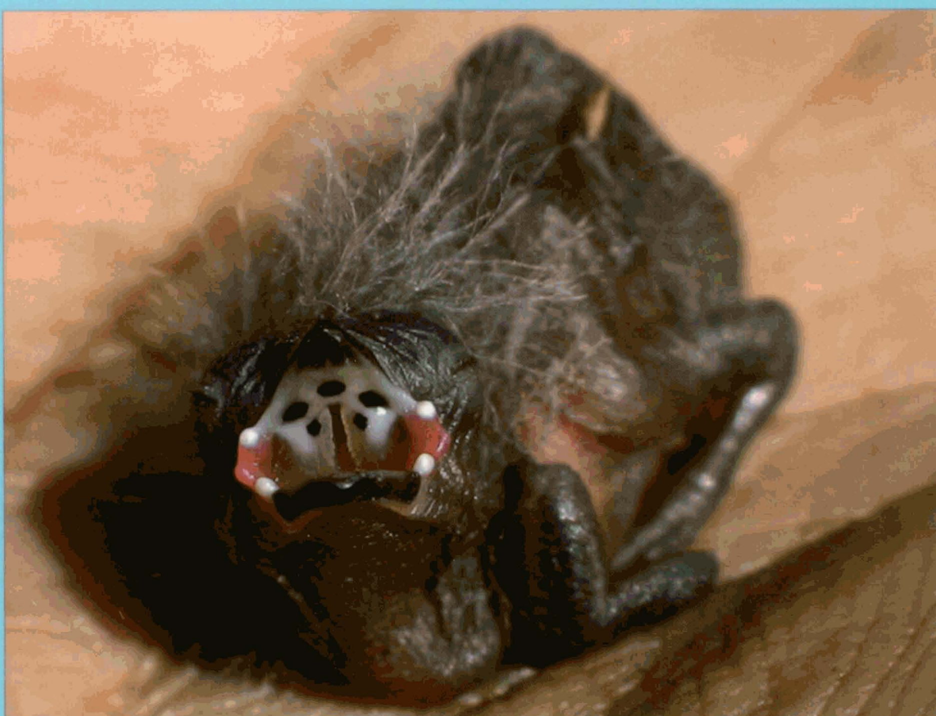
NESTLING MOUTH MARKINGS AND COLORS OF OLD WORLD FINCHES ESTRILDIDAE: MIMICRY AND COEVOLUTION OF NESTING FINCHES AND THEIR *VIDUA* BROOD PARASITES

BY

ROBERT B. PAYNE



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COVER ILLUSTRATION — *Lagonosticta rara*, Black-Bellied Firefinch

MISCELLANEOUS PUBLICATIONS
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Nestling Mouth Markings and Colors of Old World Finches Estrildidae: Mimicry and Coevolution of Nesting Finches and their *Vidua* Brood Parasites

by

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ABSTRACT

Estrildid finches have remarkable colors and patterns in the mouths of their nestlings. Certain African estrildids rear young brood-parasitic finches, the indigobirds and whydahs *Vidua*, together with their own young in a mixed-species brood. *Vidua* nestlings in the brood mimic the nestling mouth colors and patterns of the estrildid host species nestlings. The shared mouth colors, the form of the gape and the patterns of melanin markings on the palate in estrildid and *Vidua* nestlings are an evolutionary result of nestling mimicry of their hosts by the brood parasites. The question of whether the estrildid host species coevolved their nestling mouth patterns in response to their brood parasites was tested by comparing the brightness, the colors, and the pattern of markings of the gape and palate between the parasitized and unparasitized estrildid species. Compared with nestlings of other finches, nestling mouths of the African waxbills have brighter colors and more colors, as expected in a hypothesis of reciprocal coevolution. Within the waxbills, the nestling mouths were brighter and more colorful within species and more variable between species in the parasitized finches than in the unparasitized species. In addition, the mouths were brighter and more colorful in the parasitized waxbills with species-mimetic *Vidua* brood parasites than finches with species-generalist *Vidua*. However, the gape structures and the melanin markings were not more elaborate or diverse in the parasitized estrildid finches. The limited morphological response of the nestling host estrildids to their nestling-mimetic brood parasites is possibly due to behavioral constraints within each estrildid species for behavioral recognition and parental care. Other hypotheses of host nestling diversity are nest parasitism by other estrildids, habitat diversity, and phylogenetic divergence. The results suggest a limited effect of brood parasitism and a major effect of phylogeny in the diversity of nestling mouth patterns and colors.

Keywords: antagonistic mimicry, brood parasitism, character divergence, coevolution, Estrildidae, mimicry, mouth markings, parental care, *Vidua*

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Nestling Mouth Markings and Colors of Old World Finches Estrildidae: Mimicry and Coevolution of Nesting Finches and Their *Vidua* Brood Parasites

INTRODUCTION

Coevolution is an adaptive change through natural selection in the traits of species in response to its ecological interactions with other species. Coevolution is a reciprocal two-way process, where a change in one species in response to a second species is accompanied by a response of the second to the first (Ehrlich & Raven, 1964; Hamilton, 1980; Janzen, 1980; Futuyma, 1998; Davies, 2000). Coevolution recognizes an evolutionary interaction between ecologically linked organisms, where each species is a selective agent of change of the other. In pollination systems a number of species of plants and pollinators may have undergone coevolution (Thompson, 1994; Lunau, 2004), and in host-parasite or host-pathogen systems certain species-pairs may be coevolved (*e.g.*, Frank, 1994; Morand *et al.*, 1996; Sheldon & Verhulst, 1996; Clayton *et al.*, 1999; Cousteau *et al.*, 2000; Woolhouse *et al.*, 2002; Webster *et al.*, 2004). However these systems have not often considered coevolutionary interaction across a larger set of closely related and interacting species; and the mimicry system has not been examined and interpreted from this point of view.

In antagonistic associations such as the visual mimicry systems that occur in many insects, corresponding morphological traits may be selected through a coevolutionary process, but coevolution in mimicry is somewhat uncertain. In mimicry (Batesian mimicry) the mimic gains an advantage when it resembles another species (its model) (Bates, 1862; Wallace, 1869; Wickler, 1968; Turner, 1984). Within this mimetic association the model may be at a disadvantage. Although the mimic gains an advantage when it resembles the model, this mimicry does not necessarily involve a reciprocal evolutionary change of the model to the mimic. In field studies of species associations, one-way evolutionary interactions in mimicry have been described more often than have reciprocal coevolutionary interactions, both in mutualistic and in antagonistic associations between species (Futuyma & Slatkin, 1983; Gilbert, 1983; Nitecki, 1983; Clayton *et al.*, 1999; Mallet & Joron, 1999).

Fisher (1930) noted that a model species might change its visual signals to escape its mimic; nevertheless, he described no actual case of character divergence. In antagonistic coevolution, the exploiter is selected to resemble the model species, and the exploited species may be selected to escape this resemblance, with character convergence in the mimic followed by character divergence in the model, in a process of chase-away selection (Fisher, 1930; Gavrilets & Hastings, 1998; Franks & Noble, 2003; Servedio & Lande, 2003). A genetic variant in the model species that causes its characters to diverge from the mimic species might disadvantage the model species, because in losing its characters it might not be identified as the model; and the disadvantage might be greater than the advantage gained in being recognized as the model (Nur, 1980). Turner (1984: 154) proposed that "The advantage of being a mimic . . . is considerably greater than the disadvantage of being a model", and he questioned whether a model species would diverge from its mimic (Turner, 1995).

Mimicry has also evolved when one species takes resources from another and gains access to resources through its resemblance to the other species. In avian brood parasitism, where one species regularly depends on the foster care of another species in parental care, a young brood parasite gains more than its share of parental care, with the host's own young the losers in competition within the brood (Morel, 1973; Payne, 1997b; Davies, 2000). In mimicry for parental care, the model (the egg, in the songbird hosts of cuckoos; the nestling, in the estrildid hosts of *Vidua* finches) is the host offspring; the mimic is the nestling brood parasite; and the signal receiver is the foster parent (Payne, 1967). In this case the model and signal receiver are the same species.

Mimetic avian brood parasites and their hosts may be involved a process of coevolution, in a chase through time between two interacting species. In this chase the mimic pursues the model by character convergence, while the model escapes its mimic by character divergence (Payne, 1977a, 1997b, 1998b; Rothstein, 1990; Rothstein & Robinson, 1998). Nestling brood parasitic *Vidua* finches often match the mouth colors and markings of nestlings of their estrildid host species, in a species-for-species mimicry of visual patterns (Neunzig, 1929b; Nicolai, 1964, 1974, 1989, 1991). These mimics maintain a close association with their models (and hosts) over evolutionary time. A mimetic nestling *Vidua* gains parental care at a cost to the model nestling. In the best known host species, red-billed firefinch *Lagonosticta senegala*, a breeding pair has about 26% lower success in rearing their own young when a mimetic young village indigobird *Vidua chalybeata* is in the nest (Morel, 1973; Payne, 1997b, 1998b). Because the breeding hosts are less successful in rearing their own young when the brood has a young brood parasite, selection for the recognition of their own nestlings might favor nestlings that differ in appearance from the young brood parasites.

The evolution of mouth mimicry by brood parasites of their estrildid hosts may have involved (1) one-way adaptation, the

Vidua mimicking the host young; or (2) reciprocal coevolution, the estrildid finches evolving their own colors and patterns in response to the mimicry by the brood-parasite. Neunzig (1929b) introduced this hypothesis of coevolution in the nestling mouths estrildid and viduid finches, but neither he nor later curious naturalists have tested the idea. In addition to coevolution, other processes might account for diversity in nestling mouth patterns among the estrildid finches. Mouth markings might be associated with certain habitats, or they might be associated with nest parasitism between other estrildid species in natural conditions. Of course, these ideas are not exclusive. Here the focus is to test whether the diversity of nestling mouths in estrildid finches indicates a coevolutionary response to nestling mimicry in brood parasitism.

Hypotheses and predictions – A coevolutionary response of the estrildid finches to their mimetic *Vidua* species is indicated if the brood-parasitized host species have diverged in the pattern and colors of mouths of their own nestlings from the nestling mouths of their brood parasites. A character shift in the model species in response to mimicry may resemble the character divergence of ecological traits between species (Darwin, 1859; Mayr, 1963; Schluter, 2000). In coevolutionary response, we expect to see a reciprocal character shift, where the mimic species converges to the character of its model, and the model species responds by divergence of the corresponding character from its mimic, perhaps in gene-for-gene coevolution where mimic and model share homologous genes that express the corresponding traits in nestling birds (Thompson & Burdon, 1992; Frank, 1994).

The following predictions apply to this process of coevolution in the estrildid finches and their *Vidua* brood parasites. First, related estrildid species with a brood parasite will have nestlings that are more distinct from each other than do related unparasitized species. Second, the host species will have more brightly colored mouths in gape and palate, and they have more complex markings on the palate, than the unparasitized species. Third, some estrildids have species-specific brood parasites that mimic the mouths of their nestlings, whereas other estrildids have host-generalist parasites that do not mimic their host, and the degree of nestling mouth elaboration may differ between the estrildids with specialist *Vidua* and the more host-generalist *Vidua*. If so, then hosts of species-specific *Vidua* brood parasites will have more colorful and elaborate nestling mouths than do hosts of the species-generalist *Vidua*.

Specificity, bright colors and morphological elaboration of nestling mouths of estrildid finches might be accounted for by other hypotheses as well. First, certain estrildids sometimes lay in the nests of other birds, and the mouths of the nestling finches might be species-specific due to selection for the nesting birds to restrict their behavior in parental care to their own species. In that case, geographic patterns may occur in response to other species (Thompson, 1999). If so, then one would expect sympatric species of nesting estrildids to differ more from each other and to have nestling mouths more elaborate and colorful than estrildids in areas with no closely related species, through a process of evolutionary character divergence, much as suggested in estrildids that are parasitized by *Vidua* finches (Neunzig, 1929b). In this case, the divergence in mouth characters is expected to be as great in the nesting estrildids that are sometimes parasitized by other estrildids as in the estrildids that regularly host the obligate brood parasitism of *Vidua*. The hypothesis also predicts that estrildid species in areas with other species have more colorful nestling mouths than in closely related estrildid species in regions where no closely related species occur.

Second, the mouths of nestling estrildids may have evolved independently of any particular interactions with other species, perhaps due to requirements of parental care, as with more bright colors and structures being more visible to the parents in denser, more forested habitats than in open grasslands (Butler, 1898). Friedmann (1960), who did not recognize the species-specific nature of the brood-parasitic associations of *Vidua* and the estrildids (Nicolai, 1964; Payne, 1967), explained the nestling mouth markings of estrildids as visual adaptations to being seen by the nesting parents in dark habitats. Predictions of this hypothesis are that nestlings of estrildid species breeding in dense habitat will have gape structures that are larger and more brightly colored than nestlings of species in more open habitat.

Finally, the diversity in nestling mouths may follow the divergence of species in phylogeny. In fact, the visual structures of nestling gape and palate have been used to estimate the relationships among estrildid species (Neunzig, 1929a; Delacour, 1943; Steiner, 1960). The use of nestling mouths to estimate phylogeny assumes that closely related species have similar mouths, and that between species variation in nestling mouths can be accounted for by close phylogenetic relationship. Because a molecular phylogeny is available for most estrildid species, it is possible to test the assumption of mouth similarity and phylogenetic relationship.

METHODS

Systematics and sources of information. Estrildid finches include about 130 species, all in the Old World, as in recent systematic accounts (Paynter, 1968; Sibley & Monroe, 1990; Clement *et al.*, 1993; Restall, 1997; Nicolai & Steinbacher, 2001; Dickinson, 2003). In the present text, a few decisions about species limits were based on additional observations of behavior, song, and morphological differences or intergradation that were not taken into account in other systematic accounts. In this text, the term "species" is used as a singular noun (as in a phylogenetic unit) or a collective plural (as in a class of individuals that make a breeding population, and indicated by a plural verb) depending on context – much as the two senses in which Plato and Aristotle used the term "ειδος" (Balme, 1962).

Earlier estimates of species relationships among the estrildids used similarities in plumage and behaviors (Delacour, 1943;

Wolters, 1975, 1985, 1987; Morris, 1958; Immelmann *et al.*, 1965, 1977a; Mayr, 1968; Paynter, 1968; Güttinger, 1976; Goodwin, 1982) and palate markings of the young birds (Chapin, 1917; Neunzig, 1929a; Steiner, 1960). Other estimates have used chromosome morphology (Christidis, 1983, 1986a,b, 1987a) and allozymes (Kakizawa & Watada, 1985; Christidis, 1987b,c). Baptista *et al.* (1999) estimated relationships of 22 estrildid species based on combined traits of morphology, behavior and allozymes. More recently, mitochondrial DNA sequences have been compared in a phylogenetic context for most estrildid species (Sorenson & Payne, 2001b, 2002, in prep.; Payne & Sorenson, 2003; Payne *et al.*, 2002; Sorenson *et al.*, 2003, 2004; Sorenson, in prep.). In our molecular genetic analyses, the estrildid species comprise four major clades – the African waxbills, the parrotfinches, the munias and mannikins, and the Australian grassfinches. A preliminary genus-level phylogeny (Fig. 1, after Sorenson *et al.*, 2004) provides the generic groupings of estrildids in the following section, "Descriptions of estrildid finch species: Nestling mouth markings and colors". Phylogenies of certain species groups are published elsewhere (*Lagonosticta, Pytilia*, Sorenson & Payne, 2002; Sorenson *et al.*, 2003; *Lonchura, Spermestes*, Payne & Sorenson, 2003), and the details of sister-group relationships in other lineages are known from preliminary sequence data and phylogenetic analyses.

In earlier times, the mouths of nestling estrildid finches were described from the black spots and bars visible inside and around the mouths of preserved specimens and were published in black and white drawings and photographs (*e.g.*, Neunzig, 1929a; Chapin, 1917, 1954; Steiner, 1960; Immelmann, 1965; Immelmann *et al.*, 1965; Restall, 1997). In museum specimens that have been stored in alcohol, the mouth pigments other than the black spots and bars rapidly disappear – as with specimens of fish, the nestling mouth colors often are retained if the fresh specimens are fixed in neutral buffered formalin and are not transferred to alcohol.

More recently, the colors of gape and mouth have been described and these colors vary between species at least as much as the melanin spots and bars. Mouth colors and patterns of young finches were determined from published and unpublished color photographs and species descriptions. In the present study, several species were bred in aviaries and the young were observed and photographed (*e.g.*, Payne *et al.*, 2000, 2001; Payne & Payne, 2002) and many are now specimens preserved and maintained in neutral buffered formalin in the University of Michigan Museum of Zoology (UMMZ). Other specimens examined were in the bird collections of the American Museum of Natural History (AMNH, New York) and the British Museum (Natural History) (BMNH, Tring). In addition, field observations of nesting estrildids were made in Africa, Asia and Australia, and nestling estrildids in several aviary collections were observed.

Of special interest are the nestling mouths of the estrildid host species that rear nestling brood parasitic *Vidua*: these nestling mouths are mimicked by the young brood parasites (Neunzig, 1929b; Nicolai, 1964, 1987; Payne, 1973, 1982; Payne *et al.*, 2002; Sorenson *et al.*, 2003, 2004). More than 30 estrildid species in Africa are closely associated with the brood parasites, the *Vidua* indigobirds and whydahs in the family Viduidae. The occurrence of mouth markings in both the viduids and the estrildids suggests that mouth markings occurred in the common ancestors of these two families. In recent molecular systematic studies, the phylogeny of estrildid species that are associated with *Vidua* finches does not parallel the phylogeny of their *Vidua* brood parasites. That is, the matching mouth markings between each species pair of estrildid finch and Vidua finch are not the result of cospeciation or recent common ancestry. Instead, the precise mimetic resemblance between a *Vidua* and its host species indicates a much later evolution of the

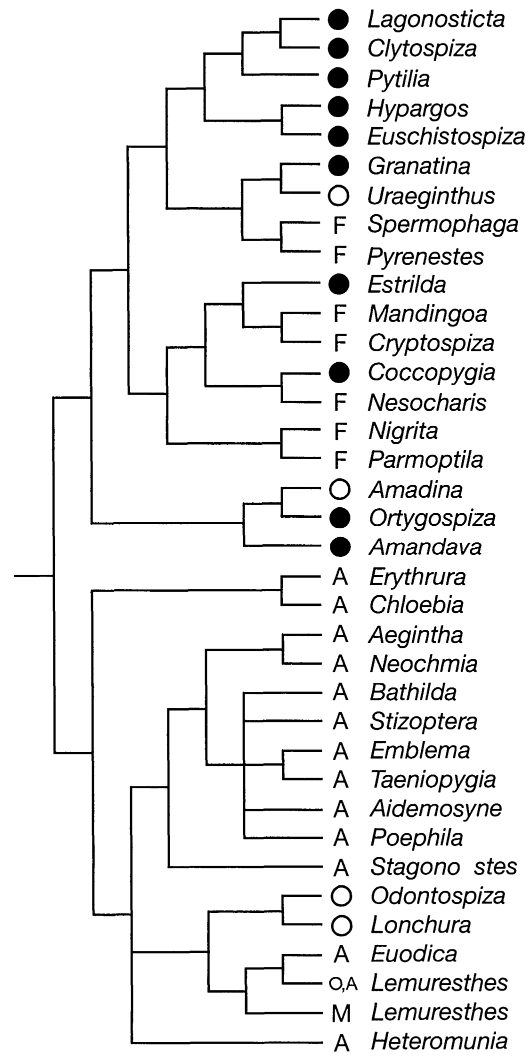

Fig. 1. Genus-level relationships within the family Estrildidae, based on phylogenetic estimates of mtDNA gene sequences (after Sorenson *et al.*, 2004). Filled circles, African host of *Vidua*; open circle, Africa, not parasitized, open habitat; F = Africa, forest habitat; A = Australasia, M = Madagascar.

specific mouth patterns in the *Vidua* species than in their estrildid hosts (Klein & Payne, 1998; Sorenson & Payne, 2001a, 2002; Sorenson *et al.*, 2003, 2004). The gape swellings and colors and the palate markings and colors of nestling mouths were used to test hypotheses of variation and coevolution in the estrildid finches, in response to each other and to brood parasitism.

Begging behaviors and parental care – Estrildid young beg for parental care in a unique behavior. They crouch, hold the mouth open, wave the head from side to side and twist the head around and upside down; the parent inserts its bill into the mouth of the young and regurgitates into the crop, in contrast to young cardueline finches, which reach the head and neck upward. In dark covered nests the young estrildids display the bright gape and palate and head movements for parental care. The begging young twists the head nearly upside down; the posture allows light from above to illuminate the palate colors and pattern, and it directs these palate colors and pattern towards the attending adult. Although estrildid species share common features of begging behavior, they differ not only in mouth markings and colors, but also in skin color, color and density of the natal down, size, begging calls and other begging behaviors (*e.g.*, Morris, 1954; Kunkel, 1959; Immelmann, 1962a; Immelmann *et al.*, 1965, 1977a; Güttinger, 1976; Zann, 1996; Nicolai & Steinbacher, 2001). All these traits may affect the acceptance and parental care given by the breeding adults to their brood (Payne *et al.*, 2001).

Once fledged and out of the nest, most estrildid young beg with the wings held against the side; they do not flutter the wings or tail (Morris, 1954; Immelmann, 1962a). Several estrildids differ from this behavior. Goldbreast *Amandava subflava* and other *Amandava* species and quail-finch *Ortygospiza* raise the wing on the side away from the adult, or on both sides if the adult is directly in front of the young bird (Güttinger, 1970; Goodwin, 1982, RBP). In begging mannikins *Spermestes*, owl finch *Stizoptera bichenovii* and some hungry zebra finch *Taeniopygia castanotis* the fledglings lift the wing on the side away from the feeding parent. Rather than indicating a close relationship between species, the wing-lift behavior may restrict competition from brood mates for parental care. A fledgling that lifts the wing on the side away from the feeding parent may screen its brood-mate and gain food that would otherwise pass to a fledgling on the far side (Immelmann, 1965). Begging fledged young with wings fluttering at the side have been seen in a few estrildids including parrotfinches *Erythrura spp*., the grassfinches *Aegintha temporalis*, *Heteromunia pectoralis*, *Stizoptera bichenovii* and *Neochmia phaeton*, a mannikin *Odontospiza* and the silverbills *Euodice spp*. (Immelmann, 1965; Güttinger, 1970, 1976; Immelmann *et al.*, 1977a; Goodwin, 1982; Restall, 1997; Nicolai & Steinbacher, 2001).

Young brood parasites *Vidua* display their mouth patterns and colors when they beg and receive parental care in the same manner as the estrildid finches (Nicolai, 1964; Kunkel, 1967, 1969; Payne *et al.*, 2001). Young *Vidua* may be more persistent and aggressive in begging than their host nestmates (Nicolai, 1964).

Morphology – As documented in the following species accounts, the skin color of young estrildids ranges from black to orange to pale pink; the skin often darkens in the first days after hatching. At hatching the nestlings vary in the length, regional extent, and amount of natal down; natal down is especially pronounced in a few waxbills such as goldbreast *Amandava subflava*. The presence of natal down varies in young nestling munias *Lonchura* even within certain species, and natal down occurs only on the back when natal down occurs at all. Natal down occurs on both head and back in African mannikins *Spermestes* species (Restall, 1997; Baptista *et al.*, 1999; Nicolai & Steinbacher, 2001).

The mouths of nestling and fledged young have distinct visual patterns and colors, and the parents see these when the young display in begging for parental care. Delacour (1943) noted that mouth patterns had been described for 46 species. These descriptions were misleading because they were based on alcoholic (spirit) specimens that had lost the colors present in life. Most current sources of information on the patterns and colors of estrildid nestling mouths are color photographs of birds reared in aviculture. In the present study, young finches were photographed in the field, and others were bred and photographed in aviaries, in a total of 37 estrildid species. The nestling mouth colors of 108 of the 130 estrildid species now are known, and the melanin patterns are known for five other species.

The corner of the mouth, the gape, is often swollen in pads, papillae, balls, globes or "reflection pearls" (Hoesch, 1939). These structures are often strikingly colored, opalescent with an underlying layer of melanin, and in contrast with the nestling skin. Pads at the corner of the gape in nestlings with gape balls are not brightly colored; these pads are often yellowish-gray. The base and the oral surfaces are often black. Inside the mouth, the palate is marked with spots and bars. The tongue is unmarked, or the dorsal surface has two subterminal spots, or it is banded or ringed (Fig. 2). Photographs often show only the dorsal surface, and others show the upper and lower surface with a black ring around the tongue. The sublingual mouth often has a black mark such as an arc, a horseshoe, "U", "V", sickle, crescent or bar.

Mouth colors of live nestlings are as variable between estrildid species as the palate spots and bars. Mouth colors of a few finches were described long ago (Butler, 1898; Bates, 1911; Swynnerton, 1916). After color illustrations and photographs were published beginning in the 1960s (Nicolai, 1964; Grzimek, 1968; Wickler, 1968) the nestling mouth colors attracted the attention of aviculturists and behavioral biologists (Ziswiler *et al.*, 1972; Mayer, 1993a-c; Beckham, 2000; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002). The gape and palate differ in color between species. Areas of the palate may have another color, white to yellow, orange, pink, red and blue; some nestling finches (firefinches *Lagonosticta*, purple

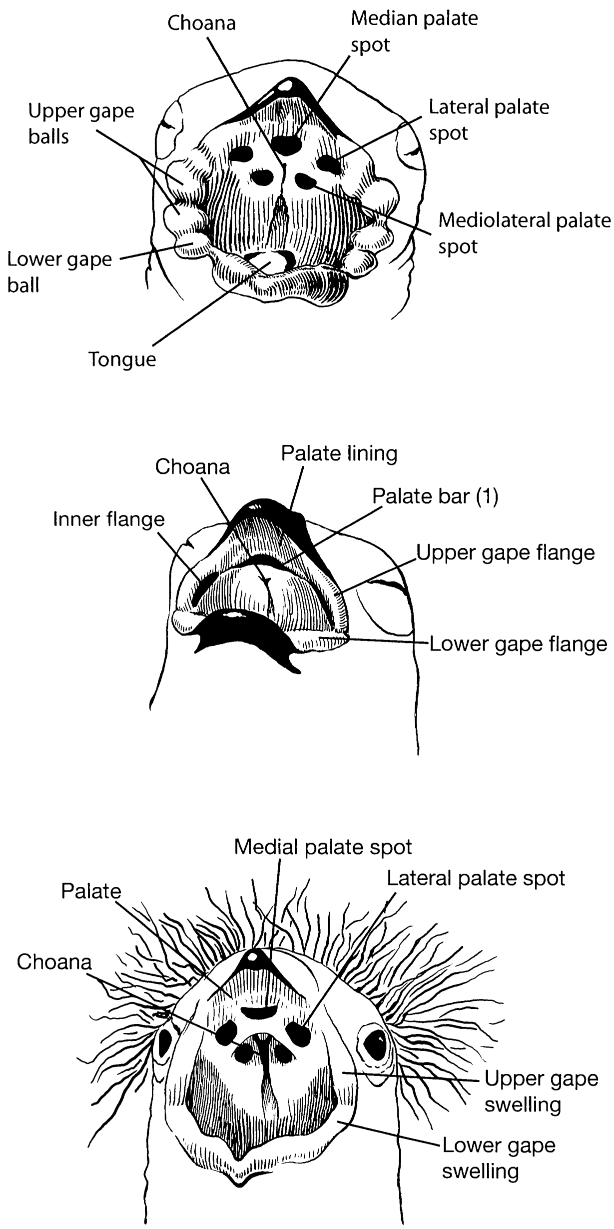

Fig. 2. Morphological traits of the mouths of nestling estrildid finches. a, *Chloebia gouldiae* Gouldian finch; b, *Lemuresthes nana* Madagascar bib-finch; c, *Amadina fasciata* cut-throat finch.

waxbills *Granatina*) have as many as three distinct and bright colors in the mouth. Colors were described from live birds in nearly all cases. Palate colors were sometimes a problem. Differences occur due to conditions of photography, to developmental changes with age of nestlings, and to differences between published descriptions. For example, the gape balls of young Gouldian finches *Chloebia gouldiae* and parrotfinches *Erythrura* spp. are uniformly blue in even light but are white especially at the center in photographs taken with a flash. In painted finch *Emblema pictum*, nestlings photographed at the same age have the palate yellowish-white or pinkish-white (Bielfeld, 1993; Puschner, 2000b); and in blue waxbills *Uraeginthus* the palate appears blue in good light but white when the photograph is overexposed, and the choana is dark in shadow with side lighting but pale with direct lighting (van Eerd, 1989; Mayer, 1992c, RBP). Melanin spots on the palate sometimes show a white ring or center when photographed with a ring flash or spot flash, but not with the flash at an angle to the palate. When known, the variation with age is described in the species accounts. Other structures and colors that vary between species in the mouths of estrildids include raised structures of colors that contrast with the palate, and the number and shape of spots and bars on the palate. In certain estrildid species the nestling tongue contrasts with the palate or has visual patterns that repeat the color motifs of the palate. The variation in nestlings described by different authors and the change of color with age, as noted in the following section, limited a comparative use of skin color.

Nestling development – In certain estrildid finches, the nestling skin color changes from pale color at the time of hatching through the first week of nestling life to become dark or nearly black. In some, the shape and color of the gape change with age. In our aviaries, nestling Peters's twinspot *Hypargos niveoguttatus* at hatching have white gape swellings, these swellings become yellow around day 5, and the lower swelling is partly orange shortly before fledging at day 18. Also, nestling goldbreast *Amandava subflava* have whitish gape flanges that become small and gray by the time of fledging. Locust finch *Paludipasser locustella* change palate pattern as they develop a second set of bars by day 6 (Irwin, 1958; Fig. 4 k, l). Mayer (1991c) illustrated a change in color of gape swellings with age in masked finch *Poephila personata*; Immelmann *et al.* (1977a) described the change in pink-throated twinspot *Hypargos margaritatus* and crimson finch *Neochmia phaeton*; and in munias *Lonchura* several species change the gape from blue to white with nestling age, *e.g.*, *L. stygia*, *L. teerinki*, *L. quinticolor* and *L. pallida* (Hofmann, 1990b; Mayer, 1991a,b,d, 1995a, 1996d; Sproule, 1994).

The palate bar of nestling munias and grassfinches develops from spots in the older embryos and hatchlings, as determined in young *Lonchura, Poephila, Bathilda, Aidemosyne* and *Stagonopleura* (=*Zonaeginthus*) (Glatthaar & Ziswiler, 1971; Steiner, 1960; Landolt *et al.*, 1975; Güttinger, 1976). In nestling *Lonchura stygia* the palate bar is incomplete at hatching and complete by day 10 (Mayer, 1991b). Within the African *Poephila* finches, nestlings of the three species differ in the degree to which spots combine into bars. Spots on bill tip and tongue sometimes are absent in small nestlings but then appear with age as in diamond sparrow *Stagonopleura guttata* (Mitchell, 1987) and they change from a pair of tongue spots in young nestlings to a bar at the time of fledging in zebra finch *Taeniopygia castanotis* (Morris, 1954). In waxbills, Goodwin (1982) described changes of spots with nestling age in blue-capped cordon-bleu *Uraeginthus cyanocephalus*.

Black spots on the gape, palate and tongue are produced by melanin. In genetic morphs (known as "mutations" in the avicultural literature, Mayer, 1987; Fucker & Fucker, 1989) that lack melanin in the plumage, nestling albino and yellow "lutino" finches lack the black spots in the mouth (Immelmann *et al.*, 1977b; Mayer, 1985). In experiments, young zebra finches that lack the spots are at a disadvantage in being fed, relative to young that have the spots (Immelmann *et al.*, 1977b; Skagen, 1988; Reed & Freeman, 1991). Also, in nestling parrotfinches *Erythrura*, the brightly colored greenish-blue balls on the gape of normal birds are yellow balls in young lutinos that lack melanin in the adult plumage (Puschner, 2001a).

In older finches the palate spots and bars persist weeks longer than the gape flanges, folds and balls, which disappear soon after the period of parental care. The small posterior or mediolateral spots in the waxbills and grassfinches are the first to disappear. The palate spots enlarge and are displayed against a bright red to yellow palate in adult red-headed bluebills *Spermophaga ruficapilla*. In contrast the spots fade to gray and disappear in adult waxbills *Estrilda astrild* and most other estrildids. The yellow bar between the 2 black palate bars is the longest-lasting trace of the young bird's palate markings in the mannikins *Spermestes cucullatus* and *S. bicolor* (Kunkel & Kunkel, 1975). The palate spots persist into adult life in blue waxbills *Uraeginthus* (Goodwin, 1965); the pale palate with dark spots is shown to another adult when a bird displays in social appeasement (Kunkel & Kunkel, 1975). In contrast to their estrildid hosts, the black palate spots of nestling brood-parasitic finches *Vidua* persist in adults only as gray spots and are not displayed in social behavior (Payne, 1973).

Melanin patterns in the mouth can vary with nestling age, and the comparative value of black markings on the inner bill, the tongue and the sublingual mouth are less well known than are the gape papillae and palate markings, and colors of the gape and mouth. Descriptions of these latter traits are more consistent between published descriptions and often are confirmed with multiple observations.

Nestling mouths differ between species owing to genetic differences between the species. Perhaps the best evidence is the appearance of hybrid nestlings (Fehrer, 1993). Steiner (1959, 1960, 1966) described their distinct mouth markings, where a nestling hybrid has a mouth with gape and palate that is intermediate in appearance between that of the two parental species. In our aviaries, one female red-billed firefinch *Lagonosticta senegala* that was reared by a Bengalese finch *Lonchura striata* later mated and nested with a male Bengalese and the pair produced a hybrid nestling, with the mtDNA of the female firefinch. The gape of the hybrid nestling was white, more swollen in the upper and lower corners than along the length of the gape or the inner fold, and the yellow palate had a continuous black bar that was wider in the middle and the ends, the locations where the 3 palate spots would appear in nestling firefinch *L. senegala*. The mouth of the hybrid was intermediate between those of the parent species (see Fig. 6 f, firefinch; g, hybrid; h. Bengalese finch).

Character scores and character indices. To compare the mouths of the young estrildids, visual pattern elements were scored as character traits from photographs and descriptions (Immelmann *et al.*, 1965, 1977a; Glatthaar & Ziswiler, 1971; Ziswiler *et al.*, 1972; Güttinger, 1976; Restall, 1997; Beckham, 2000; Nicolai & Steinbacher, 2001), and our fieldwork and captive breeding. These characters of nestling mouths are not necessarily independent. The form and size of gape swellings often but not always covary. On the palate most estrildids have either spots or bars; a few estrildids have no markings, and a few have both spots and bars. Palate spots in waxbills often appear in a ring of 5 spots (a medial spot, 2 lateral spots, and 2 small mediolateral spots). Because these spots appear in various combinations and the complete set of 5 spots are not present in all birds, the spots are scored as separate traits. Other traits were not used, as when data are missing for many species, for example the number of natal down feathers on each feather tract (Markus, 1970). Mouth characters are illustrated in Fig. 2 and are described in Table 1. Nestlings are described in the following section, and the data are listed in Table 2. Where no data are available for a particular character, the table cell is blank. Where certain traits of nestlings vary with age, or vary between descriptive accounts of a species, the more detailed text descriptions or definitive photographs are used in the comparisons. Table 2 also indicates the best estimate of sister-taxon relationship for each species in these comparisons.

Table 1. Characters used to compare the mouths of nestling estrildid finches

1	form of swelling on the upper gape (none, balls, pad or arc, entire base of gape, ridge or flange, and entire gape)
2	form of swelling on the lower gape (same as (1))
3	size of the swelling (none, small, medium, large)
4	color of gape swelling (white, yellow, orange, light blue, dark blue, red, gray)
5	second color of gape swelling (same)
6	third color of gape swelling (same)
7	oral base of swelling (mouth liner) (black, white, blue)
8	number of black medial palate spots (0, 1, 2)
9	number of black lateral palate spots (0, 2)
10	number of mediolateral palate spots (0, 2)
11	number of palate bars (0, 1, 2)
12	size of palate bars (none, small, large)
13	shape of palate bar (none, simple, complex, broken, tapered)
14	black ring around the entire inner mouth (no, yes)
15	palate spots connected (no, yes)
16	palate color (white, yellow, pink, orange, blue, black, red)
17	second palate color (same, also violet)
18	third palate color (blue, violet)
19	palate swelling (raised lateral area behind the palate spots) (no, yes)
20	tongue marks, dorsal surface (no, spots, band, ring, tongue all black)

Indices of the brightness and conspicuousness of the nestling mouths of each species and the difference between estrildid species were derived from the mouth characters in Table 2. The mouth markings were scored as in Table 3. The mouth colors yellow, orange, red, violet and light blue were scored as bright; and white, gray, dark blue, and black were scored as not bright. These indices were used to test the hypotheses of phylogeny, habitat adaptation, and coevolution in the estrildid finches both in response to each other and in response to brood parasitism by *Vidua*. Descriptions of the overall effect of the nestling mouths of estrildid species and certain comparisons between these species were summarized from the character data in Table 2, as determined in the following methods. Table 2 includes the calculated indices ***a1***, ***a2***, ***b***, ***c***, and ***d*** for each species.

Index *a1* is the number of character differences in the mouths of two closely related species, at the level of sister species. The index provides a touchstone to compare the effect of phylogeny with the effect of other determinants of differences in nestling mouths between estrildid species. The index compared the nestling mouth colors and patterns of each focal species and the most closely related species, as determined in other phylogenetic estimates (*e.g.*, Klein & Payne, 1998; Baptista *et al.*, 1999; Sorenson & Payne, 2002; Payne & Sorenson, 2003; Sorenson *et al.*, 2003, 2004). In species other than two terminal sister species, the basal species within a clade was compared with the focal species, in accord with the principles that major genetic changes between lineages occur at the time of speciation, and the basal clade has more characters like the ancestor of the clade (Futuyma, 1987; Gould, 2002). In cases where no phylogenetic estimates of the species were available, the closest match was estimated from systematic references (Wolters, 1975). When a species had no congeneric sister species, two criteria were used to determine the species compared. First, it was the species basal to the most closely related genus (as when *Chloebia* was compared with species of *Erythrura*); and, second, where a species had two (or three) other species closely related in the cladogram, it was the species with the shorter genetic distance to the common ancestor of the two (or three) (as between species of *Estrilda*, and between species of *Lagonosticta*). In each pairwise comparison, the number of character states in Table 2 that differ between a species pair was determined (from the mouth characters in Table 1, excepting no. 20, tongue marks, which varied with age and descriptions within a species). The number of nestling characters that differ between the two closely related species (possible range, 0–19) was recorded as "**index *a1***".

Index *a2*. For each species the other sympatric species with the most nearly coincident geographic distribution was determined from distribution maps (Immelmann *et al.*, 1965; Blakers *et al.*, 1984; Clement *et al.*, 1993; Restall, 1997; Nicolai & Steinbacher, 2001). A few estrildids have been introduced outside their natural region; the introduced populations are not included in a comparison of sympatry. The "other" species was restricted to an estrildid in the same major clade (*e.g.*, for *Erythrura tricolor*, in their distributional range from Timor to Tanimbar, no other parrotfinch *Erythrura* occurs even though munias *Lonchura* spp. are there; so for this comparison, no species is sympatric with the focal species). Between the two sympatric species the number of nestling characters that differed (possible range, 0–19) was recorded as "**index *a2***".

Index *b*. The number of different bright colors in gape characters (4, 5, 6) and palate characters (16, 17, and 18) for each species in Table 2 was "**index *b***". The colors yellow, orange, red, violet and light blue were scored as bright; and white, gray, dark blue, and black were scored as not bright.

Index *c* was the total number of colors in the nestling mouth, the sum of bright colors and the other colors (white, gray, dark blue and black) for each species in Table 2.

Index *d* was the sum of scores of conspicuous gape characters 1–3, and palate characters 8–15 and 19, a total of 11 characters. The sum was taken from the characters in Table 2 as scored in Table 3. This scoring gave approximately equal weight to palate spots and palate bars to avoid inflating the score for estrildids with one kind of these markings. For palate bars I recognized "1" as conspicuous and "2" as twice as conspicuous (characters 11 and 12 for the munias and mannikins); bar size (character 12) was insufficiently objective to include in the index. The sum of conspicuous characters is "**index *d***".

Phylogeny, habitat, and coevolution between estrildid finches. The nestling mouths of estrildid finches were used to compare the relative accounting power of phylogeny, habitat adaptation, and coevolution between species at risk of interspecific brood competition with another estrildid. If similarities in nestling mouths of estrildid species are mainly the phylogenetic result of recent common ancestry, then closely related species should have similar mouths. If similarities are mainly the result of adaptation to a certain regional habitat, then estrildid species that live in the same region in sympatry should have mouths more similar than species in different regions, even when the allopatric species are more closely related than the sympatric species. And if similarities are the result of coevolution between species that sometimes lay eggs in each others' nests, then closely related species should be less similar (due to character divergence) when they live in sympatry than when they are allopatric. Also, if estrildids have been selected to avoid rearing another estrildid species, then we predict nestlings of species at risk of competition between estrildid nestlings to have particularly bright or strikingly colored mouths.

Phylogeny – One approach to test the extent to which estrildid phylogeny explains the similarity in mouths between estrildid species would be to compare the actual observed **index *a1*** between sister species is significantly less than in randomly-generated indices of similarity between estrildid species. However, this approach is deferred until a more comprehensive estimate of phylogenetic relationships is available. In the present work, **index *a*** was compared with another index. If the indices of character difference between nestling mouths of species is explained to a large extent by their phylogenetic relationship,

Table 2. Mouth patterns and colors of young estrildid finches, divergence from other estrildid species, indices of conspicuousness, habitat, and role in brood parasitism

genus	species	character 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		gape above, swelling none 0 balls 1 pads, arc 2 swollen gape 3 ridge, flange 4 swollen all 5	gape below, swelling none 0 balls 1 pads 2 swollen gape 3 ridge, flange 4 swollen all 5	gape swelling none 0 small 1 med 2 large 3	gape swelling white 1 yellow 2 orange 3 blue 4 red 5 gray 6	gape 2nd color yellow 2 orange 3 blue 4 black 5 red 6 pink 7	gape 3rd color pink 7 violet 8 2nd blue 9 black 5	gape swelling liner: 1 black 2 white 3 blue	palate, spot, medial, n	palate, spots, lateral, n	spots(2), medio-lateral: small 1 large 2 lines 3 wave 4 arcs 5	palate bars, center, n	palate bar, none 0 small 1 large 2	palate bar shape none 0 simple 1 complex 2 broken 3	outer black mouth ring yes 1	palate spots connect yes 1
Amadina	erythrocephala	3	3	3	1	0	0	2	1	2	2	0	0	0	0	0
Amadina	fasciata	3	3	3	1	0	0	2	1	2	2	0	0	0	0	0
Amandava	amandava	4	4	1	1	0	0	1	2	2	1	0	0	0	0	0
Amandava	formosa	4	4	1	1	0	0	1	2	2	1	0	0	0	0	0
Cryptospiza	reichenovii	4	4	1	2	5	0	1	1	2	1	0	0	0	0	0
Cryptospiza	salvadorii	4	4	1	2	5	0	1	1	2	1	0	0	0	0	0
Cryptospiza	jacksoni	4	4	1	2	5	0	1	1	2	1	0	0	0	0	0
Estrilda	perreini	2	2	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	thomensis	2	2	2	1	0	0	1	1	2	1	0	0	0	0	0
Mandingoa	nitidula	1	1	1	1	5	0	1	1	2	1	0	0	0	0	0
Nesocharis	ansorgei	2	1	1	4	0	0	1	1	0	0	0	0	0	0	0
Nesocharis	capistrata	2	1	1	4	0	0	1	1	2	1	0	0	0	0	0
Nigrita	bicolor	1	1	2	2	0	0	1	1	2	1	0	0			
Nigrita	luteifrons	2	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Nigrita	canicapilla	1	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Paludipasser	locustella	4	4	2	5	0	0	1	0	0	3	1	1	3	0	0
Parmoptila	rubrifrons	1	1	2	2	0	0	1?	1	2	1	0	0	0	0	0
Parmoptila	woodhousei	1	1	2	2	0	0	1	1	2	1	0	0	0	0	0
Pyrenestes	ostrinus	1	1	2	2	0	0	1	1	2	1	0	0	0	0	0
Pyrenestes	sanguineus	1	1	2	2	0	0	1	1	2	1	0	0	0	0	0
Spermophaga	poliogenys	3	3	2	2	0	0	1	1	2	1	0	0	0	0	0
Spermophaga	haematina	3	3	2	2	0	0	1	1	2	1	0	0	0	0	0
Spermophaga	ruficapilla	3	3	2	2	0	0	1	1	2	1	0	0	0	0	0
Uraeginthus	angolensis	2	1	1	7	5	0	1	1	2	0	0	0	0	0	0
Uraeginthus	bengalus	2	1	1	4	5	0	1	1	2	0	0	0	0	0	0
Uraeginthus	cyanocephalus	2	1	1	4	5	0	1	1	2	0	0	0	0	0	0
Coccopygia	melanotis	2	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Coccopygia	quartinia	2	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Estrilda	astrild	2	2	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	caerulescens	2	2	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	melpoda	2	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	paludicola	2	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	nonnula	2	2	2	2	0	0	1	1	2	1	0	0	0	0	0
Estrilda	rhodopyga	2	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	troglodytes	2	1	2	1	0	0	1	1	2	1	0	0	0	0	0
Amandava	subflava	4	4	1	1	0	0	1	1	2	1	0	0	0	0	0
Clytospiza	monteiri	3	3	2	1	2	0	1	1	2	1	0	0	0	0	0
Estrilda	charmosyna	2	2a	2	1	0	0	1	1	2	1	0	0	0	0	0
Estrilda	erythronotos	2	2a	2	1	0	0	1	1	2	1	0	0	0	0	0
Euschistospiza	dybowskii	3	3	2	1	4,2	0	1	1	2	1	0	0	0	0	0
Granatina	granatina	3	3	2	1	2	0	1	1	2	0	0	0	0	0	0
Granatina	ianthinogaster	3	3	2	4	5	9	1	1	2	0	0	0	0	0	0
Hypargos	margaritatus	3	3	2	1			2?	1	2	0	0	0	0	0	0
Hypargos	niveoguttatus	3	3	2	1	3	0	2	1	2	0	0	0	0	0	0
Lagonosticta	rara	1	1	2	4	6	9	0	1	2	1	0	0	0	0	0
Lagonosticta	larvata	1	1	2	1	4	8	0	1	2	1	0	0	0	0	0
Lagonosticta	rubricata	1	1	2	1	4	7	0	1	2	1	0	0	0	0	0
Lagonosticta	rufopicta	4	4	1	1	4	0	1	1	2	0	0	0	0	0	0
Lagonosticta	nitidula	1	1	2	1	4	0	0	1	2	0	0	0	0	0	0
Lagonosticta	senegala	1	1	2	1	4	5	0	1	2	0	0	0	0	0	0
Lagonosticta	rhodopareia	1	1	1	4	4 (2nd)	0	0	1	2	1	0	0	0	0	0
Lagonosticta	sanguinodorsalis	1	1	1	1				1	2	1	0	0	0	0	0
Lagonosticta	virata	1	1	1	1	7	0	0	1	2	1	0	0	0	0	0
Ortygospiza	atricollis	1	1	2	4	5	0	1	2	2	1	0	0	0	0	0
Pytilia	afra	4	4	1	1	5	0	1	0	0	0	0	0	0	0	0

(continued)

Table 2. Continued

genus	species	16	17	18	19	20		related species	sympatric species	index a1	index a2	index b	index c	index d	habitat	brood
		palate color 1 white 2 yellow 3 pink 4 orange 5 blue 6 black 7 red	palate second color red 1 y or o 2 violet 3 blue 4 black 5 pink 6	palate third color blue 1 violet 2	palate swelling no 0 yes 1	tongue blank 1 spots 2 band 3 ring 3 black 4	n spots	most closely related	closely related sympatric	characters unlike closest (sister) species	characters unlike sympatric cousin (where not closest species)	bright colors?	n colors total (white, gray & black include)	sum, 11 characters (gape 1-3; spot 8-10; bar 11-13,15; ring 14; palate 19)	habitat forest 1 scrub 2 marsh 3 grassland 4 (dry) thicket 2 woods 2	parasite no 0 rare 1 generalist 2 specialist 3
Amadina	erythrocephala	1	2	0	0	3	5	Amafas		1		2	3	5.5	2	0
Amadina	fasciata	1	2	0	0	3	5	Amaery		1		2	3	5.5	2	0
Amandava	amandava	1	0	0	0	2	6+	Amasub	Amafor	2	0	0	2	3.3	3,4	0
Amandava	formosa	1	0	0	0	2	6+	Amaama	Amafor	2	0	0	2	3.3	2,3	0
Cryptospiza	reichenovii	1	0	0	0	2	5	Crysal	Mannit	0	3	2	3	3.3	1	0
Cryptospiza	salvadorii	1	0	0	0	2	5	Cryrei	Mannit	0	3	2	3	3.3	1	0
Cryptospiza	jacksoni	1	0	0	0	2	5	Crysal	Euscin	0	8	2	3	3.3	1	0
Estrilda	perreini	1	0	0	0		5	Esttho	Estast	0	0	0	2	5.6	2	0
Estrilda	thomensis	1	0	0	0		5	Estper	Estast	0	0	0	2	5.6	2	0
Mandingoa	nitidula	1	0	0	0	2	5	Cryrei	Cryrei	3		0	2	5.3	1,2	0
Nesocharis	ansorgei	2	0	0	0	1	5	Nescap	Nescap	2		1	3	3.3	1	0
Nesocharis	capistrata	2	0	0	0	3	5	Nesans	Nesans	2		1	3	5.3	1	0
Nigrita	bicolor	1	0	0	0	2	5	Nigcan	Nigcan	1		1	3	5.3	1	0
Nigrita	luteifrons	?	0	0	0	2	5	Nigcan	Nigcan	1				5.3	1	0
Nigrita	canicapilla	?	0	0	0	2	4	Nigbic	Parrub	1	1?			5.3	1	0
Paludipasser	locustella	7	0	0	0		5					1	3	6.6	3	0
Parmoptila	rubrifrons	2	0	0	0	1?	5	Parwoo	Nigcan	0	1?	1	3	5.6	1	0
Parmoptila	woodhousei	2	0	0	0	1	5	Parjam	Nigcan	0?	1?	1	3	5.6	1	0
Pyrenestes	ostrinus	2	0	0	0	3	5	Pyrsan	Spehae	0	2	1	2	5.6	1	0
Pyrenestes	sanguineus				0	3	3	Pyrost	(Spehae)	0	2	1	2	5.6	1	0
Spermophaga	poliogenys	2	0	0	0	3	(3)5	Spehae	Speruf	0	0	1	2	5.6	1	0
Spermophaga	haematina	2	0	0	0	1	(3)5	Speruf	Pyrest	0	2	1	2	5.6	1	0
Spermophaga	ruficapilla	2	0	0	0	3	3	Spehae	Spepol	0	0	1	2	5.6	1	0
Uraeginthus	angolensis	1	6	2	0	3	3	Uraben	Lagsen	1	9	3	5	4.3	2	1
Uraeginthus	bengalus	1	6	2	0	3	3	Uracya	Lagsen	1	8	3	5	4.3	2	1
Uraeginthus	cyanocephalus	1	4	2	0	3	3	Uraben	Graian	1	6	3	5	4.3	2	1
Coccopygia	melanotis	1	1	0	0	1	0	Coccua	Estast	1	6	1	4	2.6	2	2
Coccopygia	quartinia	1	1	0	0	1	5	Cocmel	Estrho	1	6	1	4	2.6	2	2
Estrilda	astrild	1	0	0	0	2	5	Estpal	Estmel	0	1	0	2	5.6	1,2	2
Estrilda	caerulescens	1	0	0	0		5	Esttho	Esttro	0	1	0	2	5.6	2	2
Estrilda	melpoda	1	0	0	0	2	5	Estpal	Esttro	0	0	0	2	5.6	4	2
Estrilda	paludicola	1	0	0	0	2	5	Estast	Estast	0	0	0	2	5.6	3	2
Estrilda	nonnula	1	0	0	0	2	5	Estast	Estast	1	2	0	2	5.6	4	2
Estrilda	rhodopyga	1	0	0	0	1	5	Esttro	Estast	1	1	0	2	5.6	2	2
Estrilda	troglodytes	1	0	0	0	2	5	Estmel	Estmel	0	0	0	2	5.6	4	2
Amandava	subflava	1	0	0	0	2	6+	Amafor	Ortatr	1	6	0	2	3.3	3,4	1,3
Clytospiza	monteiri	1	0	0	0	1	5	Lagrar	Lagrub	8	6	1	3	5.6	2	2
Estrilda	charmosyna	1	0	0	0	2	5	Estery	Estrho	0	1	0	2	5.6	2	3
Estrilda	erythronotos	1	0	0	0	2	5	Estcha	Estrho	0	1	0	2	5.6	2	3
Euschistospiza	dybowskii	2	0	0	0	1	3	Euscin	Lagrub	0	5	2	3	5.6	2	2
Granatina	granatina	4	0	0	0	4	3	Graian	Uraang	5	8	2	4	5.6	2	3
Granatina	ianthinogaster	4	4	1	0	4	3	Gragra	Uracya	5	6	3	4	5.6	2	3
Hypargos	margaritatus	2	0	0	0	1	3	Hypniv	Lagrub	0	4			5.6	2	1
Hypargos	niveoguttatus	2	0	0	0	1	5	Hypmar	Lagrho	0	9	2	4	5.6	2	3
Lagonosticta	rara	1	1	0	0	2	5	Laglar	Lagrub	5	3	3	5	5.6	2	2
Lagonosticta	larvata	2	0	0	0	2	5	Lagrar	Lagvir	5	5	2	4	5.6	2	3
Lagonosticta	rubricata	1	0	0	0	2	3	Lagrho	Lagrho	4	4	2	4	5.6	2	3,2
Lagonosticta	rufopicta	3	0	0	0	1	3	Lagnit	Lagsen	4	6	2	4	5.3	2	3
Lagonosticta	nitidula	3	0	0	0	1	3	Lagruf	Lagsen	4	2	2	4	5.6	2	1
Lagonosticta	senegala	2	0	0	0	1	5	Lagnit	Uraben	2	9	2	4	5.6	2	3
Lagonosticta	rhodopareia	3	0	0	0	2	3	Lagvir	Lagrub	3	6	3	4	5.3	2	3
Lagonosticta	sanguinodorsalis	1	0	0	0	2	5	Lagvir	Lagrub	1	4			5.3	2	3
Lagonosticta	virata	1	0	0	0	2	5	Lagrho	Laglar	3	4	1	3	5.3	2	3
Ortygospiza	atricollis	1	0	0	0	2	6					1	3	5.6	4	3
Pytilia	afra	1	1,6a	2	0	1	1	Pythyp	Pytmel	1	5	3	5	2.3	2	3

(continued)

Table 2. Continued

genus	species	character 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pytilia	melba	4	4	2	1	5	0	1	1	0	0	0	0	0	0	0
Pytilia	hypogrammica	4	4	1	1	5	0	1	0	0	0	0	0	0	0	0
Pytilia	phoenicoptera	4	4	1	1	5	0	1	0	0	0	0	0	0	0	0
Pytilia	lineata	4	4	1	1	5	0	1	0	0	0	0	0	0	0	0
Euschistospiza	cinereovinacea	3	3	2	1	4,2	4	1	1	2	1	0	0	0	0	0
Estrilda	atricapilla	2	2	2	1			1	1	2	1	0	0	0	0	0
Chloebia	gouldiae	1	1	3	4	2	0	1	1	2	2	0	0	0	0	0
Erythrura	coloria	1	1	2	4	2	0	0	1	2	2	0	0	0	0	0
Erythrura	cyaneovirens	1	1	2	4	2	0	0	1	2	1	0	0	0	0	0
Erythrura	hyperythra	1	1	2	4	2	0	0	1	2	0	0	0	0	0	0
Erythrura	papuana	1	1	2	4	2	0	0	1	2	1	0	0	0	0	0
Erythrura	pealii	1	1	2	4	2	0	0	1	2	2	0	0	0	0	0
Erythrura	prasina	1	1	2	4	2	0	0	1	2	1	0	0	0	0	0
Erythrura	psittacea	1	1	2	4	2	0	0	1	2	2	0	0	0	0	0
Erythrura	regia	1	1	2	4	2	0	0	1	2	1	0	0	0	0	0
Erythrura	trichroa	1	1	2	4	2	0	0	1	2	1	0	0	0	0	0
Erythrura	tricolor	1	1	2	4	2	0	0	1	2	5	0	0	0	0	0
Euodice	cantans	5	5	3	1	0	0	1	0	0	0	1	2	1	1	0
Euodice	malabarica	5	5	3	1	0	0	1	0	0	0	1	2	1	1	0
Lemuresthes	nana	3	3	1	1	0	0	1	0	0	0	1	2	1	0	0
Spermestes	bicolor	3	3	1	1	0	0	1	0	0	0	2	2	1	0	0
Spermestes	cucullatus	3	3	1	1	0	0	1	0	0	0	2	2	1	0	0
Spermestes	fringilloides	3	3	1	1	0	0	1	0	0	0	2	2	1	0	0
Odontospiza	caniceps	3	3	1	1	0	0	1	0	0	0	2	2	1	0	0
Lonchura	castaneothorax	3	3	1	1	0	0	1	0	0	3	1	1	1	0	0
Lonchura	flaviprymna	3	3	1	1	0	0	1	0	0	1	1	2	1	0	0
Lonchura	fuscans	3	3	1	1	0	0		0	0	1	1	2	1	0	0
Lonchura	grandis	3	3	1	1	0	0	1	0	0	0	1	2	1	0	0
Lonchura	leucogastra	3	3	1	1	0	0	1	0	0	1	1	2	1	0	0
Lonchura	maja	3	3	1	1	0	0	1	0	0	0	1	2	1	0	0
Lonchura	malacca	3	3	1	1	0	0	1	0	0	2	1	2	1	0	0
Lonchura	molucca	3	3	1	1	0	0	1	0	0	3	1	2	2	0	0
Lonchura	nevermanni	3	3	1	1	0	0	1	0	0	3	1	2	2	0	0
Lonchura	pallida	3	3	1	1	0	0		0	0	0	1	2	1	0	0
Lonchura	punctulata	3	3	2	1	2	0	1	0	0	2	1	2	1	0	0
Lonchura	quinticolor	3	3	1	1	0	0	1	0	0	3	1	2	1	0	0
Lonchura	spectabilis	3	3	1	1	0	0	1	0	0	3	1	2	1	0	0
Lonchura	striata	3	3	1	1	0	0	1	0	0	1	1	2	1	0	0
Lonchura	stygia	3	3	1	1	0	0	1	0	0	3	1	2	1	0	0
Lonchura	teerinki	3	3	1	1	0	0	1	0	0	3	1	2	1	0	0
Lonchura	oryzivora	3	3	2	1	0	0	1	0	0	0	1	2	1	0	0
Lonchura	fuscata	3	3	2	1	0	0	1	0	0	0	1	2	1	0	0
Heteromunia	pectoralis	3	3	1	1	0	0	1	0	0	4	1	1	1	0	0
Emblema	pictum	4	4	1	1	0	0	1	0	0	1	1	2	1	1	0
Aidemosyne	modesta	4	4	1	1	0	0	1	0	0	1	1	2	2	0	0
Bathilda	ruficauda	4	4	1	1	0	0	1	0	0	1	1	2	2	0	0
Aegintha	temporalis	3	3	2	1	0	0	1	1	1	1	0	0	2	0	0
Neochmia	phaethon	3	3	1	1	0	0	1	1	2	1	0	0	0	0	0
Poephila	acuticauda	4	4	1	1	0	0	1	0	0	5	1	2	2	0	0
Poephila	personata	4	4	1	1	0	0	1	0	2	1	1	1	2	0	0
Poephila	cincta	4	4	1	1	0	0	1	0	0	5	1	2	2	0	0
Stagonopleura	guttata	3	3	2	1	0	0	1	1	2	1	0	0	0	0	1
Stagonopleura	bella	3	3	2	1	0	0	1	1	2	1	1	1	1	0	1
Stagonopleura	oculata	3	3	2	1	0	0	1	1	2	1	1	1	1	0	1
Stizoptera	bichenovii	3	3	1	1	0	0	1	1	2	4	1	1	1	0	0
Taeniopygia	castanotis	3	3	1	1	0	0	1	1	2	5	0	0	0	0	0
Taeniopygia	guttata	3	3	1	1	0	0	1	1	2	5	0	0	0	0	0

then we expect **index *a1*** to be smaller than other indices such as **index *a2***.

Distribution and habitat – Geographic ranges of each species were used to determine their distributional overlap. Distributions of the estrildid species were taken from systematic and regional references (*e.g.*, Smythies, 1940, 1999; Immelmann *et al.*, 1965; Ziswiler *et al.*, 1972; Goodwin, 1982; Blakers *et al.*, 1984; Coates, 1990; Restall, 1997; Coates & Bishop, 1997; Nicolai & Steinbacher, 2001; Dickinson, 2003; Fry & Keith, 2004). Nearly all waxbills are African; the other estrildids are

Table 2. Continued.

genus	species	16	17	18	19	20		related species	sympatric species	index a1	index a2	index b	index c	index d	habitat	brood
Pytilia	melba	1	5	1	0	3	0	Pytlin	Uraben	6	7	1	3	2.6	2	3
Pytilia	hypogrammica	1	1,6	2	0	1	0	Pytpho	Pytpho	0		3	5	2.3	2	3
Pytilia	phoenicoptera	1	1,6	2	0	1	0	Pythyp	Pythyp	0		3	5	2.3	2	3
Pytilia	lineata	1	1,6	2	0	1		Pytafr	Pytmel	0	5	3	5	2.3	2	3
Euschistospiza	cinereovinacea	2?	0	0	0	1	5	Eusdyb	Cryjac	0 or 1	8	2	3	5.6	2	
Estrilda	atricapilla	1	0	0	0	2		Estnon	Estnon			0	2	5.6	1,2	
Chloebia	gouldiae	1	0	0	0	2	5	Erypra	Erytrich	3	3	1	3	6	2	0
Erythrura	coloria	2	0	0	0	2	5	Erytrich	Eryvir	1	?	2	3	5.6	2	0
Erythrura	cyaneovirens	2	0	0	0	3	5	Eryreg	none	0		2	3	5.3	2	0
Erythrura	hyperythra	2	0	0	0	2	5	Erypra	Erypra	1		2	3	5.3	2	0
Erythrura	papuana	2	0	0	0		5	Erytrch	Erytirch	0	0	2	3	5.3	2	0
Erythrura	pealii	2	0	0	0	2	5	Eryreg	(Erykle)	0	?	2	3	5.3	2	0
Erythrura	prasina	2	0	0	0	2	5	Eryhyp	Eryhyp	1		2	3	5.3	2	0
Erythrura	psittacea	2	0	0	0	2	5	Erypap		0		2	3	5.3	2	0
Erythrura	regia	2	0	0	0	3	5	Erypea	Erytrich	0	0	2	3	5.3	2	0
Erythrura	trichroa	2	0	0	0	2	5	Erypap	Chlgou	0	3	2	3	5.3	2	0
Erythrura	tricolor	2	0	0	0	2		Erycol		0		2	3	5.3	2	0
Euodice	cantans	1	0	0	0	1	0	Euomal	Specuc	0	4	0	2	5	2	0
Euodice	malabarica	1	0	0	0	1	0	Euocan	Lonmal	0	4	0	2	5	2	0
Lemuresthes	nana	2	0	0	0	2	0	Euomal		8		1	3	3.3	2	0
Spermestes	bicolor	1	0	0	0	3	0	Spefri	Specuc	0	0	0	2	4.3	1,2	0
Spermestes	cucullatus	1	0	0	0	3	0	Spebic	Spebic	0		0	2	4.3	2	1
Spermestes	fringilloides	1	0	0	0	3	0	Specuc	Specuc	0		0	2	4.3	2,3	0
Odontospiza	caniceps	1	6	0	0	2	0	Specuc	Specuc	1		1	3	4.3	2	0
Lonchura	castaneothorax	(1),2	0	0	0	3	0	Lonqui	Lonfla	2	2	0	2	4.3	3	0
Lonchura	flaviprymna	1	0	0	0	3	0	Loncas	Lonmal	2	1	0	2	4.3	3	0
Lonchura	fuscans	1	0	0	0		0	Lonstr	Lonatri	1	1	0	2	4.3	2	0
Lonchura	grandis	2		0	0	3	0	Lonspec	Loncast	2	2	1	3	3.3	4	0
Lonchura	leucogastra	2	0	0	0	2	0	Lonstr	Lonstr	0		0	2	4.3	1	0
Lonchura	maja	2	0	0	0	1	0	Lonpal	Lonstr	0	1	1	3	3.3	3	0
Lonchura	malacca	1	0	0	0	2	0	Lonmaj	Lonstr	0	2	0	2	4.3	3	0
Lonchura	molucca	1	0	0	0	3	0	Lonstr	Lonpal	1	2	0	2	3.3	3	0
Lonchura	nevermanni	1	0	0	0	3	0	Lonfla	Lonleu	1	2	0	2	3.3	3	0
Lonchura	pallida	1,2	0	0	0	1	0	Lonmaj	Lonpun	0	3	0	2	3.3	2,3	0
Lonchura	punctulata	2	2	0	0	2	0	Lonmol	Lonmal	3	3	1	3	4.6	2	0
Lonchura	quinticolor	2	0	0	0	2	0	Lonspe	Lonpal	2	1	1	3	4.3	3	0
Lonchura	spectabilis	1	0	0	0	3	0	Lonfla	Loncast	1	2	0	2	4.3	4	0
Lonchura	striata	2	0	0	0	3	0	Lonfus	Lonmal	0	2	1	3	4.3	2	0
Lonchura	stygia	2	0	0	0	3	0	Lonfla?	Lonnev	1	2	1	3	4.3	3	0
Lonchura	teerinki	1	0	0	0	3	0	Lonspe?	Lonleu		2	0	2	4.3	2	0
Lonchura	oryzivora	2	0	0	0	1	0	Lonfus	Lonmaj	0	1	1	3	3.6	2,3	0
Lonchura	fuscata	2	0	0	0	1	0	Lonory	Lonpun	0	1	1	3	3.6	2,3	0
Heteromunia	pectoralis	1	0	0	0	3	2	Embpic?	Loncas	?	6,2	0	2	4.3	4	0
Emblema	pictum	1	0	0	0	3	3?	Poeper	Taecas	2	4	0	2	5.3	4	0
Aidemosyne	modesta	1	0	0	2	2	(3),5	Aegtem	Aegtem	8		0	2	4.3	2,3	0
Bathilda	ruficauda	1	0	0	2	2	(3),5	Aidmod	Neopha	0	7	0	2	5.3	3	0
Aegintha	temporalis	1?	0	0	0	3	5	Aidmod	Stibic	8	7	0	2	5.6	2	0
Neochmia	phaethon	2	0	0	0	3	5	Aegtem	Aidmod	4	9	1	3	5.3	2	0
Poephila	acuticauda	1	0	0	0	2	(3),5	Poecin	Poeper	0	3	0	2	4.3	4	0
Poephila	personata	1	0	0	0	2	(3),5	Poecin	Neopha	2	5	0	2	6.3	2,4	0
Poephila	cincta	1	0	0	0	2	(3),5	Poeacu	Batruf	0	2	0	2	4.3	4	0
Stagonopleura	guttata	3	1	0	1	2	5	Zonbel	Aegtem	3	3	2	4	6.6	2	0
Stagonopleura	bella	3	1	0	1	2	5	Zonocu	Stagut	0	3	2	4	6.6	1	0
Stagonopleura	oculata	3	1,6	0	1	2	5	Zonbel	none	0		2	4	6.6	1	0
Stizoptera	bichenovii	1	0	0	0	2	5	Poeper	Taecas	3	4	0	2	6.3	2	0
Taeniopygia	castanotis	1	0	0	0	2	(3),5	Taegut	Stibic	0	4	0	2	5.3	2	0
Taeniopygia	guttata	1	0	0	0	2	(3),5	Taecas	Lonqui	0	7	0	2	5.3	2	0

mainly Australasian and Oceanic. All estrildids lay and rear their young covered nests they either build or take over from other birds. Most estrildids live in grassy scrub and around agricultural lands. Some are in semi-arid and arid scrub, bamboo thicket, open woodland, savanna with grassland, wet grassland, rice, marsh and reedbed, dry grassland, jungle and montane grassland, and others live in forest or forest edge, but within a set of closely related species, the species that are most closely related generally are in a similar habitat, and species that occur in the same geographic range generally are in a similar habitat.

Table 3. Characters and conspicuousness scores of the mouths of young estrildid finches

Character	Codes	Conspicuousness score	Character description
gape #1	2, 3, 5	1=1=1	gape shape above
gape #2	2, 3, 5	1=1=1	gape shape below
gape #3	1<2<3	0.3, 0.6, 1.0	gape swelling size
spot #8	1, 2	1	spots, medial, n
spot #9	2	1	spots, lateral, n
spot #10	1–5	1,1,1,1,1	spots, mediolateral, n
bar #11	1<2	1, 2	palate bar, presence and size
bar #13	2, 3, 4	1	palate bar, shape
ring #14	1	1	mouth ring
spot #15	1	1	connectivity
palate #19	1	1	palate swelling

The hypothesis of habitat adaptation in nestling mouths predicts that two sympatric and related estrildid species in the same region and habitat are more similar (less different) than two sister species in allopatry: that is, across these species pairs, ***a2* < *a1***. Contrariwise, the hypothesis of phylogenetic determination predicts (2x) that close relatives are more similar (less different) ***a1* < *a2***, than are two species that occur in the same area. The comparison allows both hypotheses to be rejected, and if there is an association, it tests the relative importance of phylogeny and geographic region (both a similar habitat and breeding sympatry).

Third, **index *a1*** was compared between closely related species pairs that are sympatric and species pairs that are allopatric. The hypothesis of character divergence due to risk of occasional nest parasitism by a related estrildid species (at the sister species level) predicts that nestling mouths of species in the same region are more different than are sister species in allopatry (***a1* in sympatry < *a1* in allopatry**). On the other hand the index allows a test of an alternative hypothesis, that related species are more similar when they live together than when they live apart, as they might if one mimics the other in between-species nest parasitism. That is, ***a1*** is greater (similarity is less) in sister-species pairs in sympatry than in species pairs in allopatry (***a1* in sympatry > *a1* in allopatry**). By holding constant a degree of phylogenetic relatedness, this comparison allows a test of the effect of sympatry on character similarity of the nestlings that is independent of their relatedness. A few species were excluded from this comparison where they were sympatric with another estrildid but where they occurred in different habitats (*Amadina* and *Ortygospiza*).

In addition, estrildids might have nestlings' mouths more bright and complex if they live in sympatry with another related estrildid than if they were the only estrildid species in their region, in consequence of having a risk of nest parasitism by a sympatric species. To test this idea that sympatric estrildids have more brightly colored and have more distinctive mouth markings than do finches that do not occur with a related species in the same major estrildid clade, their **indices *b, c, d***, were compared.

Host and brood parasite coevolution. Coevolution may have occurred in the estrildid host species that are mimicked by a brood parasitic *Vidua*, particularly if the interspecific effects are greater than intraspecific effects. The estrildid hosts may have responded to the challenge of mimicry by their brood parasite, by selection for distinctive mouths in their own nestlings. To test the proposal of character divergence between host species as a measure of divergence of an estrildid from a mimetic brood parasitic *Vidua*, the character differences were compared between nestlings of estrildid species, in species that were parasitized and species that were not. Criteria proposed to recognize character divergence between species as an evolutionary result of competition (Schluter, 2000) were adapted for character divergence for recognition and parental care in the estrildid finches. First, the nestling appearance of each species has a genetic basis, and is not modified by environmental differences (birds foster-reared by another species develop the same mouths as birds fostered by their own species, as in Payne *et al.*, 2001; hybrids develop mouths intermediate between those of the parent species, Steiner, 1959, 1966). Second, the species differences in nestling mouths have an effect on the success of the nestlings in being fostered between and within estrildid species (Payne *et al.*, 2001). The estrildid species have a common remote ancestry, nevertheless they are independent evolutionary units each subject to adaptive change insofar as they diverged on the order of 10^5 to 10^6 years ago (Sorenson & Payne, 2001, 2002; Sorenson *et al.*, 2003). These criteria allow a test of adaptive character divergence between the estrildid species.

Predictions of coevolution in brood parasitism can be tested by comparison of the nestling mouths in parasitized and unparasitized estrildid species. First, if estrildids are more successful in breeding when they can discriminate their own young from a mimetic nestling of a brood parasite, then we predict that the host species respond to the challenge of mimicry by evolving more complex and more colorful nestling mouths than seen in the unparasitized species. The reason is that simple mouths are easier for *Vidua* to mimic; and when the nestling *Vidua* do mimic the mouths of the nestling hosts, then the hosts can distinguish their own young and direct parental care to their own young if the mouths of their own young are more elaborate than the mimics. If parasitized estrildids are at an advantage when their own nestlings are distinctive, then we predict more colors and more bright colors in the hosts' nestling mouth than in the nestling mouths of unparasitized species. By the same reasoning, we predict a greater complexity of melanin markings and spots in the nestlings in parasitized species than in unparasitized species. As a corollary, we predict that nestlings of estrildids that are parasitized by host-specific mimetic *Vidua* differ more from each other than nestlings of estrildid species that are parasitized by less host-specific *Vidua*.

For the first prediction I compared the bright colors complied in **index *b*** across the major estrildid clades and ecological groups. For the second prediction I compared total colors, "**index *c***". For the third prediction I compared **index *d***. The taxa *Heteromunia pectoralis* and *Paludipasser locustella* were excluded because of uncertain phylogenetic relationships, and *Estrilda atricapilla* and *Euschistospiza cinereovinacea* were excluded because no field observations were available on whether they are parasitized. After an initial comparison of the results, I compared the three indices between estrildid species that had species-specialist mimetic *Vidua* brood parasites and estrildid species with the more species-generalist *Vidua*.

Statistical tests of differences between the indices of sets of estrildid finches were non-parametric chi-squared goodness-of-fit tests for homogeneity of **indices *a1*** and ***a2***, and Wilcoxon tests for the other indices (Siegel & Castellan, 1988).

DESCRIPTIONS OF ESTRILDID FINCH SPECIES: NESTLING MOUTH MARKINGS AND COLORS

1. *Lagonosticta* firefinches occur in Africa. Firefinches have red in the plumage, they have broad rectrices, and most species have white spots on the breast and flanks. The songs and calls of all ten species are distinct (Nicolai, 1964, 1982; Payne, 1973, 1982, 1998, 2004; Brunel *et al.*, 1980; Payne *et al.*, 1993; Payne & Barlow, 2004; Payne *et al.*, 2005). Phylogenetic relationships within the firefinches are well resolved (Sorenson & Payne, 2002; Sorenson *et al.*, 2003, 2004). One major clade includes *L. senegala, L. nitidula* and *L. rufopicta*; the last two allopatric species are closely related to each other and have the same songs but not the same nestling mouth patterns. The other major clade includes the other seven species, with *L. larvata* and *L. rara* in a basal clade, and the other firefinches in two sister groups, one *L. rubricata*, and the other *L. virata, L. sanguinodorsalis, L. umbrinodorsalis*, and *L. rhodopareia*. These clades indicate somewhat different species groups than the four genera of firefinches recognized by Wolters (1975, 1987). The nine firefinches for which information is available all differ in nestling skin, gape and palate colors, and palate markings.

Lagonosticta senegala red-billed firefinch are widespread across sub-Saharan Africa, absent in large forests, and often found in gardens and near human dwellings. At hatching the nestling skin is pink with pale gray natal down; the skin darkens to dark gray with nestling age. The gape has 2 white papillae on each side, separated by a narrow blue band that persists as a blue and black band after fledging. The palate is yellow or cream. Most nestlings have 3 spots on the palate (Nicolai, 1964; Immelmann *et al.*, 1965); some have 5 spots including 2 small mediolateral spots (Payne, 1973; Nicolai, 1987). When present, the mediolateral spots are much smaller in *L. senegala* than in *L. rubricata* and *L. rhodopareia*. Three-spot palates were seen in Cameroon and Zambia; both 3- and 5-spot palates were seen in captive-reared birds. The deep mouth lining is pink, the tongue is yellow and unmarked, and the lower mouth lining is pink with a black tip (Payne, 1973; Kunkel & Kunkel, 1975; Nicolai, 1987; Payne *et al.*, 2002; RBP, UMMZ, Figs. 3 a, 6 f).

Lagonosticta rufopicta bar-breasted firefinch occur in areas of grass and marsh from West Africa eastward through Central Africa and to western Kenya. Nestling skin is blackish with gray natal down; the swollen papillae are white with no black in the corner mouth and the swollen oral flange extends around the gape, the flange is white to pale bluish on the corner, and the oral surface is black on the upper and lower flange; the palate is pale pink with 3 black spots (a central spot and a pair of lateral spots), the tongue is unmarked pink, and the floor of the mouth is pink with a black sublingual chevron (Nicolai, 1972, 1987, 2001; Payne, 1982; Payne & Payne, 1994; RBP, Fig. 3 b).

Lagonosticta nitidula brown firefinch occur in south-central Africa in grass and marshy habits. The hatchling skin is black with sparse light gray natal down on head and back. The gape has 2 round white swellings one above and one below on each side of the corner of the mouth, the base of the swellings and the gape between the papillae is bright blue, the lower papilla fits in front of upper one when bill is closed. The palate is pinkish white with 3 black spots, the tongue is pink without spots, and the lower mouth is pinkish (Neff, 1966; Nicolai, 1987; Hustler, 1998; Payne *et al.*, 2002).

Lagonosticta larvata (including *vinacea* and *nigricollis*) vinaceous firefinch or black-faced firefinch occur across West Africa in upper guinea woodlands. Nestling skin is light brownish, the natal down is sparse and white; the gape has 2 white papillae at the base of upper and lower mandible, the base of papilla is blue, with a dark violet-blue papilla behind them, the papillae are connected by blue-black at the base; the palate is yellow and has 5 black spots in a ring, the 2 mediolateral spots smaller than the 3 anterior spots, the tongue is light pink with 2 black spots, and the lower mouth is pale pink with a black crescent, in both *L. l. vinacea* and *L. l. nigricollis* (Steiner, 1960; Immelmann *et al.*, 1965; Payne, 1982; Fig. 3 f).

Lagonosticta rara black-bellied firefinch occur across West and Central Africa to western Kenya. At hatching, the nestling skin is black on the head and back and reddish-black below; natal down on the head and back is light gray; in a few days the nestling skin is grayish pink. The gape has 2 small bright pale blue papillae, one above and one below the corner of mouth, each with a basal blue-black ring; the corner of the gape is a ruby- or cherry-red expanded flange between the blue papillae, with red extending into the corner of the mouth. The palate is whitish with 3 black spots and 2 smaller spots behind these, in a ring of 5 spots. The upper mandible has a black bar near the tip; the inner mouth is pink, the tongue is pink with 2 black spots joined by a band below the tongue, and the tip is pale blue like the gape papillae, the lower mouth is pale with a black crescent. In side or frontal view the closed mouth has blue papillae and a red gape. This description applies to nestlings in northern Nigeria and nestlings in captive-bred

Fig. 3. Mouths of young *Vidua* indigobirds and their estrildid hosts. a, *Lagonosticta senegala*, Choma, Zambia (photo by D. M. Lewis); b, *L. rufopicta*, Cape Coast, Ghana; c, *L. rubricata*, Banyo, Cameroon; d, *L. rara forbesi*, Zaria, Nigeria; e, *L. rhodopareia jamesoni* (cf. Payne, 1973); f, *L. larvata*, Zaria, Nigeria; g, *Vidua chalybeata* ; h, n, *Vidua wilsoni*, Bukuru, Nigeria; i, *Vidua camerunensis*; j, *L. rara rara*, Tibati, Cameroon (C. Balakrishnan); k, *Vidua larvaticola*, Zaria, Nigeria (d, e, k, M. F. Gartshore, cf. Payne, 1982); l, m, *Vidua nigeriae*; Bukuru, Nigeria; o, *Vidua camerunensis*, Tibati, Cameroon (C. Balakrishnan); p, two hybrid *V. camerunensis x V. chalybeata*; q, r, *Vidua purpurascens*, Lochinvar National Park, Zambia; s, *Euschistospiza dybowskii*; t, u, *Clytospiza monteiri*, Ngaoundere, Cameroon; v-x, *Hypargos niveoguttatus* (captives – c, e, g, i, p, s, v, w, x, RBP).

offspring of dark-plumaged *L. r. forbesi* from West Africa (Burkard, 1968; Payne, 1982; Fig. 3 d). In contrast, nestlings of the same age in northern Cameroon and Zaire, the paler-plumaged Central African *L. r. rara*, have the skin pinkish gray, natal down on the head and back is light gray, the small gape papillae are white with no trace of blue, the gape is pink to light red at the base of the papillae, in the corners, and into the side of the mouth (Chapin, 1917, 1954; C. Balakrishnan; RBP, Fig. 3 j).

Lagonosticta rubricata African firefinch are widespread across Africa in mesic habitats of grass and grassy woodland. At hatching, the nestling skin is black to gray-black, violet-black on the abdomen; the natal down is light gray; the gape has a pair of small, round, white papillae, each blue at the base, one above and one below the corner of the mouth, a swelling between the gape papillae is pink (when the mouth is closed, the pink swelling is apparent behind the two white papillae; the pink area is slightly longer than the blue base of the papillae – not much longer than the papillae as it is in *L. rara*); the palate is yellowish white with 3 black spots and 2 smaller black mediolateral spots forming a ring of 5 spots, the tongue is pink with a black bar, and the lower mouth is pale pink with a black crescent (Swynnerton, 1916 (where called "*rhodopareia*"); Payne, 1982; Mayer, 1996c; Puschner, 2000a; RBP, UMMZ, Fig. 3 c). Nestling mouths are similar in the subspecies *L. r. congica* (Fig. 3 c), *haematocephala* (Fig. 4 f, l) and *polionota* (Fig. 4 r, x). Older nestlings and fledglings have a brighter yellow palate. The 3 anterior spots in older juveniles spread to form a black mouth lining in the adults.

Lagonosticta rhodopareia Jameson's firefinch occur in semi-arid grassy woodlands in East and southern Africa. The nestling skin is blackish, the natal down sparse and light gray; the gape has 2 small white papillae, one above and one below on each side, the papillae become light blue with age, have a narrow dark blue band at base, and are separated by broad pinkish-violet oral flange; the palate is pink with 5 black spots, the tongue is pink with a black bar, the lower mouth is pale pink with a black crescent (Swynnerton, 1916; Payne, 1973; Payne *et al.*, 1993; Nicolai, 1987, 2001; RBP, UMMZ, Fig. 3 e). The palate spots of juveniles spread into a black palate in the adults.

Lagonosticta virata Mali firefinch occur in eastern Senegal and Mali in dry grassy, rocky woodlands. Nestling skin is dark gray to purplish black, natal down is light gray; the corner of the gape is grayish pink and has 2 small bluish-white papillae; the palate is yellowish white with 5 black spots in a ring with the anterior 3 spots larger than the 2 spots behind, the tip of the upper bill has a black rim, and the tongue is whitish with black spots. A nestling preserved in alcohol at BMNH has lost its color (the mouth is all white), and in Table 2 the colors are from an earlier description of this bird, although the "grayish pink" or "brown" gape colors are uncertain because of the observer's colorblindness affecting red photopigments (I. Hinze, 2001, pers. comm.).

Lagonosticta sanguinodorsalis rock firefinch live on rocky hills in northern Nigeria. Nestlings have not been described. In grown juveniles the soft corner of the gape is grayish pink and the gape has 2 small whitish papillae (color may have changed from the younger nestling; the gape is similar to that of fledged *L. rhodopareia* in Zambia); the palate is yellowish white with a ring of 3 large black spots in front and 2 smaller black spots behind, the inner mouth is pink, and the tongue is whitish with black spots (Payne, 1998a).

Lagonosticta umbrinodorsalis umber firefinch (Chad firefinch) occur on wooded rocky hillsides in southwestern Chad (Brunel *et al.*, 1980; Payne & Louette, 1983). The nestlings have not been described.

2. Twinspots are not all each other's closest relatives, although the following three genera are closely related. *Clytospiza* are basal to the firefinches *Lagonosticta*, whereas *Hypargos* and *Euschistospiza* are sister genera to that clade (Sorenson *et al.*, 2003, 2004; Fig. 1).

Clytospiza monteiri brown twinspot of Central Africa occur in open woodland. Nestlings have dark skin with natal down on the head and body, the gape has 2 thick white swellings on each side, constricted at the corner into a bilobed form, white externally and yellow inside with a black spot on the oral surface of each swelling; the white palate has 5 black spots (the mediolateral spots are smaller), the pink tongue is unbanded or has a dark band, and the lower mouth is pinkish with a black crescent (Chapin, 1917, 1954; Steiner, 1960; Neff, 1975, 1977; Fig. 3 t, u).

Hypargos niveoguttatus Peters's twinspot occur from East to south-central Africa in lowland thickets. Nestlings have pink skin with sparse gray natal down, a gape with 2 large white swellings on each side constricted by a white gape corner, the lower swelling develops a lateral spot that turns yellow by day 5 and orange by the age of fledging, and the gape swellings lack a black oral surface; the palate is yellow with 3 black spots, the tongue and the inner and lower mouth are pink and unmarked (Payne *et al.*, 1992; Fig. 3 v-x).

H. margaritatus pink-throated twinspot of southeastern Mozambique and northeastern South Africa occur in lowland thickets. Nestlings have pinkish skin with long natal down on the head, a gape with large white swellings, 2 on each side and lined with black, a yellow palate with 3 black spots, and the rest of the mouth and tongue are reddish. The gape swellings change to blue-green within a few days after hatching and blue after fledging (Burkard, 1968; Immelmann *et al.*, 1977a; Brickell & Koen, 1996).

Euschistospiza dybowskii Dybowski's twinspot live in grassy, rocky thicket areas in West Africa. Nestlings have purplish-black skin with sparse gray natal down; the gape has 2 large white swellings on each side (the upper swelling is blue in young nestlings) with a base of light blue and internally with a black spot, and the corner of the gape has a yellow papilla pad between the white swellings; the palate is yellow extending to

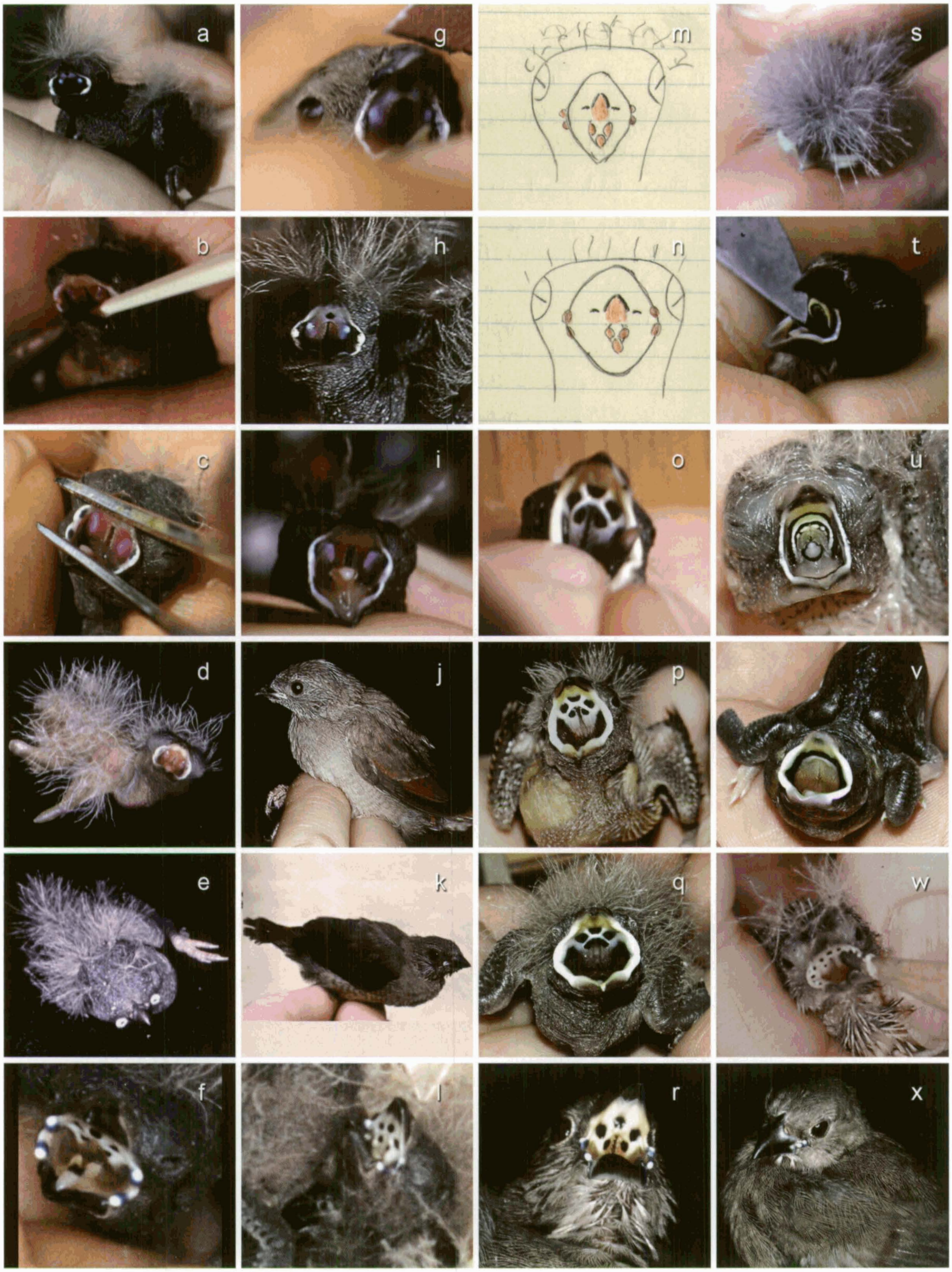

Fig. 4. Mouths of young *Pytilia*, brood-parasitic *Vidua* paradise whydahs, and other estrildids. a, *Pytilia melba*, Lusaka, Zambia; b, *P. afra*; c, d, e, *P. hypogrammica* (c, Tibati, Cameroon, C. Balakrishnan), f, l, *Lagonosticta rubricata haematocephala*; g, *Vidua paradisaea*, fledged young, Lochinvar National Park, Zambia; h, nestling *V. paradisaea*, Lake Baringo, Kenya; i, j, *Pytilia phoenicoptera*; k, hybrid *Pytilia hypogrammica* x *P. phoenicoptera*); m, n, *Paludipasser locustella* (Midlands, Zimbabwe, M. P. S. Irwin, Irwin, 1958 and field notes); o, p, *Amadina fasciata*, q, s, *Amadina erythrocephala*; r, x, *Lagonosticta rubricata polionota*; t, *Spermestes cucullatus*, Bukuru, Nigeria; u, *Spermestes bicolor*; v, *Euodice cantans*; w *Amandava amandava* (captives – b, d, e, f, i, j, k, l, o, r, w, x, RBP; p, s, u, v, R. Beckham).

the gape, the palate has 5 black spots (with the 2 mediolateral spots small), the bill tip is blackish; the tongue is pinkish with 2 black spots and a yellow tip, and the lower mouth is pink with a black crescent (Kujawa, 1965; Immelmann *et al.*, 1965; RBP, Fig. 3 s).

E. cinereovinacea dusky twinspot in the Albertine rift region of East Africa and in Angola live in thickets. Nestlings have a gape flange like *E. dybowskii*; the palate has 5 black spots; the tongue has 2 black spots and there is a black sublingual chevron; the mouth colors are not described (Steiner, 1960; Immelmann *et al.*, 1965; Baars, 1967).

3. *Pytilia*. Five pytilia species occur across Africa, usually one in an area, two or three in western Mali (Bamako, Tienfala). *Pytilia melba* melba finch (green-winged pytilia) live in semi-arid open woodland across sub-Saharan Africa. *Pytilia afra* orange-winged pytilia are in more mesic woodland in south-central Africa, *P. lineata* red-billed pytilia (lineated pytilia) are in Ethiopia, *P. phoenicoptera* red-winged pytilia (aurora finch) are in open woodland from Sudan west to Senegal, and *P. hypogrammica* yellow-winged pytilia occur in the same region, usually in more humid woodland than the last species. Phylogenetic relationships among these species are known from molecular genetics, with *P. melba* basal to the others, and *P. lineata* basal to the other three (Sorenson *et al.*, 2004).

P. melba nestling skin is black, the sparse natal down is pale gray; the gape has a slightly swollen white flange above and below, continuous across the gape, the outer and inner base of the flange is black; the bill tip is black, the palate is white and has a black spot in the center, the mouth lining behind the hard palate is bright pink, the sides and lower mouth are black, a luminous pale blue spot appears on each side of the black palate, and the tongue is pink at the base and has a dark band and whitish tip (Nicolai, 1964, 1991; Markus, 1970; Immelmann *et al.*, 1977a; RBP, Fig. 4 a).

P. afra nestlings have the skin blackish on the head and grayish pink on the back, the natal down is pale gray; the gape flange is whitish gray, less swollen than in *P. melba* and without black markings on the oral surface; the anterior palate is whitish with no central spot, the bill tip is black, the posterior mouth lining is bright pink, the posterior palate is bright grayish pink with a large oval violet (or purplish pink) spot on each side, the tongue has a yellow base and tip separated by a red band, and the lower mouth is yellow to pink with a black chevron (Nicolai, 1964; Markus, 1970; RBP, Fig. 4 b).

P. phoenicoptera, *P. lineata* and *P. hypogrammica* nestlings are similar to each other in appearance. The skin is dark gray on the head and pink on the body turning blackish with age, the natal down is pale gray; the gape flange is white, the upper and lower lobes with a black spot on the inner lining, the black is visible between the flanges when the mouth is closed; the anterior palate is yellowish white with no central spot, the bill tip is black, the posterior mouth lining is bright pink with red edges on the choana, the rear palate is pinkish red with a large oval violet spot on each side, the tongue is pink with no black marks (the dorsal surface has a red band), and the lower mouth is pink with a black chevron (Chapin, 1917; Nicolai, 1964, 1968, 1977, pers. comm.; Immelmann *et al.*, 1965; C. Balakrishnan, RBP, Fig. 4 c, d, e, i, j). Hybrid *P. phoenicoptera x P. hypogrammica* that we bred in captivity have the same mouth as the two parent species (Fig. 4 k). Brightness of the rosy palate varies with nestling condition: in *P. phoenicoptera* the palate is paler in nestlings with mite ectoparasites, and the color fades soon after death (Chapin, 1917; Payne, 1997b).

4. *Granatina* purple waxbills and *Uraeginthus* blue waxbills comprise a clade (Sorenson *et al.*, 2004; Fig. 1). Each *Granatina* species has a species-specific brood parasite. *Uraeginthus* blue waxbills generally do not, yet occasionally the blues are parasitized, to judge from song mimicry of *U. bengalus* by adult male steel-blue whydahs *Vidua hypocherina* in Kenya (Payne, 1997a), by song mimicry of *U. angolensis* by adult male shaft-tailed whydah *Vidua regia*, and from fledged *V. regia* in broods of *U. angolensis* in Botswana (Harrison *et al.*, 1997; R. J. Nuttall, pers. comm.). In addition, *U. cyanocephalus* are associated by habitat with straw-tailed whydah *Vidua fischeri* in southern Sudan (Nikolaus, 1979), and in captivity they have reared the young of other estrildid finch species and *Vidua* indigobirds (Payne *et al.*, 2001). Phylogenetic relationships among the five waxbills are known from molecular genetic studies (Sorenson *et al.*, 2004).

Granatina granatina violet-eared waxbill occur in semi-arid regions of southern Africa. Young have blackish skin and long sparse grayish-white natal down; the gape has a dark blue oval swelling and a smaller pale blue ventral swelling, the two connected by a dark blue band; the palate is whitish with an orange center, the orange is bordered anteriorly by 3 black spots, one in the center and one on each side, the rest of the palate is pale blue laterally, the inner mouth is black, the tongue is black at hatching then changes to orange or yellow or even whitish with black spots in the fledgling, and there is a sublingual black band (Nicolai, 1964; J. Schuetz; Fig. 5 w, x).

Granatina ianthinogaster purple grenadier live in semi-arid regions of East Africa. Young at hatching have purplish-black skin and light gray or fawn natal down; the gape has a blue dorsal swelling and a smaller pale blue ventral swelling and a band around the gape is dark blue to purplish-black (the open mouth shows 2 small pale blue swellings on each side of the gape), and the oral surface is black; the palate center is whitish with 3 black spots, the tip of the palate is dark gray, the medial palate behind the spots is orange grading to whitish and laterally to pale blue and the rest of palate is black, the inner mouth is black, the tongue is white with a black bar near the rear, then it turns black with white edges, and the inner lower mandible is black (Neunzig, 1929b; Nicolai, 1964; RBP, UMMZ, Fig. 5 v).

Uraeginthus angolensis southern blue waxbill occur in southern Africa as far northward as southern DR Congo and Tanzania. Hatching young have pink skin pink, the natal down is long

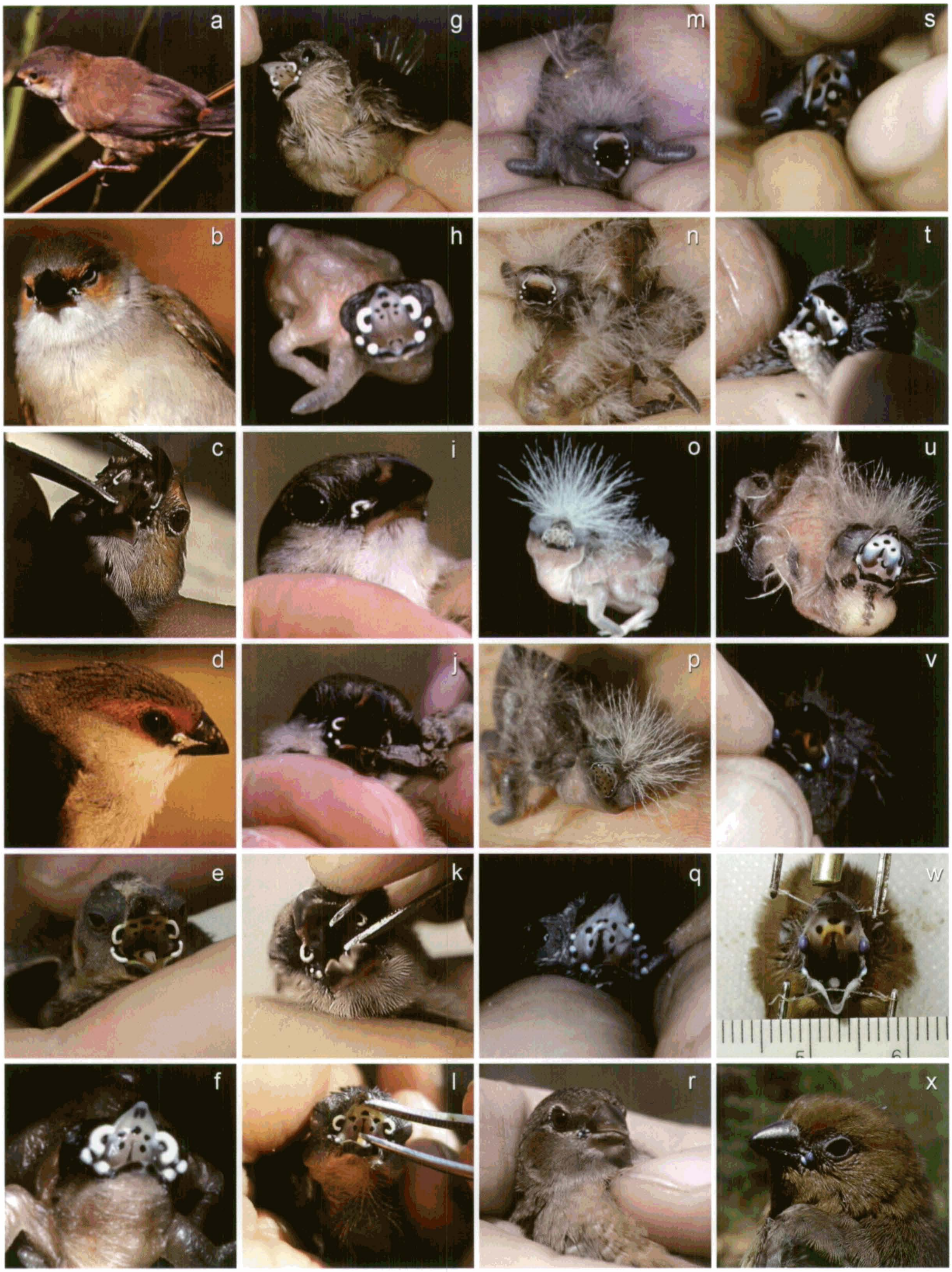

Fig. 5. Mouths of young waxbills and the brood-parasitic generalist pin-tailed whydah *Vidua macroura*. a-c, *Estrilda melpoda* (a, Mole National Park, Ghana; b, Tibati, Cameroon; c, Cape Coast, Ghana); d, *E. astrild*, Lochinvar National Park, Zambia; e, *E. nonnula* Tibati, Cameroon (C. Balakrishnan); f, *E. troglodytes*; g, h, *E. rhodopyga*; i-l, *Vidua macroura* (i, Bukuru, Nigeria; j, Cape Coast, Ghana; k, l, Tibati, Cameroon, C. Balakrishnan); m, n, *Coccopygia quartinia*; o, p, *Amandava subflava* (p, Tibati, Cameroon, C. Balakrishnan); q, r, *Ortygospiza atricollis* (r, Ngaoundere, Cameroon); s, *Uraeginthus angolensis*, Lochinvar National Park, Zambia; t, *U. bengalus*, Vom, Nigeria; u, *U. cyanocephalus*; v, *Granatina ianthinogaster*; w, x, *Granatina granatina*, South Africa (Justin Schuetz) (captives – f, g, h, m, n, o, q, u, v, RBP).

and light yellowish-brown to gray, the gape has an inconspicuous oval blue-black swelling on the upper mandible and a black border inside the mouth, the gape corner has a narrow grayish-white band, and a slight swelling is on the lower mandible between the paler base and distal edge. The center of the palate is white grading to pinkish in front and pale bluish behind, the whitish area with 3 black spots, the inner bill tip with 2 large black spots, the inner mouth black; the tongue pale pink with a black ring and bluish gray tip, and the lining of the lower mouth whitish with a black crescent (Skead, 1975; van Eerd, 1989; RBP, Fig. 5 s). By the time the contour feathers erupt the skin is blackish; by fledging the edge of the gape is paler, the swelling on the upper gape is more blue than black, the lateral palate and inner mouth are black, and the tongue tip is pale gray.

Uraeginthus bengalus red-cheeked cordon-bleu occur from Senegal eastward to Kenya, Tanzania and central DR Congo. Nestlings at hatching have the skin pink, the natal down long and light yellowish-brown to gray, the gape flange on the upper mandible with an inconspicuous dark blue oval papilla with a black border inside the mouth, the gape corner is a thin purplish to grayish-white line; below the gape is a blue swelling on the lower mandible with a black band across the outer ridge. The palate is whitish grading to pink in front and pale blue behind, the palate has 3 black spots, the mouth behind the palate is black as is the choana, the inner bill tip has 2 large black spots; the tongue is pink with a black ring and a bluish gray tip, and the lining of the lower mouth is whitish with a black crescent near the tip. By the time of fledging, the upper gape papilla is lighter blue and has a white anterior end, and the gape and inner mouth are paler (Chapin, 1917; Kev Roy, RBP, Fig. 5 t).

Uraeginthus cyanocephalus, blue-capped cordon-bleu (blue-headed cordon-bleu), occur in semi-arid regions of East Africa, locally sympatric with *U. bengalus*; usually *U. cyanocephalus* are in more arid habitats. Nestlings at hatching have pink skin with three conspicuous broad black stripes on the throat (a pattern unique among the estrildid finches), the natal down is long, dense, pale buff to gray; the mouth has a small blackish oval swelling above the gape, the swelling is bordered bluish white at the corner of the mouth, the gape has a grayish-white band, a smaller black swelling is on the outer edge of the lower bill, which has the basal and distal edge whitish. The palate is whitish blue and behind this area the mouth grades to sky blue and violet, the palate has 3 black spots, the inner bill tip is blackish, the inner mouth cavity is pink, the tongue is pink with a black ring and bluish white tip, and the lower mouth lining is pale pink with a black crescent near the bill tip. Little change occurs with age; the dark gape papillae with grayish borders are inconspicuous (Mayer, 1992c; RBP, Fig. 5 u).

5. *Pyrenestes* seedcrackers and *Spermophaga* bluebills occur in mesic forests and thick bush of West Africa to East and Central Africa. The seedcrackers and bluebills comprise a clade (Sorenson *et al.*, 2004; Fig. 1).

Pyrenestes ostrinus eastern (black-backed) seedcracker nestlings have a gape with 3 fleshy balls and a smaller papilla between the middle and lower balls, the top ball bright yellow and the lower balls whiter to pale yellow, all the structures bordered black; and a pale palate with 5 spots (the posterior pair very small), a band around the tongue and a black crescent on the mandible (Chapin, 1917, 1954; Smith, 1990). *P. sanguineus* western (brown-backed) seedcrackers nestlings have a dark blackish-red skin with sparse natal down on the head and body, the mouths are similar to those of eastern seedcrackers with yellow gape balls (Saarlouis-Fraulautern, 1977; Silzer & Silzer, 1980; Wiegand, 1999).

Spermophaga ruficapilla red-headed bluebill occur in Central Africa from southern Sudan to northwestern Angola. Nestlings have pale yellowish-flesh skin and sparse natal down on the head and back at hatching; the gape has 3 small yellow ball-like swellings; the palate is yellow, 2 small black marks are near the bill tip, the palate has 3 large black spots, the tongue has a narrow dark bar and there is a sublingual mark (Chapin, 1954; Kunkel, 1967, 1968). *S. haematina* western bluebill occur in West and Central Africa. Nestlings have pale skin with natal down on the head and back, the gape margin is pale yellow with 2 thick swellings above and a thick swelling below, the upper swellings are separated by a black spot that extends into the oral cavity; 2 small marks are near the bill tip, the palate is yellow with 3 large round black spots, the tongue is unmarked pink and yellow, and a dark crescent is below the tongue (Bates, 1911; Chapin, 1917; Ullrich, 2004; AMNH 0290). *S. poliogenys* Grant's bluebill of Central Africa are known as young only from older juveniles in which the gape swellings had regressed; the palate was yellow with 3 black spots, the posterior palate lacked spots and the tongue had a dark band (Chapin, 1917, 1954; Kunkel & Kunkel, 1975). The mouths of young *Pyrenestes* and *Spermophaga* are similar, having the gape with yellow balls and the palate with black spots.

6. *Parmoptila* and *Nigrita* comprise a clade (Sorenson *et al.*, 2004; Fig. 1). Phylogenetic relationships among the species are incompletely known.

Parmoptila antpeckers (flowerpecker finches) are forest living, slender-billed insectivorous estrildids in West and Central Africa. The western and eastern forms of *Parmoptila*, *rubrifrons* and *jamesoni*, are sexually dimorphic, the males with a red crown and rufous underparts, the females with a brown crown and spotted underparts; the central African *P. woodhousei* males and females are nearly monomorphic in plumage with a rufous face and scaly brown underparts.

Parmoptila (rubrifrons) jamesoni Jameson's antpecker occur in northern, central and east-central DR Congo to western Uganda and northwestern Tanzania. Young birds have a gape with 3 yellowish balls (or lobes, or wattles), the gape itself black, and the interior of mouth pale yellow with 5 black spots on the palate and a black crescent mark below the tongue (Chapin, 1917, 1954). *P. (r.) rubrifrons* red-fronted antpecker young are undescribed. *P. woodhousei* Woodhouse's antpecker occur in Central Africa from Nigeria east of the Cross River to Cameroon, Central African Republic, DR Congo and Angola. A feathered young spirit specimen of *P. woodhousei* in BMNH taken by G. L. Bates in Cameroon has 3 large lobes on the gape (2 on the upper mandible, 1 on the lower) and a fourth smaller lobe in a lateral position at the base of the lower mandible; the black base of the balls extends between the globes inside the mouth; the yellow palate has 3 large spots and 2 smaller spots behind them, and the tongue is unmarked. Another bird, the type specimen of *Lobornis alexandri* Sharpe 1874, from Nigeria, a feathered young preserved in spirits, had 3 white lobes or wattles on the gape; the specimen was made into a dry skin after it was sketched in color; the sketch is in Tring (Sharpe, 1874, 1885; Chapin, 1954; BMNH 1874.5.18.3). The bird is a young *P. woodhousei*; and *Lobornis alexandri* is a synonym of *P. w. woodhousei* Cassin, 1859; as in Sclater (1930). Both specimens were preserved in alcohol, the pickled white gape balls perhaps were yellow in life, as in Chapin's description of *jamesoni*.

Nigrita nigritas are insect-eating finches of forests and forest edge and have a more finch-like (less slender) bill than *Parmoptila*. *Nigrita bicolor* chestnut-breasted nigrita occur in West and Central Africa. Young birds have blackish skin, a whitish gape with 4 small lemon-yellow balls at each side, the base of each ball is black; the palate is whitish with 5 black dots, the posterior pair small (Chapin, 1917, 1954; Kleefisch, 1990; van den Elzen, in litt.). *N. luteifrons* pale-fronted nigrita occur from southern Nigeria to Central Africa. Nestlings have the gape margin black with 4 white balls, 1 at the angle of the gape, 2 above the angle and 1 below; the palate spots and tongue spots are as in *Estrilda* (Bates, 1911). *N. fusconota* white-breasted nigrita occur in West and Central Africa east to Kenya; the nestlings are undescribed. *N. canicapilla* gray-headed nigrita in West to Central and East Africa have nestlings with grayish white natal down, a gape with 4 white papillae at each side, and a palate with 5 black spots (Chapin, 1917, 1954; Immelmann *et al.*, 1965; Kleefisch, 1984).

7. *Coccopygia* swee waxbills occur in East and southern Africa. Our understanding of swees as three distinct species is supported not only by distinct plumage but also by behavioral observations in the aviary. When these swees live together in an aviary, each shows sexual interest only in their own kind (Pajain, 1975; Goodwin, 1982). *Coccopygia quartinia* yellow-bellied swee waxbill live in open habitats in East and Central Africa. Nestlings have blackish skin on the head and the region where feathers develop, with the other skin area dark pink, the long gray natal down dense in patches on the head, back and thighs, a black gape with a bluish-white swollen arc above, with the proximal end curved ventrally to end in a white ball, and the lower gape with 2 balls of white to bluish-white, the palate unmarked, creamy white distally and bright reddish pink proximally, the tongue, lower mouth and edge of the mandible unmarked gray (UMMZ, RBP, Fig. 5 m, n). *C. melanotis* southern black-eared swee waxbill live in shrubby grass habitat. Nestlings have long gray natal down, a gape black bordered with white, a pale unmarked palate, and a plain or barred tongue, and as far as known are identical to *C. quartinia* (Immelmann *et al.*, 1965; Herkner, 1987; Maclean, 1993; Puschner & Rösel, 2001). *C. bocagei* Angola swee waxbill nestlings have not been described.

8. *Nesocharis* olive-backs are birds of forest or forest edge. *N. capistrata* olive-backed (white-cheeked) olive-back nestling skin color and natal down have not been described; the mouth has a gape with a curved upper arc with the proximal end curved ventrally to end in a white ball, and the lower gape with 2 balls, all pale bluish green backed by black; the pale yellowish palate has 5 large black spots, and the pink tongue has a dusky band (Chapin, 1917, 1954; T. Kleefisch fide R. van den Elzen). *N. ansorgei* white-collared olive-back of east-central Africa have natal down on the head and back, a swollen gape with a curved arc of light green-blue above and 2 light green-blue balls below, all separated by black; the black base of the upper arc extends into the oral cavity; the yellow palate has a single black spot, and the yellowish tongue and lower mouth are unmarked (Chapin, 1954; Kunkel & Kunkel, 1975; AMNH 0535). *N. shelleyi* Fernando Po (Bioko) olive-back live in southern Cameroon and Bioko; the young are undescribed.

9. *Mandingoa* green twinspots and *Cryptospiza* crimsonwings form a clade (Sorenson *et al.*, 2004; Fig. 1). *Mandingoa nitidula* green twinspots live in forests and thickets in West, Central and East Africa southward along the coast to eastern South Africa. Nestlings have yellow skin when young and the color changes with age to gray; they have long whitish-gray down. The gape on each side of the mouth has 3 bluish-white papillae edged inside with black, the palate is whitish with 3 black spots and 2 small posterior spots, and the tongue has 2 black spots sometimes connected by a line (Bates, 1911; Chapin, 1917, 1954).

Cryptospiza crimsonwings are birds of forest undergrowth in Africa. Some crimsonwings occur in areas with no others or with little geographic overlap between species; all four crimsonwings occur in the Albertine montane region of Central Africa (Hall & Moreau, 1970). *Cryptospiza reichenovii* red-faced crimsonwing nestlings have 4 small, pale yellow gape papillae, 2 above and 2 below, on each side of the gape, on the oral surface each papilla is lined with black; the palate is yellow with 3 large spots and 2 small spots behind them; the tongue has 2 spots, and under the tongue is a pair of spots; the nestling skin and down are undescribed (Chapin, 1954; Eisentraut, 1963; Markus, 1970; Sieberer, 1972; Kunkel & Kunkel, 1975). *C. salvadorii* Abyssinian crimsonwing have the nestling skin pale, the natal down on head and body is pale, the gape has 4 yellow papillae, the palate is yellowish white with 3 large spots and 2 smaller spots behind them, and the tongue has 2 spots (Chapin, 1954; Immelmann *et al.*, 1965, 1977a; Neff, 1978). *C. jacksoni* dusky crimsonwing have nestling mouths as in *C. reichenovii* (Chapin, 1954). *C. shelleyi* Shelley's crimsonwing nestlings are undescribed.

10. *Estrilda* waxbills occur in grassy areas through Africa and two or three species often live together within each species' geographic range. The molecular phylogeny indicates these form a monophyletic clade recognized as *Estrilda*. Within these waxbills are four sub-clades and these correspond to the four genera recognized by Wolters (1975). These sets are *Estrilda* Swainson 1827 (10.1), *Krimhilda* Wolters 1943 (10.2), *Brunhilda* Reichenbach 1862 (10.3), and *Glaucestrilda* Roberts 1922 (10.4). The first two (10.1, 10.2) are each others' closest relatives, and the second two (10.3, 10.4) are each others' relatives.

10.1. *Estrilda astrild* common waxbill, *E. rhodopyga* crimson-rumped waxbill, *E. paludicola* fawn-breasted waxbill, *E. troglodytes* black-rumped waxbill and *E. melpoda* orange-cheeked waxbill all live in open grassy areas in Africa, the first species throughout non-forested areas, the second in semi-arid regions of East Africa, the third in moist grassy areas in Central Africa, and the fourth and fifth together across semi-arid central and West Africa. Nestlings are naked, pink, and without natal down (Skead, 1957; Immelmann *et al.*, 1965; Goodwin, 1982). The mouth gape has a C-shaped arc swelling above, and the lower mouth has 2 white papillae. When the mouth is closed, the anterior lower papilla fits into the arc-like papilla of the upper mandible, and the posterior papilla is behind the upper arc. In front and in side view, the gape appears as a black spot surrounded by a white swelling. The palate is pink and has a ring of 5 spots, the lower gape has 2 white rounded papillae with black between them, and the tongue is pink with a black bar. A few days after hatching the skin darkens to pinkish gray (Bates, 1911, 1930; Chapin, 1917, 1954; Immelmann *et al.*, 1965; Goodwin, 1982; Mayer, 1999a; Lievens, 2004; J. Schuetz *E. rhodopyga*, RBP *E. astrild, E. troglodytes*, *E. rhodopyga, E. melpoda*, Fig. 5 a-h).

10.2. *Estrilda nonnula* black-capped waxbill of open woodlands in Central Africa, and *E. atricapilla* black-headed waxbill of forest clearings occur in Central Africa. Nestlings are pale pink and nearly naked. The gape has a swollen curved arc above, white with a black margin and black inner surface above the gape, and another swollen arc with a black lining below (the gape end of the arc is bluish white in the hatchling). When the mouth is closed, the upper arc lies in front of the lower arc. The pinkish- to yellowish-white palate has a ring of 5 black spots, the tongue has 2 black spots, and the lower mouth has a black crescent (Bates, 1911; Chapin, 1917, 1954; Urlepp, 1996; Mayer, 1997, 1998a; C. Balakrishnan, RBP, Fig. 5 e).

10.3. *Estrilda erythronotos* black-cheeked waxbill of semi-arid thorn country in East and southwestern Africa and *E. charmosyna* pink black-cheeked waxbill of thornbush thickets in northeast Africa occur together in southern Kenya (van Someren, 1978; Nicolai, 1989). In both species the nestling skin is black with light gray natal down, the gape has a swollen curved white arc above and a white arc below extending to a swollen ridge along the jaw, each arc lined black on the buccal surface; the palate is white with 5 black spots, the flesh-colored tongue has black spots; the overall mouth pattern is black and white (Immelmann *et al.*, 1965; Nicolai, 1989, 1990; Mayer, 1996b).

10.4. *Estrilda caerulescens* lavender waxbill of West Africa, *E. perreini* gray waxbill of south-central Africa and *E. thomensis* Cinderella waxbill of western Angola and northern Namibia occur in semi-arid regions in scrub habitat. *E. caerulescens* have a bluish-white swollen gape flange on the upper gape and another on the lower gape, the gape swellings lined inside the mouth with black (more extensive on the lower swelling), the gape swellings are nearly continuous with no black between them; the pale pink palate has a ring of 5 black spots, the posterior 2 smaller than the central and lateral spots, and the tongue has a dorsal black bar. Fledglings have the gape flange creamy white (Immelmann *et al.*, 1965; Puschner, 2001b; UMMZ, RBP). *E. perreini* nestlings are flesh-colored with sparse down on the head and back; the skin turns gray in 3 or 4 days (Pöhland, 1969). Nestling mouths of *E. perreini* and *E. thomensis* are similar, *E. perreini* having the same spot pattern and gape as *E. caerulescens* (Verheyen, 1953; Immelmann *et al.*, 1977a) and the gape arcs are seen in fledged *E. thomensis* (Pöhland, 1970). As far as known from the incomplete photographs and descriptions of the last two species, the nestlings and mouth patterns are the same in these three species.

Four other waxbills at times have been considered distinct species (Sibley & Monroe, 1990): *Estrilda nigriloris* black-faced waxbill along the Congo River in DR Congo, perhaps a local color form of *E. atricapilla*); *E. (paludicola) poliopareia* Anambra waxbill in southern Nigeria; *E. (p.) ochrogaster* Abyssinian waxbill; and *E. rufibarba (E. troglodytes rufibarba*: or *E. rhodopyga rufibarba*) in the southern Arabian peninsula. Their nestling gape and palate markings and colors are unknown.

11. *Ortygospiza* African Quail-finch populations comprise a single species *O. atricollis*, not two species *O. atricollis* and *O. gabonensis*, as in certain recent systematic treatments. Quail-finch occur in open habitats in sub-Saharan Africa in mesic and semi-arid regions, mostly in seasonally wet fields where they nest during the dry season, especially near flood plains. They regularly nest on the ground. Across the geographic range there is complete intergradation in face pattern between the extreme forms, some with white chin and white eye-ring, others with less conspicuous white plumage marks, others with a white chin and no white eye-ring, and the darkest forms with no white on the chin or around the eye. All have red bills as breeding adults. White-chinned and black-chinned quail-finch have the same songs (Stjernstedt, 1993, 1994). Because white-chinned and black-chinned plumage populations of *Ortygospiza* do not differ in songs and calls, do not differ in bill color, and do not breed separately in sympatry, and their mtDNA gene trees are not reciprocally monophyletic (Payne & Sorenson, 2003), they appear to be a single species.

Nestling quail-finch *Ortygospiza a. atricollis* and *O. a. pallida* have pink skin and gray natal down. The gape has round pale blue papillae, 2 on each side of the upper mandible and 1 on the lower, each separated by black at the base and along the gape fold between the papillae, the corner of the gape has a swollen gray pad; the blue papillae and black matrix form a bold checkerboard pattern on the closed mouth. The palate is pinkish-white to yellowish-white with a ring of 6 black spots, formed by 2 spots side by side in the center of the palate, a lateral spot on each side of it, and 2 smaller mediolateral spots. The tongue is pink with 2 black spots and a black tip. The colors and patterns of mouth and palate of young quail-finch appear to be the same across their distributional range (Serle, 1938; van Someren, 1956; Schifter, 1964; Kunkel, 1966; Nuttall, 1992; Payne & Payne, 1994; RBP, Fig. 5 q, r – 5 q = *O. a. pallida*, 5 r = *O. a. atricollis*). Nestling *O. a. fuscata* (of the black-chinned "*gabonensis*" complex) are the same, with 3 greenish blue balls on each side of the gape and a yellowish palate with 6 black spots, as in Chapin (1954).

12. *Paludipasser locustella* locust finch once were considered congeneric with *Ortygospiza* quail-finch. However, the molecular genetic data and phylogenetic analysis indicate they may be only distantly related (Payne & Sorenson, 2003), and here they are recognized as distinct genera. Locust finch occur in wet grasslands mainly in Central Africa and west to Nigeria. Nestling skin color is unknown; short natal down is on the head. The gape has a small red globe bordered black below at 1 day and 2 days of age; with 2 small red globes on either side from day 3 to day 6. Locust finch differ from other waxbills in having lines rather than spots on the palate. The palate is whitish, the center of the palate is bright red, and the center is bordered by a U-shaped arc, bright red in color with black edges. By day 3 the arc divides medially into 2 bow-shaped lines, and a black transverse line appears at the lateral base of the arc, the line extending halfway to the edge of the mouth; in Table 1 the lines are coded as modified lateral palate spots. The pale tongue has red spots on either side and on the tip; by day 3 the tongue spots are more intense red than the gape wattles (Irwin, 1958; Fig. 4 m, n).

13. *Amandava* finches occur in Africa and in Asia. *Amandava amandava* red avadavat (strawberry finch) are in southern and southeast Asia where they live in damp grass and reedy areas and are often in flocks (Smythies, 1940). Nestlings are pink-skinned with long white natal down. The gape is inconspicuous and whitish, the swelling contrasts with the blackish bill; the inner surface of the upper and lower gape each have 3 black spots; the palate is yellowish white with 3 or 4 small spots (the medial spot is single or double) and 2 smaller spots behind these forming a ring of 5 black spots; the tongue has 2 lateral spots, and there is a sublingual crescent (Steiner, 1960; RBP, Fig. 4 w). When the bill is closed, the black spots on the inner gape are seen against the white gape swelling.

Amandava formosa green avadavat (tiger finch) occur in India. Nestlings are sparsely covered with natal down, the gape has a narrow white flange with black spots as in *A. amandava*, a pale palate with 4 small spots (the center spot is double) and 2 more spots behind these, the tongue with 2 black spots and a black tip, and the lower bill with a short black crescent and 2 black spots. At fledging the gape flange is dull gray (Kunkel, 1962; Immelmann *et al.*, 1965; Hofmann, 1990a).

Amandava subflava goldbreast (orange-breasted waxbill, zebra waxbill) occur in Africa in open grassy areas, especially seasonally wet grasslands; they either build a nest or they nest in an old covered grass nest of other small birds. Nestling goldbreast at hatching are pink-skinned with long white down, long especially on the crown; the skin changes to dark gray before the feathers erupt while the white tufts of down contrast strongly with the gray skin. The mouth has an inconspicuous narrow whitish gape flange with 3 black spots on the inner surface of the upper flange and 3 on the lower flange; a whitish palate with 2 large black arcs in front of a ring of 5 small black spots, 3 on the palate and 2 smaller spots behind; a whitish tongue with 2 black spots and a black tip, and a sublingual crescent (Chapin, 1917; Immelmann *et al.*, 1965; C. Balakrishnan photos, RBP, Fig. 5 o, p). In frontal view the closed nestling mouth shows 2 black spots surrounded by a whitish gape. The gape swelling becomes small, inconspicuous and gray by the time of fledging. The details are the same in nestlings bred in our aviary by the West African subspecies *A. s. subflava* with the bright orange belly in male plumage and by the East African *A. s. clarkei* pale with the belly mostly yellow. The two subspecies have different brood parasites – *A. s. subflava* has the indigobird *Vidua raricola* and *A. s. clarkei* has the pin-tailed whydah *V. macroura*, both *Vidua* species with nestling mouths unlike those of the goldbreast hosts (*V. macroura*, Fig. 5 j-l).

14. *Amadina* thick-billed waxbills comprise two species that live in semi-arid habitats. *Amadina fasciata* cut-throat finch are widespread from west to east and southern Africa. Nestlings have dark grayish skin with long, dense pale gray natal down on the head and back; the gape flange is swollen and white, the white continuous on the inner surface (no black streaks); the palate is white and continuous with the white gape swellings, the palate has 5 large black spots on a bold network of white, area anterior to the spots is yellow and the palate behind the posterior pair of spots shades to reddish black, the lower mouth is black, and the tongue is pink with a broad black band (Güttinger, 1976; Beckham, 2000; RBP, Fig. 4 o, p). *Amadina erythrocephala* red-headed finch of South Africa are allopatric with the previous species. Nestlings have purplish-black skin with long, dense gray to white natal down on the head and back; the mouth is like that of *A. fasciata* (Markus, 1970; Immelmann *et al.*, 1977a; Oppenborn, 1998; Beckham, 2000; RBP, Fig 4 q, s).

15. *Erythrura* and *Chloebia* comprise a distinct clade of estrildid finches (Sorenson *et al.*, 2004; Fig. 1). *Chloebia gouldiae* Gouldian Finch occur in northern Australia; the plumage is green, yellow, and purple. The plumages of *Erythrura* parrotfinch species are green, blue and red. Some parrotfinches are terrestrial and feed on grasses; others are arboreal and feed on figs (Ziswiler *et al.*, 1972). Nestlings are naked at hatching and the skin is orange to pink. In *Chloebia gouldiae* and in the *Erythrura* parrotfinch species in which nestlings have been described, the gape is swollen and yellow and has 2 large and ornamental balls 1–2 mm in diameter, swellings of opalescent blue with black at the base. These balls reflect light and look like blue pearls; the upper ball is behind the lower one when the mouth is closed. Inside the mouth, the lining of the gape flange is black near the gape balls; in *Erythrura* the black is not extensive. In *Chloebia gouldiae* the variation in description of nestling mouths and the change in tongue marks with age (as in certain *Erythrura* species descriptions below) call into question the reports of species differences in nestling parrotfinches *Erythrura* as in Ziswiler *et al.* (1972).

Chloebia gouldiae Gouldian finch nest in holes in a tree. Nestling skin is orange to pink and naked. The gape has conspicuous large balls of opalescent blue, one above and one below the corner of the mouth, the balls with a black base, and a smaller yellow ball or swelling is at the gape; when the mouth is closed the lower ball is anterior to the upper one and the three form a triangle. The whitish palate has a ring of 5 black spots: a medial one, a large lateral pair and a smaller mediolateral pair. The upper bill tip has a black mark on either side, the inner mouth is pink, the pink tongue has 2 black spots above connected by a black band below, and there is a black lower mouth or crescent (Butler, 1898; Kühn, 1994; Beckham, 2000; Hofmann, 2000; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002; RBP, UMMZ, Figs. 2 a, 6 a).

Erythrura parrotfinch species occur from southeast Asia through Wallacea and the Pacific. Several species live on islands where they are the only parrotfinch, and others are sympatric with other parrotfinch species. The relationships among species have been proposed with details differing in nearly all reviews that were based on plumage and bill shape, and some reviews recognized two or more genera (Ziswiler *et al.*, 1972; Wolters, 1975; Nicolai & Steinbacher, 2001). The mtDNA analysis of parrotfinches indicates three clades and two subclades (certain species are yet to be sequenced): (1) *Erythrura prasina* and *E. hyperythra*; (2) *E. psittacea*; (3) *E. tricolor, E. regia* and *E. pealii*, and (4) *E. coloria*, *E. trichroa* and *E. papuana*; with (1) basal to the others and (3) and (4) as sister sub-clades. *Erythrura hyperythra* tawny-breasted parrotfinch are widespread from the Malay Peninsula, Java, Lombok, Flores, Sumbawa and Borneo to Sulawesi and the Philippines (Luzon, Mindoro). *E. prasina* pin-tailed parrotfinch are widespread in southeast Asia, Sumatra, Java and Borneo. *E. viridifacies* green-faced parrotfinch occur in the Philippines in Luzon and Negros. *E. tricolor* tricolored parrotfinch occur from Timor to Tanimbar. *E. trichroa* blue-faced parrotfinch are in Sulawesi, the Moluccas, New Guinea, the Bismarck Archipelago, western Oceania and northeastern Queensland. *E. coloria* red-eared (Mt. Katanglad) parrotfinch are in the mountains of Mindanao. *E. papuana* Papuan parrotfinch (with *E. trichroa*) are in New Guinea, *E. psittacea* red-throated parrotfinch are in New Caledonia. *E. pealii* Fiji parrotfinch are in Fiji, *E. cyaneovirens* red-headed parrotfinch in Western Samoa, and *E. regia* royal parrotfinch on Banks Is and Vanuatu; these last three are often considered conspecific, *E. cyaneovirens* (Dickinson, 2003). *E. kleinschmidti* pink-billed parrotfinch occur in Fiji. Nests of parrotfinches are bulky dark globes with a side entrance and often are built in trees (Ziswiler *et al.*, 1972; Hannecart & Letocart, 1980; Coates, 1990; Nicolai & Steinbacher, 2001).

Nestlings as far as known have similar nestling skin, gape and mouth patterns and colors in all species (Table 2). Nestling skin is orange to pink, and naked without down. The gape has conspicuous blue balls on the upper corner of the mouth and another on the lower with a small yellow flange between them. The blue balls are darker at the base but this base is limited to the ball (whereas *Chloebia* has black extending between the balls and inside the mouth), and does not appear to be a separate color, but rather a result of melanin at the base of the reflecting balls (Chun, 1903). The yellow palate has a ring of 5 black spots; one medial, a large lateral pair, and usually a mediolateral pair (Fig. 6 b-e). Species have been said to differ in size of the balls on the gape, the number and size of mediolateral palate spots, the marks on the tongue and below it, and the presence of a dark spot near the bill tip (Sarasin, 1913; Nicolai, 1967; Ziswiler *et al.*, 1972; Albrecht, 1990; Pistor, 1990; Kühn, 1994; Reinwarth, 1992; Wyrsch, 1992; Neff, 1995; Mayer, 1995d; Puschner, 2000c,d; Nicolai & Steinbacher, 2001). These traits differ with age and condition of observation, and photos show the color intensity of the gape balls to vary with the angle of light. The photographs available do not support the species differences described by Ziswiler *et al.* (1972). Young *E. kleinschmidti* have not been described, and young of a few other parrotfinches species are incompletely known (Nicolai & Steinbacher, 2001).

16. *Heteromunia pectoralis* pictorella finch live in northern Australia, and are distinct in plumage, with black face, gray-brown back and wing plumage, males with white breast and females with the breast scaled with black. Their relationship among the other estrildid finches is unresolved. *Heteromunia* were basal to both Australian grassfinches and munias *Lonchura* in a protein electrophoretic estimate (Kakizawa & Watada, 1985), they were basal to the munias in another protein estimate (Christidis, 1987a), and they were within the grassfinches in a chromosomal banding estimate (Christidis, 1986a). In our preliminary estimate of the generic relationship of estrildid finches, *Heteromunia* and the grassfinches and munias occur in an unresolved polytomy (Sorenson *et al.*, 2004; Fig. 1). The

Fig. 6. Mouths of young estrildid finches. a, *Chloebia gouldiae*; b, c, *Erythrura psittacea*; d, *Erythrura trichroa*; e, *Erythrura papuana*, New Guinea (Bruce Beehler); f, *Lagonosticta senegala*; g, hybrid *Lagonosticta senegala* x *Lonchura striata*; h, i, *Lonchura striata*, Bengalese finch (i, albino); j, *Lonchura castaneothorax*; k, *L. oryzivora*; l, *L. m. malacca*; m, *L. nevermanni*; n, *Poephila acuticauda*; o, *Lemuresthes nana*; p, *Taeniopygia castanotis*; q, *Stizoptera bichenovii*; r, *Stagonopleura guttata*; s, *Bathilda ruficauda*; t, *Aidemosyne modesta* (captives –a, b, c, d, f, g, h, p, q, r, RBP; i, j, k. l, m, n, o, s, t, R. Beckham).

plumage is sexually dimorphic, in contrast to the munias and like certain grassfinches such as zebra finch. Courtship displays of *Heteromunia* differ from displays of munias and are more like displays of an Australian-New Guinea grassfinch, the crimson finch *Neochmia phaeton* (Güttinger, 1976). The song is a simple pair of notes, which a male gives in a forward bowing movement somewhat like a singing *Lonchura* (Hall, 1962; Immelmann, 1965; Restall, 1997). *H. pectoralis* occur in moist country and in dry interior country and spinifex grassland. Nestlings are pink, naked without natal down, as in most munias *Lonchura*. The mouth has a narrow gape flange, slightly swollen and white with the gape corner bluish white, the upper and lower swellings lined with a streak of black; the yellowish-white palate has a single narrow black bar, and the tongue is whitish with black spots or a black ring and black tip (Immelmann, 1965; Güttinger, 1976; Restall, 1997; Nicolai & Steinbacher, 2001).

17. Australian grassfinches: Grassfinch nestlings have sparse natal down. They lack the bright globe-like protuberances at the gape, which varies from a thin flange to quite swollen in the case of *Stagonopleura guttata* diamond firetail. The nestling palate varies among grassfinches, even between *Poephila* species that are similar in plumage and behavior. *Poephila* and a few other genera have mainly lines on the palate whereas other grassfinches have spots, either elongate or round. The species distributions are mapped in Blakers *et al.* (1984). The incomplete taxon sampling and the comparison of different characters have led to inconsistent suggestions about generic relationships (Christidis, 1986a, 1987b; Baptista *et al.*, 1999). Phylogenetic relationships are not well known (Sorenson *et al.*, 2004; Fig. 1).

Stagonopleura guttata diamond firetail (diamond sparrow) occur in southeastern Australia. Nestlings have pale pink skin with sparse white natal down on head and back. The white swellings of the gape are outlined black and marked inside with a large black spot on the upper and lower swellings, showing as a black line between the white swellings when the mouth is closed. The palate is pinkish white with a diamond-shaped mark formed by a small black medial spot and 2 pairs of small black spots all connected by a thin black line, behind the hard palate is a pair of prominent white elongated white swellings on the side and a whitish curved transverse ridge in the midline (Immelmann, 1965; Nicolai & Steinbacher, 2001; RBP); Immelmann (1965) illustrated 2 spots on the tongue; the tongue in 1–2-day nestlings is barely marked (RBP, UMMZ, Fig. 6 r).

Stagonopleura oculata red-eared firetail live in evergreen forest in extreme southwestern Australia, where they are the only indigenous estrildid finch. *S. bella* beautiful firetail occur in mesic southeastern coastal Australia and in Tasmania where they are the only estrildid finch (Blakers *et al.*, 1984). Nestlings of both species have pale pinkish or yellowish skin and whitish natal down. The conspicuous gape swellings are white, each with an inner black spot. The pinkish palate has an elongated medial black spot and 2 elongated lateral black spots, 2 small black spots are behind the palate, the 5 palate spots are joined by a dark gray line that forms a diamond, open posteriorly. Behind the diamond a pair of contrasting white swellings rise in high relief and extend backward near the upper gape swelling, and a whitish curved transverse ridge is in the midline. The anterior mouth has 2 parallel lines, the tongue has 2 spots and there is a black sublingual crescent (Immelmann, 1965; Landolt *et al.*, 1976; Mitchell, 1987, in litt.; D. Myers, in litt.). The nestling gape swellings and palate patterns and colors are the same as in diamond firetail *S. guttata*.

Neochmia phaeton crimson finch occur in northern Australia and southern New Guinea. Nestlings are light-skinned at hatching with a trace of natal down; the skin changes from flesh color to nearly black by day 4. The mouth has a yellowish-white swollen corner of the gape with 2 large black spots on the medial surface of the upper and lower swellings, a creamy yellow palate with 3 elongate spots and 2 small spots behind these, the palate bright yellow around the posterior spots, the tongue has 2 black spots or a black bar, and a black crescent below (Mitchell, 1962, in litt.; Immelmann *et al.*, 1977a; Nicolai & Steinbacher, 2001; D. Myers, in litt.). The black mouth spots persist in the adult (anatomical spirit specimen with open mouth, AMNH 4519, Western Australia). In the New Guinea *N. p. evangelinae*, which also occur in the Cape York region of Australia, the young have the same details of skin and mouth (Rand, 1942).

Poephila grassfinches of northern Australia comprise *Poephila acuticauda* long-tailed finch and *P. cincta* black-throated finch, two allopatric species, and *P. personata* parson finch or masked finch which occur with the other two. *P. personata* nestlings have dark pink skin with sparse natal down, a gape flange blue at hatching and white by fledging, and a whitish palate with a short bar in the middle and a lateral bar on each side, and a pair of mediolateral spots (Immelmann, 1965; Mayer, 1991c; Beckham, 2000; I. Mitchell). *P. acuticauda* nestlings have pink to black skin with sparse light gray natal down, an unswollen bluish-white to white gape flange; the yellowish-white palate has a long black bar constricted near the ends, behind the long bar is a pair of mediolateral arcs (sometimes fused in the center), the tongue has 2 spots or a band, and a black V is under the tongue (Immelmann, 1965; Schönborn, 1984; Mayer, 1999b; Beckham, 2000; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002; I. G. Mitchell, in litt.; D. Myers, in litt.; Fig. 6 n). *P. cincta* nestlings at 2 days of age have black skin with sparse light gray natal down, a whitish gape flange, and a whitish palate with a black bar that narrows near the ends (Immelmann, 1965; Mayer, 1994c; I. G. Mitchell, in litt.). The fusion of black markings on the palate differs between *P. personata* which has short bars and the other two species; *P. cincta* has a long palate bar and mediolateral arcs much like *P. acuticauda* (Zann, 1976). *P. a. acuticauda* and *P. a. hecki* are alike (N. Burley, pers. comm.). All three species have black streaks on the oral surface of the gape swellings, a pair of black spots on the tongue and a black V under the tongue.

Bathilda ruficauda star finch occur in northern Australia from Shark's Bay eastward to isolated populations in the York Peninsula; before 1901 they also occurred through eastern Queensland. Nestlings have pale pink skin with sparse whitish natal down on the back, the gape has slightly swollen white flanges, bordered black and lined inside the mouth by 2 black bars on each side; the yellowish-white palate has a narrow bar of black and 2 small spots behind the bar, a black ring is around the tongue, and a crescent is under the tongue (Steiner, 1960; Sperl, 1996; Beckham, 2000; Puschner, 2002a; Fig. 6 s).

Aidemosyne modesta plum-headed finch (cherry finch) live in inland eastern Australia. Nestlings have pink skin and sparse whitish down on the back, the gape flanges are slightly swollen and light blue (with age changing to white), inside the gape are 2 black bars; the palate and a raised ridge and ring around the mediolateral spots are white, and the mouth cavity is pale pink (Schwanke, 1997); the markings resemble those of *Bathilda ruficauda* except the spots and bars on the palate and gape are broader (Steiner, 1960; Immelmann, 1965; Beckham, 2000; Fig. 6 t).

Emblema pictum painted finch occur in the Kimberley region of Western Australia and through the arid center of Australia in spinifex habitat. Nestlings hatch with naked pinkish skin; the gape is an inconspicuously swollen flange strikingly marked inside with a thin black line (barely visible in fledged young), the black line extending to the tip of upper and lower mandible; inside the mouth are 2 black parallel streaks on the anterior end of the upper mandible, the whitish palate has a thin long black bar in front of a raised white crest and a pair of small black spots, the tongue has a black ring and black tip, and under the tongue is a thin black crescent (Mitchell, 1987; Bielfeld, 1993; Mayer, 1993c; Puschner, 2000b; Nicolai & Steinbacher, 2001).

Aegintha temporalis red-browed finch occur in non-arid eastern Australia from the York Peninsula coastwise to South Australia. Nestlings have flesh-colored skin and sparse bluish natal down; the gape has grossly swollen corners with 2 large black spots on the inner surface of the swellings, the palate has 3 elongate spots in front and 2 small spots behind, the tongue has a dark bar and under the tongue is a black crescent (Steiner, 1960; Immelmann, 1965; Nicolai & Steinbacher, 2001).

Taeniopygia guttata and *T. castanotis* zebra finches differ from each other in plumage, courtship displays and song (even when the nestlings are cross-fostered and reared by the other form, they develop the song characteristics of their genetic species, Clayton, 1990a); and in an aviary where they are free to choose a mate of either kind, they mate assortatively (Böhner *et al.*, 1984; Clayton, 1990b,c). *Taeniopygia castanotis* Australian zebra finch occur throughout most of non-forested Australia. Nestlings have pink skin with sparse natal down on the head and back, The gape is slightly swollen and constricted in the middle, a black line is inside the swelling, the upper line extends forward to nearly meet at the bill tip, the lower line extends less than halfway to the tip; the palate is pinkish- to yellowish-white and has 3 round spots and a pair of short arcs behind the lateral spots, the tongue has 2 black dorsal spots (changing with age to a dorsal bar), and the mouth has a black sublingual crescent (Morris, 1954; Immelmann, 1965, 1968; Zann, 1996; Beckham, 2000; Vriends & Heming-Vriends, 2002; RBP, Fig. 6 p). Timor zebra finch (Lesser Sunda zebra finch) *T. guttata* Timor zebra finch occur on Timor and other islands in the Lesser Sundas (White & Bruce, 1986). Nestlings have skin color, natal down, and a mouth like nestling Australian *T. castanotis* (Ullrich, 1997; Beckham, 2000; Nicolai & Steinbacher, 2001).

Stizoptera bichenovii double-bar finch (owl finch) occur in Australia within the range of zebra finch. Sometimes recognized within the zebra finch genus *Taeniopygia, S. bichenovii* and *Taeniopygia* do not form a monophyletic lineage either in the combined-character analysis of phylogeny of Baptista *et al.*, (1999), where they are associated with *Poephila cincta*, or in our molecular genetic analyses, where they are with *Poephila personata* (Sorenson *et al.*, 2004; Fig. 1). Nestlings have dark pinkish gray skin, short gray down on the head and back; the slightly swollen white gape has a black medial surface on each flat flange, inside the mouth the pinkish-white palate has 3 elongated black spots and 2 small black arcs in the mediolateral position (the arcs open posteriorly, rather than anteriorly as in *T. guttata* and *T. castanotis* zebra finches), 2 black spots on the tongue and a black spot below, and a black sublingual crescent (Immelmann, 1965; Beckham, 2000; Nicolai & Steinbacher, 2001; RBP, Fig. 6 q).

Oreostruthus fuliginosus crimson-sided mountain finch (mountain firetail) occur in forested highlands of New Guinea. Fledged young have orange-yellow swellings on the lower gape (Coates, 2001); otherwise the young are undescribed.

18. *Lonchura* munias. The most species-numerous estrildids are the munias *Lonchura*. They vary in plumage, most species having a combination of brown, black and white, thick bills, and large feet and toes with which the birds climb on grass stems, especially rice (Restall, 1997). Phylogenetic relationships among most species have been determined in mtDNA sequence analyses, and the following numbered sections indicate these munia clades and the species relationships within these clades. Here the term "munias" is used for all these Australasian birds, rather than "nuns" or "mannikins," and this last term is restricted to finches in the African genus *Spermestes*. Within the genus *Lonchura* the clades are as follows: clade 18.1 is basal, next is 18.2, and then 18.3 and 18.4 ((a,b)(c)) (Payne & Sorenson, 2003). The cladistic positions of the Indian *L. kelaarti* in clade 18.2 and several New Guinea munias in clade 18.4.c are tentative and have yet to be determined in genetic analysis.

Most *Lonchura* nestlings are naked or have sparse natal down on the back, and the palate has a black bar. Munias differ in other mouth markings; only one species has bright patches of color inside the mouth. The gape swelling has not received much attention in descriptions or photographs and it appears to vary mainly in size. Most young munias have a simple pale swollen fold at each side of the gape. In several species a bold black outline is on the naked face at the folds of the gape; the facial outline is unknown in other species where only the inner surface of the mouth has been photographed in the unfeathered nestling.

18.1. In munias the basal clade consists of four species. *Lonchura tristissima* streak-headed munia are New Guinea birds. The southern form *L. t. leucosticta* white-spotted munia has been considered a distinct species (Sibley & Monroe, 1990). The plumages differ, hybrids occur where the ranges meet, and they are often considered a single species (Immelmann *et al.*, 1977a; Coates, 1990; Nicolai & Steinbacher, 2001; Dickinson, 2003). The nestlings are undescribed in detail. Nestling *L. t. leucosticta* have flesh-colored skin and are naked at hatching, and they have a white gape flange bordered black and a yellowish palate (Bielfeld, 1982; Mayer, 1992a; Nicolai & Steinbacher, 2001). Hybrid nestling *L. t. leucosticta x Taeniopygia castanotis* have a swollen pale gape, 3 spots or a broken black bar on the palate and an unmarked tongue and lower mouth (Restall, 1997).

Lonchura oryzivora Java sparrow occur on Java and nearby islands, with introduced populations elsewhere; and *L. fuscata* Timor sparrow are on Timor, Semau and Roti. The two earlier were recognized as a separate genus *Padda.* Nestling *L. oryzivora* have pink skin with sparse natal down on the head and back (UMMZ) or only on the back (Baptista *et al.*, 1999), or are naked and lack down altogether (Beckham, 2000; Nicolai & Steinbacher, 2001); nestling *L. fuscata* are naked (Nicolai & Steinbacher, 2001). Both have a broad white swelling around the gape, the gape is yellowish on the oral surface or has 2 small black streaks on each side of the gape, the yellow to whitish palate has a single broad black bar; the tongue and area below are unmarked (Güttinger, 1976; Restall, 1997; Beckham, 2000; Mayer, 2000c; Nicolai & Steinbacher, 2001). Domesticated white plumage phase *L. oryzivora* lack the black mouth markings and lack melanin in the eyes (Beckham, 2000; UMMZ, Fig. 6 k).

18.2. *Lonchura punctulata* scaly-feathered munia are known as spice finch, spotted munia or nutmeg finch in the avicultural trade. The natural distribution includes India, Sri Lanka, China and southeast Asia through Malaysia and Indonesia through Sulawesi and the Lesser Sunda Islands, and the Philippines and the birds have been introduced elsewhere. Nestling skin is purplish gray with sparse gray natal down on the back; the mouth gape is whitish, somewhat swollen, bordered black and with black markings on the oral surface; the palate is whitish with a black bar, behind the bar the mouth is yellowish white, the tongue is pink with an incomplete black ring, and a black crescent is below (Moynihan & Hall, 1954; Immelmann *et al.*, 1977a; Bielfeld, 1992; Baptista *et al.*, 1999; Beckham, 2000; RBP).

Lonchura kelaarti hill munia occur in southern India and Sri Lanka, where they are common in clearings in forests and in gardens and towns (Restall, 1997). Young at hatching have light flesh-colored skin with sparse light gray natal down on the back, the palate is pale yellow with slate black markings much as in *Lonchura punctulata*; further details are lacking (Nicolai & Steinbacher, 2001).

18.3. *Lonchura striata* white-rumped munia (striated munia, sharp-tailed munia) occur in southern, eastern and southeast Asia and in Sri Lanka. Nestlings have pink skin, and they vary from being naked to having as much natal down as in *L. punctulata*; the mouth has a simple gape of white, bordered and black on the oral surface, a yellow palate marked with a single curved bar and 2 small spots behind the bar, and a ring around the tongue (Mayer, 1995c; Baptista *et al.*, 1999; UMMZ, Fig. 6 h). The nestling mouth is the same in different subspecies in Sri Lanka and eastern China, and in dark domesticated Bengalese finch (Restall, 1997). In pied- and white-plumage strains of Bengalese finch the nestling pigment is reduced or lacking, the skin is pink even in older nestlings, the palate is whitish; the palate bar sometimes is broken into discontinuous lines or is missing, and marks on or under the tongue vary as well (Restall, 1997; Beckham, 2000; RBP, Fig. 6 i).

Lonchura leucogastra white-bellied munia occur in the Malay Peninsula, Borneo, and the Philippines (Dickinson *et al.*, 1991). They sometimes breed in colonies with as many as six nests in a tree (Smythies, 1999). A forest bird, destruction of habitat has caused much loss of populations, especially in the Philippines. Nestlings have pink skin sometimes with one or two tufts of down on the back, a whitish flanged gape, the yellowish palate with a narrow black arc extending laterally nearly to the gape and with 2 mediolateral spots, the tongue unmarked or with 2 black spots, and the lower mouth with a long black arc extending nearly to the gape (Steiner, 1960; Immelmann *et al.*, 1977a; Mayer, 1992a; Restall, 1997; Nicolai & Steinbacher, 2001).

Lonchura molucca black-faced munia occur in Sulawesi, the Moluccas, and throughout the Lesser Sunda Islands. In geographic distribution they complement *L. striata*, a closely related species. Nestling *L. molucca* have flesh-colored skin with one or two tufts of white down on the back (Nicolai & Steinbacher, 2001). The gape flange is white, bordered black and lined black, and constricted at the mouth corner; the whitish palate has a narrow black bar that tapers in the midline and at the ends, a pair of black arcs are behind the blade bar, and the tongue has a black tip and black spots that join below (Beckham, 2000).

Lonchura fuscans dusky munia occur in Borneo and the Natuna islands, and early records indicate they once were in the Philippines (Cagayan Sulu) (Dickinson *et al.*, 1991). They nest in dark sites, in dense foliage of a tree, and in crevices as high as 75 m in Niah caves. Nestlings have pink skin, natal down is lacking or consists of a few tufts of light gray natal down on the back, the gape is swollen, blue-white gape at hatching and white at fledging (the buccal lining is not visible in photographs), and the palate is whitish with a long black bar and 2 spots behind the bar (Mayer, 1984; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002). The nestling mouth in this forest- and cave-living species is like that of other munia species in more open grassy habitats.

Lonchura leucogastroides Javan munia occur in Java, Bali and Lombok. Their geographic distribution complements the more northern *L. striata*, except that both munias occur in Sumatra where *L. leucogastroides* may have been introduced (van Marle & Voous, 1988). They live in cultivation, rice fields and grassy scrub. Nestlings have pink skin, bare or with one or two tufts of down, the gape flange is white bordered black outside and lined black inside the mouth, the palate is yellowish and has a black bar, the tongue has 2 spots and a black mark is under the tongue (Restall, 1997; Mayer, 1998b; Nicolai & Steinbacher, 2001).

18.4.a. The next three munias are allopatric, are each others' closest relatives (Restall, 1997; Payne & Sorenson, 2003) and are probably conspecific. *Lonchura malacca* black-headed munia (tricolored nun) occur in central and southern India and in Sri Lanka. Nestling *L. (m.) malacca* have a gape flange of bluish-white changing to white with age, the gape with a thick black line on the inner surface above and below; the palate is pale yellowish-pink with a black band extending laterally and 2 indistinct blackish spots behind the band, a tongue with 2 small spots and a black tip, and a chevron under the tongue (Mayer, 1992b,d, 1993b; Ullrich, 1998; Beckham, 2000; Fig. 6 l). *L. (m.) atricapilla* chestnut munia of northern India, south-east Asia and southern island Asia from the Philippines through most of Indonesia have a white gape flange bordered with black streaks on the inner surface, a whitish palate with a black band, a tongue with 2 small spots, and a narrow sublingual chevron (Restall, 1997). In *L. (m.) ferruginosa* white-headed munia of Java, the nestlings' mouth has not been described, the skin is pinkish, and apart from two tufts of down the nestlings are naked at hatching, as in other nestling *L. malacca* (Nicolai & Steinbacher, 2001).

L. maja white-headed munia and *L. pallida* pale-headed munia have complementary geographic ranges, *L. maja* in the Malay archipelago, Sumatra and Java, and *L. pallida* in Sulawesi and the Lesser Sunda Islands east to Timor and Wetar. *L. pallida* nestlings have pink skin and lack natal down, a swollen blue gape changing to white by day 10 and bordered with black, a pale yellow palate with a black arc, an unmarked tongue and a short mark under the tongue (Mayer, 1991d; Restall, 1997; Nicolai & Steinbacher, 2001). *L. maja* nestlings have pink skin at hatching, either naked or with tufts of natal down, a bluish-white gape flange bordered black, a yellow palate with a black arc, an unmarked tongue and a mark near the bill tip (Mayer, 1994a; Restall, 1997; Beckham, 2000; Nicolai & Steinbacher, 2001).

18.4.b. Another set of munias *Lonchura* occurs across a wide region from the Malay Archipelago to New Guinea and Australia. *Lonchura spectabilis* hooded munia occur in New Guinea, New Britain, and Long and Rooke islands. They build covered grassy nests in grass or bushes, and breeding sometimes is in colonies (Coates, 1990). Nestlings have naked pale pink skin, a blue-white gape lined with black, a pale pinkish palate with a black curved bar and 2 black mediolateral lines, a black ring around the tongue and a black sublingual mark. At fledging time the gape edge is white (Güttinger, 1976; Mayer, 1990; Dingelstedt, 1997).

Lonchura teerinki Grand Valley munia (black-breasted munia) occur in northwestern central New Guinea. Their plumage color and the visual pattern of black head, breast and flanks and a yellowish rump, resemble the larger munias in northern New Guinea and the Bismarck Archipelago (*L. grandis* and *L. melaena*). Young nestlings have flesh-colored skin with sparse white down on the back, the mouth has a blue gape flange (the flange is white at 17 days at fledging) with a black lining, the palate is pinkish-white with a single long black line and 2 black spots behind the line, the tongue is yellowish-white with a black ring and black tip, and the bill tip is black (Hofmann, 1990b; Mayer, 1991a; Nicolai & Steinbacher, 2001).

Lonchura castaneothorax chestnut-breasted munia live in New Guinea and northern and eastern Australia, in habitats of savanna and grassland (Coates, 1990). Newly hatched nestlings have pink skin, usually bare or with one or two tufts of natal down, a blue-white gape slightly swollen and lined inside with black, the upper gape mark a long teardrop and the lower one a simple spot, a pale yellow palate with a short medial black bar formed by 3 spots), a spot on each side of the base of the lower bill, the tongue with a black ring, and a black sublingual crescent (Immelmann, 1965; Mayer, 1995b, 2000a; Beckham, 2000; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002; Fig. 6 j).

Lonchura quinticolor five-colored munia (chestnut-and-white munia) occur in Indonesia in Teman Negara (Lesser Sunda Islands) from Lombok, Sumbawa, Flores and Alor to Sumba, Roti, Moa, Timor, Sermata and Babar (White & Bruce, 1986). Nestlings have light flesh-colored skin nearly naked with one or 2 tufts of natal down; the gape flange is blue at hatching and changes to white by 10 days, the flange is bordered black and lined with 2 black vertical bars. The yellow palate has a pair of long and narrow black lines, the anterior bar incomplete in the midline, a tongue with lateral spots, and a black bar on the under surface (Mayer, 1995a; Restall, 1997; Nicolai & Steinbacher, 2001).

Lonchura flaviprymna yellow-rumped munia occur in northern Australia in swampy grasslands along the coast and inland, in reedbeds, long grasses, the edges of swamps and marshes, and in scrub country near water. In northwestern Australia near the Kimberley Research Station, about 10% of nesting birds are seen in mixed-species pairs: they interbreed and produce hybrid offspring with *L. castaneothorax* (Immelmann, 1962b; Restall, 1997; Nicolai & Steinbacher, 2001). Nestling *L. flaviprymna* have naked pink skin at hatching, the gape is bluish white turning white with age, the palate is whitish with a curved black bar and behind the bar are 2 small spots, the tongue has a black ring and there is a broad sublingual black crescent (Restall, 1997; Mayer, 2002).

Lonchura nevermanni gray-crowned munia occur in the trans-Fly region of southern New Guinea. Non-breeding birds are sociable, feeding in grassy marshland and roosting together at night, hunched together or piled into a nest. At breeding time the birds separate into pairs; the members of a pair build a nest of grasses and reed leaves, they share in incubation, and they feed the young. Nestlings have pink skin, with tufts of down on the back (the down disappears in older nestlings); the gape flange is bluish-white bordered black and lined black, constricted at the mouth corner; the whitish palate has a single black bar that tapers to a point in the midline and at the ends, a pair of elongated spots are behind the white ridge behind the black palate bar, and the tongue has a black tip and black spots on the dorsal surface joined below (Mayer, 1996a; Coates, 1990; Restall, 1997; Nicolai & Steinbacher, 2001; R. Beckham; Fig. 6 m).

Lonchura stygia black munia live in south central New Guinea in low wet grassland, tall grasses and reedbeds, and on floating mats of rice grass in lagoons and swamps (Restall, 1997). The munia are social, in flocks of 20 or more birds, sometimes with *L. caniceps* gray-headed munia and *Neochmia phaeton* crimson finch. Nestlings have pink skin, usually without natal down or with tufts of down on the back, the gape flange is bluish-white to white, bordered and lined black; the palate is pinkish-white at hatching and yellow at 10 days, the palate bar is incomplete at hatching changing with age to a complete bar, 2 short lines are behind the bar, and the tongue has a black band and black tip. The black inner lining of the nestling gape shows in frontal view (Mayer, 1991b, 1996d; Nicolai & Steinbacher, 2001; Ullrich, 2002).

Two other species pairs of *Lonchura* munias occur in New Guinea. *Lonchura caniceps* gray-headed munia and *Lonchura vana* gray-banded munia are closely related, one in eastern New Guinea and the other in the Arfak region. *L. caniceps* build a covered grassy nest placed in dense shrubs or trees, and they have bred in captivity; *L. vana* have not been seen to nest (Restall, 1997). *Lonchura montana* western alpine munia or Snow Mountain munia and *L. monticola* eastern alpine munia occur in montane New Guinea. *Lonchura monticola* build a nest like other munias, neatly woven of rushes and grass and built in a tree (Restall, 1997); *L. montana* nest in grasses by water (Bell, 1971; Beehler *et al.*, 1986). The nestling mouths have not been described.

A final set of munias *Lonchura* in New Guinea and the Bismarck Archipelago are mainly allopatric. *Lonchura grandis* grand munia of northern and eastern New Guinea is a large bird with a very large bill, living in wet grass and nesting in trees (Coates, 1990). Nestlings are naked, the gape flange is white, the inner lining of the flange has 2 elongate black spots, the yellow palate had a single long black line and 2 black spots behind it, and the tongue is yellow with a black ring (Mayer, 2000b; Ullrich, 2002; R. Beckham). *Lonchura melaena* thick-billed munia occur in the southern Bismarck Archipelago (New Britain) and Buka, and *Lonchura forbesi* New Ireland munia occur on New Ireland. Nestling *L. melaena* and *L. forbesi* are unknown.

Lonchura hunsteini Hunstein's munia are small-billed munia in the northern Bismarcks (New Ireland and New Hanover) (Coates, 1990; Mayr & Diamond, 2001). They live in lowland grasslands. The form *nigerrima* is considered to be a subspecies of *L. hunsteini* (Coates, 1990). The nestlings are undescribed.

19. *Spermestes* and *Odontospiza* mannikins form a clade distinct from the munias. Three species of *Spermestes* occur in Africa, *Spermestes cucullatus* bronze mannikin widespread through sub-Saharan Africa except in dense forest and the arid southwest, *S. bicolor* black-and-white mannikin in more mesic regions, and *S. fringilloides* magpie mannikin in eastern Africa in areas of rice and bamboo.

Spermestes nestlings have sparse gray natal down, a gape flange and a double bar on the palate (Nicolai & Steinbacher, 2001). *S. bicolor poensis* and *S. b. nigriceps* (black-and white mannikin and rufous-backed mannikin) have the gape slightly swollen in a bluish-white band and a black margin. The palate is yellowish white with a double curved bar, the anterior bar longer, and between the bars is a raised yellow-white ridge, the upper bill has a black tip, and the tongue has a black band (Bates, 1911; Chapin, 1917, 1954; Beckham, 2000; Mayer, 2001; Fig. 4 u). *S. fringilloides* have the same pattern, the corners of the gape are bluish-white and lined with black, the palate has a double bar, the tongue has 2 spots or a band, and 2 black bars are the lower mouth (Chapin, 1917, 1954; Serle, 1950; Steiner, 1960; Markus, 1970; Restall, 1997; Baptista *et al.*, 1999; Mayer, 2001; Nicolai & Steinbacher, 2001). *S. cucullatus* have the same pattern (Chapin, 1917, 1954; Kunkel & Kunkel, 1975; Güttinger, 1976; Restall, 1997; Mayer, 2001; RBP, Fig. 4 t).

Odontospiza caniceps (*"Lonchura griseicapilla"* auct.) pearl-headed mannikin (gray-headed silverbill, pearl-headed amadine) occur in semi-arid East Africa. Nestling skin is dark pink with sparse whitish natal down; the mouth has a thin bluish-white gape flange bordered black and lined medially with 2 elongate black spots; inside the mouth is whitish with 2 parallel black streaks near the tip, the palate is whitish with a black double arc, the 2 arcs widely separated by white; the mouth cavity is pinkish, the bluish-white tongue has 2 black spots and a band on the lower surface, and 2 crescents are below the tongue (Mayer, 1994b; Restall, 1997; Baptista *et al.*, 1999; Hofmann & Mettke-Hofmann, 1999; Nicolai & Steinbacher, 2001; Puschner, 2002b).

19. *Lemuresthes nana* Madagascar munia (bib-finch) is the only naturally occurring estrildid finch on Madagascar. Nestlings have pinkish skin and no natal down. The gape is slightly swollen and white to yellowish white with teardrop-shaped black spots inside the gape, one on the upper flange and one on the lower; the palate is yellow with a long, narrow curved black bar, the tongue has a pair of small black spots, a black mark is below the tongue and a black line occurs along the sides and tip of the lower mouth (Steiner, 1960; Güttinger, 1976; Beckham, 2000; Giebing, 2000; Mayer, 2001; Figs. 2 c, 6 o).

20. *Euodice* silverbills. *Euodice cantans* African silverbill occur across sub-Saharan Africa north of the central forest and south to Tanzania, and eastward into southern Arabia. *E. malabarica* Indian silverbill are in dry and barren areas and desert oases from the eastern Arabian Peninsula to Pakistan, India and Sri

Lanka. *E. cantans* nestlings are naked with a blue-black skin; some have sparse natal down on the back. The mouth has a thick and swollen white gape, the palate is yellowish white, a broad black band (corresponding to the palate bar of other munias) extends from the palate around the sides of the mouth and gape swelling to the lower jaw where the band narrows, and a field of small, uncolored papillae is on the palate behind the parachoanal ridge (Fig. 2 b). *E. malabarica* nestlings are similar (Steiner, 1960; Glatthaar & Ziswiler, 1971; Güttinger, 1976; Immelmann *et al.*, 1977a; Baptista *et al.*, 1999; Beckham, 2000; Nicolai & Steinbacher, 2001; Vriends & Heming-Vriends, 2002; Fig. 4 s).

RESULTS

Traits of the natal skin and down, the nestling gape and mouth patterns and colors, and the geographic distribution and habitat vary among the estrildid finches. The mouth characters of nestlings (Table 2) were compared to test ideas about the evolutionary significance of this variation: phylogeny, habitat, coevolution in response to nest parasitism between estrildid species, and coevolution in response to brood parasitism by their *Vidua*. The characters were compared by way of indices for each species and between pairs of species (**indices *a1*, *a2*, *b*, *c*,** and ***d***).

Phylogeny – The variation in estrildid nestling mouth patterns and colors may be explained by species divergence in phylogeny, and the mouth markings have been used as independent estimates of phylogenetic relationships among species (Neunzig, 1929a; Delacour, 1943; Steiner, 1959, 1960, 1966). Earlier proposals about the evolution of nestling mouth patterns in estrildid finches were based on the assumption that *Vidua* finches were not host-specific, and they viewed the evolution of mouth patterns as independent of brood parasitism (Chapin, 1917; Hoesch, 1939; Friedmann, 1960).

Although a molecular phylogeny of the estrildids is still incomplete, the results available indicate that the mouth markings tend to follow the estimates of phylogeny. The form of gape swellings and flange and the pattern of black markings on the palate are more similar within than between the clades and lineages shown in Fig. 1. The waxbills have palate spots (except in the three species of *Coccopygia* and in four *Pytilia*), with variations in the number of spots (1 in *Pytilia melba*, 3 very large spots in *Amadina*, 3 or 5 in most estrildids, and 16 in *Amandava*) (Figs. 4, 5). The gape is more variable, with small to large papillae in firefinches *Lagonosticta* (except in *L. rufopicta*, which have an upper and a lower swelling on each side of the gape). *Amandava* lack distinct colored gape papillae, whereas *Amadina* have a swollen flange. The similarity in nestling mouths of *Amandava amandava* and *A. subflava* (Figs. 4 w, 5 o, p) is consistent with their close phylogenetic relationship, and the nestling mouths do not differ because of association with a brood parasite (Indian *A. amandava* are not parasitized, whereas *A. subflava* have two *Vidua* species). The gape papillae are pale blue in some estrildids (*Nesocharis*, *Ortygospiza*), and yellow and orange in some twinspots (*Euschistospiza, Hypargos*) (Fig. 3 s, v, w, x, Fig. 5 q, r). Locust finch *Paludipasser locustella* have bright red lobes on the gape and the red palate is marked with bars rather than spots (Fig. 4 m, n).

In parrotfinches *Erythrura* and Gouldian finch *Chloebia*, the nestlings have black spots on a yellow to whitish palate and a large blue globe above and below the gape (Fig. 6 a-e).

In Australian grassfinches the nestling gape varies from a thin flange to broad swellings, and the gape is conspicuously swollen only in firetails *Stagonopleura* (Fig. 6 n, p, q, r, s, t). The palate has spots in estrildids with a swollen gape, and bars in estrildids with a thin, flanged gape.

Finally, in most munias and mannikins the gape is a slightly swollen flange and the palate has bars (Fig. 4 t, u; Fig. 6 h, j-m). Asian and African silverbills *Euodice* have a broad mouth and conspicuously swollen gape (Fig. 2 b, Fig. 4 s).

Within a few clades the nestling mouths differ markedly, in particular in the firefinches *Lagonosticta*, where the species mouths are similar only within the clade *L. rubricata-virata-sanguinodorsalis-rhodopareia*. Estrildid finches with similar nestling mouths generally appear to have close phylogenetic relationships (Baptista *et al.*, 1999; Sorenson & Payne, 2001b; Payne & Sorenson, 2003; Sorenson *et al.*, 2003, 2004; Fig. 1).

Habitat – Palate markings and gape papillae of nestling estrildids are directed toward the parent in parental care. These signals may allow the parent to see their nestlings in a dark place (Butler, 1898; Hoesch, 1939; Friedmann, 1960). Estrildids rear their broods in covered nests often concealed in dense vegetation. The balls or globes on the gape in parrotfinches *Erythrura* and Gouldian finch *Chloebia gouldiae* are particularly striking, as even in a darkroom with little light they appear to glow: these structures reflect light rather than luminesce, as when external light is excluded, the globes produce no visible gleam (Chun, 1903; Ziswiler *et al.*, 1972). Because all estrildids use covered nests where the sun does not shine directly on the begging young, the differences between nestlings of estrildid species may require some explanation beyond the structure of the nest.

A prediction of the hypothesis that low light levels are associated with nestling mouth patterns is that the patterns are brighter and the gape globes are more prominent in estrildids living in dense vegetation than those in more open habitats, and in estrildids that build dense larger nests than birds with less dense nests. Forest-living green twinspot *Mandingoa* and crimsonwings *Cryptospiza* have small inconspicuous gape balls of bluish-white or yellow; yet blue gape balls also occur in quail-finch *Ortygospiza* which nest in open grassy habitat. Finally, several African estrildids live in forests: *Parmoptila, Nigrita, Spermophaga, Pyrenestes* and some *Spermestes bicolor* (Fig. 1), yet these birds have no more prominent gapes and bright colors than the estrildids in more open habitats (Table 2). In Australasia, some estrildids that nest in dense vegetation have bright gape balls, notably parrotfinches *Erythrura* which build large nests in closed vegetation (Ziswiler *et al.*, 1972; van Balen, 1987; Nicolai & Steinbacher, 2001) and Gouldian finch *Chloebia gouldiae* which always nest in tree holes and long-tailed finch *Poephila acuticauda* which sometimes nest in tree holes (Tidemann *et al.*, 1992, 1999). Further, the gapes are more conspicuous in Australian firetails *Stagonopleura* that live in forests and build large nests with thick walls, than in grass-finches in more open habitats with a smaller nest and thinner and more light-penetrating walls (Table 2). Gape swellings are not conspicuous in munias *Lonchura*, and none have bright colors or complex mouth patterns. Forest-living munias do not have greater elaborate markings or gape structures than do the munias living in open habitats (Table 2). In the Malay Peninsula, Sumatra, Borneo and the Philippines, white-bellied munia *L. leucogastra* (Restall, 1997) live both in forest and in forest edge, rice fields and wet grasslands (Dickinson *et al.*, 1991; Nicolai & Steinbacher, 2001). In New Guinea, streak-headed munia *L. tristissima* are in forest clearings or open land between forest and marsh, or bamboo, and not in forest itself. Most munias live in open grassland, cultivated fields, rice paddies, reed beds and rank grasses. All munias use covered nests, yet no munias have bright gapes. In the estrildids the large, bright gape papillae and colored gape markings are associated more closely with phylogenetic lineage than with habitat and nest structure.

Opportunistic nest parasitism by estrildid finches – Nest parasitism between estrildid species might lead to natural selection for divergence of nestling mouths (K. Immelmann, pers. comm.). Even so, in his fieldwork, Immelmann did not observe or report nestlings of one species in the nest of another species (Immelmann, 1962a, 1965, 1968; Immelmann & Immelmann, 1967).

Field observations suggest opportunities for nest parasitism between sympatric species. Estrildids sometimes lay eggs in the old nests of other species, in Africa (Lynes, 1924; Bates, 1930; Jackson & Sclater, 1938; Moreau & Moreau, 1939; Bannerman, 1949; Hoesch & Niethammer, 1940; van Someren & van Someren, 1945; Chapin, 1954; Calder, 1955; Friedmann, 1960; van Someren, 1956; Morel & Morel, 1962; Eisentraut, 1963, 1968; Benson *et al.*, 1964; Immelmann *et al.*, 1965; Immelmann & Immelmann, 1967; Mundy & Cook, 1974; Woodall, 1975; Payne, 1977b, 2004; Paxton, 1996; Hustler, 1998), in Asia (Legge, 1880; Phillips, 1948; Sharma, 1987; Roberts, 1992; Restall, 1997; Smythies, 1999), and in Australia and New Guinea (Immelmann *et al.*, 1977a); at least 30 species of estrildids have been reported to do this. At Vom, Nigeria, three active nests of red-cheeked cordon-bleu *Uraeginthus bengalus* and two active nests of African silverbill *Euodice cantans* were observed in abandoned nests in a colony of Heuglin's masked weaver *Ploceus heuglini* (RBP). Along the upper Zambezi River, an egg of cut-throat finch *Amadina fasciata* appeared in a deserted nest of brown-throated weaver *Ploceus xanthopterus*, and an egg of goldbreast *Amandava subflava* was on the flat top of an active nest of tawny-flanked prinia *Prinia subflava* (four goldbreast eggs were laid a few m away in a grassy nest built by goldbreast; the goldbreast reared their own young to fledge (K. Hustler, pers. comm.). And yet in none of these cases was one estrildid species known to rear another estrildid species's young.

Phylogeny, habitat, and character divergence – In estrildid species for which the most closely related species did not have the most corresponding geographic distribution, the estrildid often had a nestling mouth more similar to its sister species than to the estrildid with the most closely corresponding range (**index** $\boldsymbol{a1 < a2}$, $n = 57$; $\boldsymbol{a1 = a2}$, $n = 15$; $\boldsymbol{a1 > a2}$, $n = 6$). Excluding cases where $\boldsymbol{a1 = a2}$, a chi-square test of homogeneity indicates $\chi^2 = 44.9$, $\mathbf{df} = 1$, $P < 0.001$. The test comparison rejects the null hypothesis of homogeneity of data. The test also strongly rejects the hypothesis that nestling mouths are more similar than expected at random when the species live in the same habitat. Further, closely related sister-species of estrildid finches that live in allopatry are typically in similar habitat anyway, because of a recent common ecological association with the habitat (this applies to nearly all closely-related species as outlined in the earlier section "Descriptions of estrildid species"). On the other hand, the results are consistent with the hypothesis that species differences in nestling mouth colors and patterns are determined mainly by phylogenetic relationship, and the differences are less in the more closely related species.

The hypothesis of coevolution between estrildid species led to predictions that the nestling characters are more colorful and more distinctive in species that occur in the same area as another estrildid, and that character divergence occurs between species that occur and breed in the same area. In the first, we predicted that nestlings of *Erythrura* parrotfinch species have more colorful mouths and more complex mouth gapes and black markings (**indices b, c, d**) where they occur with another parrotfinch than where no others occur; that Australian zebra finch *Taeniopygia castanotis* are more colorful than Timor zebra finch *T. guttata*; that southeastern Australian firetail *Stagonopleura bella* are more colorful than southwestern Australian *S. oculata*; Javan munia *Lonchura oryzivora* are more colorful than Timor *L. fuscata*; that the African mannikins *Odontospiza* and *Spermestes* and Australian pictorella finch *Heteromunia pectoralis* are more colorful than Madagascar *Lemuresthes nana*; and that blue waxbills *Uraeginthus bengalus* and *U. cyanocephalus* which occur together in East Africa are more colorful than *U. angolensis* which is only in southern Africa. None of these predictions of coevolution between estrildid species were realized, and the prediction was less successful than one based on phylogeny as a determinant of nestling traits.

The test of character divergence was whether sister species that live in sympatry are more different in nestling mouths than sister species that live in allopatry. In 43 species of estrildids, the most closely related species had similar and overlapping geographic ranges, and in 61 species the most closely related species was allopatric. Nestling mouths on average differed somewhat more in sympatric sister species (mean = 1.58 ± 2.12 sd) than in allopatric species (mean = 1.20 ± 1.72). In both groups the character differences ranged from 0 to 8; and in a chi-square test of the two groups where the character differences were binned into (0,1) vs (2–8), the difference was not significant ($\chi^2 = 0.96$, $P > 0.5$). Again the results indicate a more important determinant role of phylogeny than of any response between sympatric estrildid species.

Nestling mimicry by *Vidua* brood parasites. – Nestlings of many brood-parasitic *Vidua* finches mimic their nestling estrildid hosts, and they are such close visual mimics that in some cases it is not possible to distinguish the host and parasite nestlings by mouth markings and colors alone (Nicolai, 1964, 1969, 1974, 1989; Skead, 1975; Payne, 1982, 2004). Each species group of brood-parasitic *Vidua* finches is associated primarily with a single clade of estrildid hosts. *Vidua* species are not closely related each to its estrildid host, and the species phylogeny of *Vidua* does not parallel that of their estrildid species. In addition, the species associations of *Vidua* and estrildid hosts result from histories of host shifts by the *Vidua*, rather than by a contemporary co-speciation of brood parasite and host (Klein & Payne, 1998; Sorenson & Payne, 2001a, 2002; Sorenson *et al.*, 2003).

Table 4 lists the brood-parasitized estrildid finches and their *Vidua* brood parasites, as documented elsewhere (Sorenson *et al.*, 2003, 2004; Payne, 2004), for the estrildids for which more than one case of parasitism is known (the blue waxbill species *Uraeginthus* are rarely parasitized). The adult male indigobirds mimic the songs of their foster species, and in some cases this song mimicry, which is learned from the foster parent (Payne *et al.*, 1998a), is the only evidence that a particular indigobird species is reared by a particular host species (Payne *et al.*, 1992, 1993, 1998a; Payne & Payne, 1994, 1995; Payne, 2004).

In each set the nestling brood parasites are similar in mouth pattern to their host nestlings: the paradise whydahs with *Pytilia* (*Vidua paradisaea* and *P. melba*, Figs. 4 f and 4 a – note 4 f was identified by size only, the largest nestling in nest of *P. melba*; and not by molecular genetics or by rearing the bird (a predator took the brood); *V. obtusa* and *P. afra* (*V. obtusa*, RBP photos of juveniles at Lochinvar NP, Zambia, resemble *P. afra*, Fig. 4 b; and *V. interjecta* and *P. hypogrammica* (Nicolai, 1977; Payne, 2004). Nestling and fledgling shaft-tailed whydah *Vidua regia* mimic the mouth pattern and colors of the young of their hosts, violet-cheeked waxbill *Granatina granatina* (Nicolai, 1964; Skead, 1975), and nestling straw-tailed whydah *V. fischeri* mimic the mouth patterns and colors of the young of their hosts, purple grenadier *G. ianthinogaster* (Nicolai, 1969).

The indigobirds parasitize mainly the firefinches *Lagonosticta* (Table 3) and the young in many of these indigobird species mimic the mouths of their host species. (1) *V. chalybeata* are associated with *L. senegala* (compare Fig. 3 g with Figs. 3 a, 6 f). The young indigobird in Fig. 3 g was reared in captivity from a pair of *V. chalybeata amauropteryx* in 1973, and it developed the adult male breeding plumage and the red bill and foot colors of *amauropteryx* (UMMZ 222537).

(2) *V. chalybeata* on the upper Zambezi River also are associated also with *L. nitidula* – the mouth of a nestling indigobird in a nest of this host is like those of *V. chalybeata* in the nest of *L. senegala*, and is illustrated elsewhere (Payne *et al.*, 2002).

(3) *V. wilsoni* are associated with *L. rufopicta*, Fig. 3 h, n with Fig. 3 b – these two short-tailed *V. wilsoni* (UMMZ 233851, 233852) fledged from a nest together with two *L. rufopicta*, Rayfield fish farm, Nigeria, 25 November 1995.

(4) *V. purpurascens* are associated with *L. rhodopareia*, Figs. 3 q, r with Fig. 3 e – this juvenile *V. purpurascens* was netted together with juvenile *L. rhodopareia* and other indigobirds at Lochinvar National Park, Zambia, on in June 1972, and it was kept in captivity with other juvenile indigobirds until they attained adult plumage; this male had the purple plumage and whitish bill and feet of *V. purpurascens* (UMMZ 219766).

(5) *V. larvaticola* are associated with *L. larvata*, Figs. 3 k; f, the juvenile *V. larvaticola* was noosed in a fledged family group

Table 4. Estrildid finches and their *Vidua* brood parasites

Estrildid host	*Vidua* brood parasite
Lagonosticta senegala	*Vidua chalybeata*
L. nitidula	*V. chalybeata*
L. rufopicta	*V. wilsoni*
L. rubricata	*V. funerea* (S Africa), *V. camerunensis* (W Africa)
L. rhodopareia	*V. purpurascens*
L. larvata	*V. larvaticola*
L. virata	*V. larvaticola*
L. sanguinodorsalis	*V. maryae*
L. rara	*V. camerunensis*
Clytospiza monteiri	*V. camerunensis*
Euschistospiza dybowskii	*V. camerunensis*
Hypargos niveoguttatus	*V. codringtoni*
H. margaritatus	*V. codringtoni*
Ortygospiza atricollis	*V. nigeriae*
Amandava subflava	*V. macroura* (S Africa), *V. raricola* (W Africa)
Granatina granatina	*V. regia*
G. ianthinogaster	*V. fischeri*
Estrilda astrild	*V. macroura*
E. charmosyna	*V. hypocherina*
E. erythronotos	*V. hypocherina*
E. melpoda	*V. macroura*
E. paludicola	*V. macroura*
E. rhodopyga	*V. macroura*
E. troglodytes	*V. macroura*
Coccopygia melanotis	*V. macroura*
C. quartinia	*V. macroura*
Pytilia melba	*V. paradisaea* (S Africa), *V. orientalis* (W Africa)
P. afra	*V. obtusa*
P. hypogrammica	*V. interjecta*, *V. togoensis*
P. phoenicoptera	*V. interjecta*
P. lineata	?
Spermestes cucullatus	*V. macroura*

of *L. larvata* near Zaria, Nigeria, on 18 December 1976 (Payne, 1982; UMMZ 235475).

(6) *V. camerunensis* are associated by song mimicry with several host species, each male *Vidua* mimicking the song of one estrildid host species (Payne *et al.*, 2005). *V. camerunensis* in Cameroon mimic the mouth of *L. rara* (Figs. 3 o; j). At Tibati, Cameroon, I caught a juvenile indigobird at a call-site of a male indigobird (the male mimicked songs of *L. rara*; the date was 24 November 1992), the juvenile had raspberry red mouth flanges, small bluish-white gape papillae, an absence of dark blue or black on the gape, and a paler pink anterior palate with 5 spots (UMMZ 232498). Two other juvenile indigobirds caught at Tibati in late November 2003 by C. Balakrishnan also had pink mouth flange corners and small white gape papillae (Fig. 3 j). In another case, a wild-caught captive adult male *V. camerunensis* mimicked songs of *L. rubricata*, and bred in our aviaries with a female indigobird received in the same shipment. The indigobirds are thought to be from western West Africa (Guinea and neighboring countries), the source of most finches exported in the bird trade (Payne & Barlow, 2004; Payne *et al.*, 2005). Nestlings from this indigobird pair (UMMZ adults 238824, 238826) mimicked the mouth of *L. rubricata* (Fig. 3 i; c). Nestling mouths of young *V. camerunensis* that parasitize other hosts, the twinspots *Clytospiza monteiri* and *Euschistospiza dybowskii* (Fig. 3 s, t, u), are unknown, as are the mouths of nestling indigobirds in nests of *L. rubricata* at Tibati. More fieldwork is needed to compare the nestling mouths of these indigobirds in West and Central Africa.

(7) Nestling mouths of *V. codringtoni*, the indigobird that mimics songs of Peters's twinspot *Hypargos niveoguttatus* (young twinspots are in Fig. 3 v-x), are undescribed: a juvenile indigobird captured by D. M. Lewis in June 1972 at Lochinvar NP, Zambia, was not photographed, but it had a mouth "different from" that of juveniles of the other local indigobirds *V. chalybeata* and *V. purpurascens*. *V. codringtoni* is the only other indigobird in this locality (Payne *et al.*, 1992, 1993). The juvenile molted into *V. codringtoni* adult male breeding plumage (UMMZ 219769) and this male mimicked songs of *H. niveoguttatus* (Payne *et al.*, 1992).

(8) *V. funerea* are associated with *L. rubricata* in southern Africa. No photographs or specimens are known. Nestlings in Malawi and Zimbabwe match the mouth pattern and colors of *L. rubricata* (Payne *et al.*, 1993; Payne, 2004).

By way of contrast, juvenile indigobirds that were captured in family groups with other known host-song-mimicked estrildid species had mouth colors that did not match their host species' young (*Vidua nigeriae* with quail-finch *Ortygospiza atricollis*, and *V. raricola* with goldbreast *Amandava subflava*, both in Nigeria) (Payne, 2004). In the best-documented case, a juvenile indigobird (UMMZ 233861) netted on 10 October 1995 in a family group of quail-finch had a single frontal palate spot (the central spot was not double as in quail-finch), and the gape papillae blue with a black base were only 2 in number, not 3 as in the quail-finch (compare Fig. 3 l, m with Fig. 5 q, r).

Finally, in the aviary a mixed-species pair of indigobirds (male *V. camerunensis* that mimicked songs of *L. rubricata*, UMMZ 238825, female *V. chalybeata* bred for second generation in captivity, UMMZ 238821), bred and produced several offspring, hybrid *V. camerunensis x V. chalybeata* (UMMZ 237285, 237286, 237287, 237288, 238828, 238829). The hybrid nestlings had a mouth pattern with pale yellowish palate and white, blue-based gape papillae that were intermediate in size between those of *V. chalybeata* and *V. camerunensis* (Fig. 3 p; g, i).

Pin-tailed whydah *Vidua macroura* nestlings mimic the nestling mouths of several host waxbills *Estrilda*. In the specimens, photographs and drawings that are available, young *V. macroura* all match the mouths of the five closely-related species of waxbills *Estrilda* that are perhaps its most common host species (*V. macroura* Fig. 5 i-l; *Estrilda* species Fig. 5 a-h). Young *V. macroura* have an arc-like papilla on the upper mandible and 2 white rounded papillae on the lower gape, a black background between the 3 papillae, a light pink palate with 5 spots, and an unmarked tongue. *Estrilda* hosts of *V. macroura* at Cape Coast, Ghana, are *E. troglodytes* and *E. melpoda* (MacDonald, 1980). In other sites where *V. macroura* were observed, at Tanji, The Gambia, *E. troglodytes* and *E. melpoda* occur (C. R. Barlow, pers. comm.; RBP); at Mole National Park, Ghana, *E. melpoda* is common (Greig-Smith, 1977; RBP), and at Bukuru, Nigeria, *E. troglodytes* is common but no mixed broods were observed there. At Lukolwe mission, northwestern Zambia, where *V. macroura* are common in the breeding season, *E. paludicola* are the only waxbill (Britton, 1970; RBP). At Lochinvar National Park, Zambia, juvenile *V. macroura* are like those in West Africa (RBP photos) and match the mouth pattern of their local host species *E. astrild* (Fig. 5 d), as do whydahs that parasitize this waxbill in Natal (J. Schuetz, photos). On the other hand, at Tibati, Cameroon, where the parasitized waxbill is *E. nonnula* (C. Balakrishnan, pers. comm.), the whydah has the same mouth as in these previous host associations (Fig. 5 d), even though *E. nonnula* has a different gape (Fig. 5 e).

Finally, steel-blue whydah *Vidua hypocherina* nestlings mimic the mouths of two sister species of hosts, the waxbills *Estrilda charmosyna* and *E. erythronotos*, which have nearly identical mouth patterns and colors (Nicolai, 1989, 1990).

In all these birds, the parental care that can be provided by the foster parents to the brood is thought to favor nestling *Vidua* with mouths that mimic the host broodmates. In experimental tests, mimetic nestlings with mouths like those of the host nestlings have an advantage over non-mimics in certain conditions. In aviary experiments, nestling indigobirds *V. chalybeata* that matched the mouths of nestlings of the firefinch hosts in mixed-species broods were equally likely to fledge and survive to independence in broods cared for by firefinches as were the young firefinches themselves (Payne *et al.*, 2001). In contrast, nestlings of other species did not survive as well when they were in mixed-species broods as when they were the only nestlings in the brood. And in broods where they were the only nestlings, the indigobird nestlings that mimicked the mouths of their host firefinch nestlings were more successful in being reared than were the non-mimetic nestlings of other species (Payne *et al.*, 2001). In other experiments, Australian zebra finch *Taeniopygia castanotis* reared both normal nestlings and nestlings that lacked the normal zebra finch mouth pattern when food was available, but they preferentially reared young with the normal mouth pattern when food was scarce (Immelmann *et al.*, 1977b; Skagen, 1988; Reed & Freeman, 1991). Nicolai (1964) noted several cases where the foster estrildids did not rear young of other estrildid and viduid species in their nests. In host-specific *Vidua* finches that mimic the mouth patterns and colors of their host species, the nestling mouths of brood parasites could evolve through natural selection by an accumulation of small steps. Furthermore, in nestling *Vidua* that do not mimic their host, perhaps because the association between brood parasite and host is recent, the nestlings are reared by the foster parents.

Coevolution of nestling estrildids and their *Vidua* brood parasites. Neunzig (1929b) proposed that the mouth patterns of brood-parasitic finches were selected to match the mouth patterns of their host species. The proposition suggests that species differences between host nestlings are a coevolutionary response to *Vidua* brood parasitism. A consequence is that nestling mouths may differ more between the species of parasitized estrildids than between the unparasitized estrildids, insofar as the parasitized species from time to time have escaped their mimetic brood parasite by divergent coevolution. As Mitchell (1987) presented the case for diversity among the mouths of nestling estrildids, "The real reason was indicated long ago by Neunzig (1929) who pointed out that the mouth-markings of the estrildines were extremely similar to those of their specific brood parasites, the parasitic whydahs or viduines. It has always been an advantage for the Viduine to have the same mouth-markings as the host and for the Estrildine to have mouth markings which are different."

Table 5 summarizes the comparisons of the mouths of the estrildid finches. Because only the waxbills are regular hosts of the brood-parasitic *Vidua*, the most appropriate comparison of nestling mouths is within the waxbills. Waxbills differ from the other estrildid clades in the number of bright colors, both on the gape and on the palate; in other clades most species have only a single color on the gape and on the palate (Tables 2, 5). In the waxbills the mean bright color score **index *b*** is 1.3 in both the parasitized species and the unparasitized species, and the Wilcoxon-test statistic of the data in Table 2 indicates no significant difference between these two groups ($z = 0.06$, ns). However, the statistic indicates significantly more colorful mouths in hosts of *Vidua* specialist species than in hosts of *Vidua* generalists ($z = 4.83$, $P < 0.001$). Grassfinches of the Australian region, finches that appear to be the closest ecological counterpart of the African waxbills, are considerably less colorful than are the waxbills, and most other estrildids have fewer bright colors than waxbills (means, $b = 0.3$ in nestling silverbills and mannikins, 0.4 in nestling munias *Lonchura*, 0.5 in nestling grassfinches); nestling parrotfinches are more brightly colored with their blue gape papillae and bright yellow palates (mean, $b = 1.9$).

In total mouth colors, **index *c***, which includes both the bright colors and the range of black, gray and white, the waxbill host species have more colors per nestling on average than do unparasitized waxbill species (Wilcoxon $z = 4.25$, $P < 0.001$). Within these host species, the host species of the *Vidua* species-specific mimics also have a larger number of nestling colors on average than hosts of the *Vidua* generalists ($z = 1.61$, $P < 0.05$).

The number, size and complexity of the nestling gape and palate melanin markings (conspicuous characters, **index *d***) do not differ between parasitized and unparasitized waxbill species ($z = 0.94$, $P > 0.17$). Waxbills with host-specific *Vidua* do not have more complex morphological structures (index d) than waxbills with host-generalist *Vidua* ($z = 0.66$, $P > 0.25$, ns). Not all parasitized waxbills have mouths with complex melanin markings. *Pytilia*, hosts of the paradise whydahs, have no black mouth markings or (one species) have one spot; the nestling *Pytilia* have complex mouth colors. *Lagonosticta* firefinch hosts of the indigobirds have complex nestling mouth markings. Contrariwise, the parasitized purple waxbills *Granatina* are not more strikingly marked than the unparasitized blue waxbills *Uraeginthus*. Mouths of swee waxbills *Coccopygia*

Table 5. Comparison of nestling mouth markings and colors in estrildid finches

Species groups	n	Character indices: bright colors *b:* mean, sd	all colors *c:* mean, sd	overall conspicuousness *d:* mean, sd
waxbills, unparasitized	24	1.25 ± 0.94	3.75 ± 0.99	4.51 ± 1.78
waxbills, host specialist	22	1.86 ± 1.04	3.73 ± 0.99	4.78 ± 1.35
waxbills, host generalist	9	0.22 ± 0.44	2.44 ± 0.88	4.93 ± 1.32
parrotfinches	11	1.91 ± 0.30	3.00 ± 0.00	5.39 ± 0.22
grassfinches	14	0.50 ± 0.85	2.50 ± 0.85	5.60 ± 0.78
munias *Lonchura*	17	0.47 ± 0.51	2.59 ± 0.62	4.00 ± 0.47
mannikins (Africa, S Asia)	7	0.29 ± 0.49	2.29 ± 0.49	4.36 ± 0.57

species are unmarked with melanin spots, although swees are parasitized by the same species (*Vidua macroura*) that parasitizes the waxbills *Estrilda*. Mouths of *Estrilda* species are nearly the same whether or not they are parasitized. In other waxbills, the parasitized African goldbreast *Amandava subflava* and the unparasitized Asian *A. amandava* and *A. formosa* have the same mouth pattern apart from a double rather than single medial palate spot in the Asian birds. The complex mouth pattern of *A. subflava* appears to be a retained ancestral trait, rather than an escape from mimicry by its brood parasites (indigobird *Vidua raricola* and whydah *V. macroura*). Finally, in the other waxbill with a species-specific brood parasite, quail-finch *Ortygospiza atricollis* with the indigobird *V. nigeriae*, the mouth patterns of host and parasite young differ (Payne & Payne, 1994; Payne, 2004; Figs. 3 l, m; 5 q, r). There is no compelling or independent reason to account for the nestling goldbreast or quail-finch mouth pattern as an escape from mimicry by their *Vidua* brood parasites. Australian grassfinches, the ecological counterparts of African waxbills, have no brood parasites and yet they are no less complex in nestling mouths than in the African waxbill hosts (Table 5). Grassfinches have more complex nestling mouths on average, in gape structure and in melanin traits, than do the other estrildids, and the melanin patterns are more closely associated with phylogenetic relationship than with brood parasitism.

DISCUSSION

Estrildid finches have elaborate nestling mouths and a great variation among these species. The variability in nestling mouths of estrildid finches appears to be greater than that in other groups of songbirds with distinctive mouth patterns and colors, including the cardueline finches (Newton, 1972; Harrison, 1978; van den Elzen, 1983), grass-warblers *Cisticola* (Lynes, 1930; Hoesch, 1939; Tye, 1997), larks and sunbirds (Swynnerton, 1916).

Specificity and elaboration of the nestling mouths are associated with phylogeny. Gape papillae and palate colors and spots occur in the African waxbills, enlarged gape papillae and a yellow palate with spots occur in the parrotfinches; gape flanges and variable palate markings but rarely any bright mouth colors occur in the Australian grassfinches; and gape flanges and palate bars but no bright mouth colors occur in the munias and mannikins. Estrildid species and lineages differ in ornamentation of the nestling gape, and in mouth colors, patterns, or both. A more detailed phylogenetic estimate of certain species is necessary for further comparisons.

Habitat does not appear to affect the species variation in nestling mouths. The nestling mouths of species living dark and dense habitats are not more brightly marked. Closely related species that live in sympatry and in the same habitat are not more different than between less closely related species that do not.

Brightness and diversity of the palate colors of nestlings are greater in the waxbills than in other estrildid lineages, and the waxbills are hosts of the brood parasitic finches. Within the waxbills, the species that are parasitized have more colorful nestling mouths than species that are not parasitized. In contrast, the gape and the melanin markings, features that were thought to suggest a coevolutionary escape of the estrildids from their brood parasites (Neunzig, 1929b), do not differ in kind between the parasitized and unparasitized waxbill species. It is the nestling mouth colors that provide evidence of coevolution of the estrildid finches and their brood parasites.

Behavioral constraints in parental care. Nestling mouths of estrildid finches do not differ with the risk of being nest-parasitized by a closely-related estrildid species. However, an evolutionary response to occasional nest parasitism might be based not on nestling begging, but rather on the breeding pair's parental behavior toward their brood. One prediction of this idea is that nesting estrildids do not rear nestlings of other species, and another is that heritable variation occurs for behaviors in parental care.

One domesticated estrildid finch clearly illustrates heritable variation for behavior in parental care. Over the past four centuries, aviculturists have selected a strain of *Lonchura striata*, "Bengalese finch", to breed in captivity and to rear nestlings of other estrildid finches, as when the others breed but fail to rear their own young (Immelmann *et al.*, 1977b; Baptista, 1978; Black, 1987; Nicolai & Steinbacher, 2001). The gape and palate colors and markings of nestling Bengalese finch are much as in the wild *L. striata*; it is the behavior of the adults that has been selected. Immelmann reported that estrildids, except domesticated Bengalese and domesticated zebra finch, do not rear the young of other species. He reported (Immelmann, 1968: 88, my translation), "In natural conditions, zebra finches rear only the young of their own species. If one places nestlings of another species into a brood, they will not be fed and most will be tossed at once from the nest. In the domestic animal the Schema [that is, the mental representation of the releaser] of the young bird has changed so much that every now and then a nestling of another species can be reared, though only when one has taken the precaution to remove the bird's own young and there is no possibility that the parent can compare the foundling with its own young. Later [in domestication] the Schema was enlarged, as in Bengalese, so the bird will rear nearly any young finch (often as well as the young of its own species) and so birdlovers are fond of using these as foster parents for their rare estrildid finches."

In *Critique of Pure Reason*, Kant (1781) developed the term "Schema" as a mental prior that places appearances into a class: the Schema "releases" the class and it restricts its scope (Caygill, 1995). The ideas derive from long philosophical concern with the innate and sensory bases of knowledge in humans. Lorenz (1935) used the ideas as well and established their use in ethology.

Although Immelmann anticipated that mouth markings were releasers of species-specific parental behavior, neither his studies of domesticated zebra finches, his field studies in Australia, or his observations of captive breeding wild birds described cross-species fostering to wild zebra finches (Immelmann, 1959, 1962a,b,c). In his later experimental work, Immelmann *et al.* (1977b: 217) noted, "The results thus give the first experimental evidence that the mouth markings actually have a releasing function for the feeding of the nestlings." In that study the foster birds were domesticated zebra finches; they reared nestlings of a mutant strain that lacked the normal nestling mouth markings, although when food was scarce the mutant nestlings were at a disadvantage relative to care given to the normal nestlings in a mixed brood.

Bengalese finch and domesticated Australian zebra finch are not the only estrildids that can rear young that look unlike their own nestlings. Other species rear nestlings of several species when the eggs or nestlings are placed into nests of foster parents. For example, nestlings of other species have been reared by a foster pair of another species, as the firefinch *Lagonosticta rubricata* have reared the young of other estrildids (Immelmann *et al.*, 1965), and in experimental tests where the eggs were cross-fostered between a firefinch *L. senegala*, a blue waxbill *Uraeginthus cyanocephalus* and goldbreast *Amandava subflava*, the foster parents reared each others' nestlings (Payne *et al.*, 2001). In the aviary, breeding estrildids that fail in their own nesting sometimes adopt the nestlings or fledged young of their own or other species (Immelmann *et al.*, 1965; Orrell, in Immelmann, 1982; Goodwin, 1982), even finches that differ in appearance and are not closely related, as when bronze mannikins *Spermestes bicolor* adopt the fledged young of goldbreast *Amandava subflava*. A second prediction of biased parental behavior is that hybrids, with their deviant mouth markings, are not reared successfully. In contrast to this prediction, many hybrid young estrildids of various parental species have been reared in aviculture (Fehrer, 1993). In the field the munias *Lonchura castaneothorax* and *L. flaviprymna* sometimes breed with each other and rear their hybrid young, and *Lonchura nevermanni* and *L. stygia* rear their hybrid young as well, even though the parental species differ from each other and from hybrids in nestling mouth markings (Immelmann, 1962b; Restall, 1997).

Because estrildids only infrequently lay in the nests of other birds in natural conditions, it seems unlikely that the diversity of mouth colors and patterns of estrildid finches is an evolutionary response to occasional nest parasitism by other estrildid finches. There is no strong evidence of divergent evolution of nestling mouths in response to occasional nest parasitism between estrildid species. Finally, it is unlikely that the estrildids diverged through selection to distinguish their own young from another nesting species for the following reason. For each case where an estrildid might lay its eggs in the nest of another to rear as a foster parent, there is an equal case for the "foster" species to lay its own egg in the nest of the first species. With a mixed behavioral strategy, where a bird at one time is a donor and another time is a receiver of alien young in its nest, the advantage in having a distinct appearance in its role as a foster species would be a disadvantage in its role as an occasional nest parasite.

Mouth mimicry and coevolution in *Vidua* brood parasite and estrildid host – The brood parasite young imprint to their foster species, and the parasite-host association between *Vidua* and estrildid species is maintained by the female when she returns to parasitize the host species that fostered her as a young bird (Payne *et al.*, 2000). Mimetic young that match the visual elements in the mouth pattern of their host species have a higher probability of receiving parental care and surviving to independence (Morel, 1973; Payne *et al.*, 2001). Greater brightness and color diversity of the nestling mouths of the parasitized estrildids were predicted in a test of coevolution of nestling mouths in the estrildid finches and their brood parasites. Each is a selective agent of evolutionary change of the other species. The hosts can rear or can fail to provide parental care to the young *Vidua*, and the young *Vidua* can affect the survival of the host brood by competitive behavior in a mixed brood. Brood-parasitic *Vidua* affect the fitness of the host finches both when females remove the egg at the time of laying, and when a *Vidua* nestling is in the brood and competes for parental care. The effect of having a nestling *Vidua* indigobird in the brood is to decrease the survival of nestling hosts by about 25% (Morel, 1973; Payne, 1998b), and in the best-known species, the firefinch *Lagonosticta senegala*, about 30% of nests are parasitized by the indigobird *V. chalybeata* (Morel, 1973; Payne, 1977b). Despite the benefit to *Vidua* young when they mimic the host young and to an effect of the *Vidua* on the breeding hosts, there is only limited evidence that estrildid nestling hosts have been selected to diverge in appearance from their mimics, or that the mimetic system of the brood parasitic finches is a case of coevolution between host and brood parasite.

Certain behaviors of the foster adult estrildid finches in parental care could limit the success in the *Vidua* finches that shift to a new host-parasite association and do not mimic the nestlings of the new host species (Nicolai, 1964; Payne *et al.*, 2001; Sorenson *et al.*, 2003). Nevertheless, the parental care of estrildid finches does not vary greatly between species, and the begging behaviors of most estrildid young are similar. Estrildid nestlings and fledglings beg by twisting the head and waving the open mouth in front of the parent, which then regurgitates into the open mouth of the young. A few estrildids do not beg in this manner (bluebills *Spermophaga*, Kunkel, 1959, 1967, 1968) and are not *Vidua* hosts; although in this case the lack of brood parasitism can be attributed to the bluebills' forest habitat. Begging behavior of certain estrildid young varies in twisting the head and use of the tongue. Nevertheless, species differences in behavior of young estrildids have not completely prevented host shifts of *Vidua* onto these species. For example, after they fledge from the nest, young quail-finch *Ortygospiza atricollis* and goldbreast *Amandava subflava* beg by raising a wing on the side far from the parent; nevertheless, these two estrildid species are hosts of indigobirds *Vidua nigeriae* and *V. raricola* (Payne & Payne, 1994).

Apart from a unique thrusting and sideways movement of tongue on the palate in several species of *Pytilia* (except in *P. melba*, Güttinger, 1976), there appear to be no conspicuous differences in begging behaviors that would affect whether a *Vidua* young is at a disadvantage in a mixed-species brood. The genus *Pytilia* has seen successful host shifts of paradise whydahs between melba finch *P. melba* and other species (Klein & Payne, 1998; Sorenson & Payne, 2002; Sorenson *et al.*, 2004). In addition, the indigobirds (*Vidua chalybeata* and nine other species) are known to mimic the songs of their foster species and to parasitize the host broods of at least 15 species of estrildid finches. All indigobird species have the same begging calls as young, even though their host species differ from other host species in the nestling begging calls. Begging calls of young indigobirds match the begging calls of one clade of firefinch *Lagonosticta* hosts (*L. rubricata, L. rhodopareia, L. virata*), closely related species that may have retained the begging behavior of the host lineage of the ancestral indigobirds (Payne & Payne, 2002).

Most *Vidua* species mimic the nestlings of their host species, yet not all *Vidua* are nestling mimics. The degree of mimicry of pin-tailed whydah *Vidua macroura* varies with the waxbill host. Young whydahs in several areas all have the same mouth pattern with 2 globes on the gape at the base of the lower mandible. The young whydahs resemble the young of certain *Estrildid* host species more closely than other host species (swees *Coccopygia*, goldbreast *Amandava subflava*, mannikins *Spermestes* spp.) (Friedmann, 1960; Macdonald, 1980; Brosset & Erard, 1986; Payne, 2004).

Occasional cases of parasitism with fledged young *Vidua* have appeared in broods of red-cheeked cordon-bleu *Uraeginthus bengalus*, southern blue waxbill *U. angolensis* and black-cheeked waxbill *Estrilda erythronotos* (Harrison *et al.*, 1997; Payne, 1997a). A nestling paradise whydah *Vidua paradisaea* appeared in a nest of purple grenadier *Granatina ianthinogaster*; the nestling *V. paradisaea* and a nestling straw-tailed whydah *V. fischeri* were taken by a predator (Nicolai, 1969). One population of village indigobird *V. chalybeata* has shifted from their old host red-billed firefinch *Lagonosticta senegala* to a new host brown firefinch *L. nitidula* along the Zambezi River (Payne *et al.*, 2002). In addition, the indigobirds have succeeded in shifts from firefinches *Lagonosticta* to parasitize other clades of waxbills. For example, *Vidua raricola* is with host goldbreast *Amandava subflava*, *V. nigeriae* with quail-finch *Ortygospiza atricollis*, *V. codringtoni* with the twinspots *Hypargos niveoguttatus* and *H. margaritatus* (Payne *et al.*, 1992, 1993; Payne & Payne, 1994; Payne, 2004), and populations of *V. camerunensis* with other twinspots *Clytospiza monteiri* and *Euschistospiza dybowskii* (Payne & Payne, 1994, 1995; Payne *et al.*, 2004). Niche shifts to new host species in the remote past are clear in the cladistic branching sequence of the indigobird species, as the branching sequence does not parallel that of their firefinch host species (Klein & Payne, 1998; Payne *et al.*, 2002; Sorenson & Payne, 2002).

Hoesch (1939) stated that time has been insufficient for evolution of host-specific mimicry; rather, the mouth markings of young *Vidua* evolved earlier and the parasites sought out host species with nestlings similar to their own. His was a statement of incredulity: he could not imagine a starting point for this evolution. He pointed out that the unparasitized grass-warblers *Cisticola* have marked nestling mouths, so by analogy the nestling mouths of estrildids should be independent of any interaction of host and parasite. In fact, *Cisticola* are hosts of the brood-parasitic cuckoo-finch *Anomalospiza imberbis* (Roberts, 1917, 1939; Chapin, 1954; Vernon, 1964), *Anomalospiza* is the sister clade of *Vidua*, and the common ancestors of the parasitic finches and estrildids probably had mouth markings (Sorenson & Payne, 2001a, 2002; Lahti & Payne, 2003). *Cisticola* perhaps evolved nestling mouth markings in response to their early finch brood parasites.

Data from molecular genetics suggest that the clades comprising the brood-parasitic finches and the nesting estrildids diverged long ago, more than 10 million years (Sorenson & Payne, 2001a). Time has been sufficient for the evolution of host-specific mimicry in the *Vidua* finches, even though time within each species-specific host-parasite association may have been insufficient for all *Vidua* to match the details of their host species. Because the *Vidua* have speciated much more recently than their host species (Klein & Payne, 1998; Sorenson & Payne, 2002; Sorenson *et al.*, 2003), time was adequate for the estrildid hosts to have diverged in response to the mouth mimicry of their brood parasites. Fisher reasoned that "Close [Batesian] mimicry can therefore be established only if the rate of modification of the model has been less than that of the mimic", and the selective advantage to the mimic is greater than the disadvantage to the model (Fisher, 1930, p. 148). In the host estrildids, the mouth colors and patterns of nestlings may provide their parents the information to make decisions in allocation of parental care. Symmetry of the mouth melanin spots may indicate developmental normality of their offspring (pattern asymmetry may indicate a problem), and brightness of mouth colors in the live nestlings may indicate both their normality and their condition (health and hunger) (Kilner & Davies, 1998; Davies, 2000; Payne *et al.*, 2001).

Divergence from the norm may disadvantage a nestling in receiving parental care, and the effect would be even greater when a nestling *Vidua* is in the brood. Conservative behavior for parental care in the host species for their own nestlings may account for the absence of two-way coevolution of the mouth patterns in host and brood parasite. Mimicry is successful for the brood parasite; whereas escape from mimicry by the host is limited by the greater importance of providing parental care to their brood than to discriminate among the young in the brood. Much as in rejecting their own eggs in the hosts of other brood parasites (Lotem, 1992; Lotem *et al.*, 1995), the risk of rejecting their own young may constrain an evolutionary response of the estrildid finches to the nestling mimicry by their brood parasites.

Coevolution between mimics and models in other animals – Coevolution may occur in other brood parasites and their hosts, as in cuckoos, where the cuckoo eggs often mimic the eggs of their hosts. The hosts show defensive behaviors toward an adult cuckoo, and the hosts vary in response in evicting a cuckoo egg in their nest (Rothstein & Robinson, 1998; Nakamura *et al.*, 1998; Soler *et al.*, 1998; Davies, 2000; Payne, 2005). The behavior differences between individuals within a host species – and even between species – may be owing not to coevolution, but rather to the birds' individual experiences, in particular to their behavioral encounters with cuckoos (Lotem *et al.*, 1992; Payne, 1997b). A collective individual experience, acquired by each host female, may account for regional differences in the behavior of nesting females towards a cuckoo egg placed in their nest, in populations where cuckoos breed and in populations where there are no cuckoos (Davies & Brooke, 1989; Payne, 1997b).

The evidence for coevolution is somewhat stronger in the case of egg polymorphism in cuckoos and hosts. Where known, differences between females in egg color and pattern are determined by maternal genetic differences (Gosler *et al.*, 2000). Several brood-parasitic cuckoo species are polymorphic in egg color and pattern, where each egg morph of the cuckoo is a mimic of a different host (Southern, 1954; Friedmann, 1968; Rothstein, 1990; Davies, 2000). In Europe, the eggs of common cuckoo *Cuculus canorus* often match the eggs of the host nest where they lay, as noted in 1850 (Kunz, 1850), described in detail by Baldamus (1853, 1892) and explained as a result of selection by the host parent, which removes from the nest any eggs unlike its own, by A. Newton (1896).

In Africa, field biologists have long been aware of egg mimicry by brood-parasitic cuckoos, notably diederik cuckoo *Chrysococcyx caprius*. The eggs of certain weaver finches *Ploceus* differ remarkably in color and pattern between females. Bates (1911, 1930) attributed the variation between females' eggs in African weavers *Ploceus* as an adaptation to allow a female to direct her care to her own and avoid caring for the young of another weaver, as two or more species nested in the same breeding colony. Swynnerton (1918) then described "Evidence for the view that polymorphism in the host's eggs may be of use against cuckoos" such as *Chrysococcyx caprius* which parasitize weaver nests, and he carried out field experiments on host egg recognition and rejection of eggs unlike their own in another weaver species. Nesting weavers removed the egg that did not match their own. Next, Victoria (1972) found that village weavers *Ploceus cucullatus* reject eggs unlike their own, and suggested that the polymorphism in weaver eggs is due to cuckoo parasitism ("it may be that the adaptive value of the village weaverbird's polytypic eggs is to reduce parasitism"). In response to the mimicry by cuckoos of weaver eggs, some weaver species have evolved highly variable eggs, where each female lays eggs of one color and pattern, and most weavers' eggs differ from those of a female cuckoo. As a result of egg polymorphism and egg rejection, most female weavers escape the costs of cuckoo parasitism (Payne, 1967, 1977; Victoria, 1972; Freeman, 1988; Rothstein, 1990; Din, 1992; Lahti & Lahti, 2002). In an alternative hypothesis, the diversity in egg color in weavers has been selected not through brood parasitism by the cuckoos, but through between-female nest parasitism by the weavers (Jackson, 1998).

Another possible means of host escape from the costs of mimicry is behavioral development. A female may recognize her own eggs by learning what they look like when she first lays her eggs in the nest; she accepts these eggs and rejects eggs of different appearance that appear later in the nest (Rothstein, 1974; Lotem *et al.*, 1995). Although female imprinting might work for eggs, it is less likely to provide reliable information about the first-hatched young, as the brood parasites have short incubation periods and often hatch before the host species (Lotem *et al.*, 1992, 1995; Payne, 1997b).

In classical Batesian mimicry, the distasteful model and its tasteful mimic are visually conspicuous, and the visual signal is directed towards a predator, which like the mimic would benefit in discrimination between the model and mimic (Fisher, 1930; Mallet & Joron, 1999). If a predator avoids attacking a brightly colored butterfly, either because the predator had an experience with the brightly-colored model and found it distasteful, or because the predator had an aversion to insects other than the common cryptic insects (Fisher, 1930; Sherratt & Beatty, 2003), then an unrelated edible species that resembles the distasteful species may have a survival advantage. The model in turn may change through natural selection when the model diminishes the resemblance (Fisher, 1930). If a model has a large number of mimics, the model might escape its mimics through selection for alternative visual morphs (Owen, 1970, 1971, 1980). The African butterflies *Danaus chrysippus*, *Acraea encedon* and *A. encedana*) were thought to be distasteful models in which new morphs have a survival advantage when old morphs were swamped by a mimic (Smith, 1980; Gilbert, 1983). Each of these butterfly species now is regarded as a complex of races, where each morph first evolved in one region and later dispersed and hybridized with another in a broad region of contact, and where *Acraea* are intermediate in taste on a palatability spectrum between the *Danaus* models and the other species that mimic all three model species (Owen *et al.*, 1994; Smith *et al.*, 1997). In general, a coevolutionary escape from a mimic is more likely when the mimic is common and when the mimic is detrimental to the model, as when a mimic puts its model at risk to predators that take the edible mimic, then attack and damage its model as well. The coevolutionary process in these polymorphic model butterflies is similar to that in the cuckoo-parasitized *Ploceus* weaver finches, in that new morphs have been selected that differ from earlier mimics, their Batesian mimics in the butterflies and cuckoo egg-mimics in the weavers.

In the estrildid finches, the *Vidua* brood parasites colonized their host species long after the nesting estrildids first evolved their own distinctive mouth patterns. Nestling mouth mimicry by *Vidua* has evolved at a rapid rate, much as speciation in the *Vidua* has been more rapid and recent than in their hosts (Klein & Payne, 1998; Payne *et al.*, 2002; Sorenson & Payne, 2002; Sorenson *et al.*, 2003). In the case of the estrildids, nestling estrildids with new and distinctive mouth patterns that diverge in response to a mimetic brood parasite would be at a disadvantage in comparison with nestlings having the old mouth pattern. Nestlings with the new signal patterns might not be recognized as the parents' own brood, and they might receive inadequate parental care. The host species are constrained from divergence in signals in response to their *Vidua* brood parasites if only because the mouth pattern of their young functions in the host species' own parental care. Further, a degree of signal generalization by the nesting parent may allow the imperfect mimic brood parasite to gain an advantage over the non-mimic brood parasite.

Character convergence in nestling mimicry in the brood parasites is more in evidence than is character divergence in their estrildid hosts. If the host nestlings in fact have diverged in response to their *Vidua*, the host estrildids have left little trace of this divergence, as the brood parasitic *Vidua* have kept up with the progressive evolutionary change by the hosts, and the estrildids have been constrained by the need for providing parental care to their own young.

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