HOST-PARASITE INTERACTIONS:
ON THE PRESUMED SYMPATRIC SPECIATION OF *VIDUA*

Introduction:

Ernst Mayr once wrote, "sympatric speciation is like the Lernaean Hydra which grew two new heads whenever one of its old heads was cut off" (1963:451). This observation, from his landmark text *Animal Species and Evolution*, marks the beginning of his systematic confutation of all evidence and theory pertaining to the possibility of sympatric speciation available at that time. Much has changed, however, in the field of biology since '63, but his point still remains valid: since Darwin's original vague descriptions on the requirements for speciation, many have forwarded models involving speciation in sympatry only to have them later disproved – or at least highly questioned – by the academic community (White, 1978; Coyne & Ore, 2004). As of late, a new surge of interest and research has once again made its way into the journals and texts. Recent publication, such as Via (2001), have attempted to review and bolster the newest evidence for speciation in sympatry; do these examples simply represent another head on the immortal hydra or has the tide shifted so much that we can accept the possibility of this type of speciation? Coyne & Orr (2004) doubt much of this new evidence; however, they offer that the likelihood of this mode in specific cases is increasing with each new paper published.

Recently, yet another possible example has been described by science, which may offer some of the most compelling support for sympatric speciation. The system does not rely upon genetic changes to promote assortative mating, but instead offers an example where learned behavior may be crucial to mate selection (Beltman *et al.*, 2003; Beltman *et al.*, 2004). What herein follows is a review of this system and its implications; the work, done mostly by University of Michigan resident Robert Payne and Michael Sorenson of Boston University, is upon the many subspecies and sister species of the African indigobirds, *Vidua* spp. (Sorenson *et al.*, 2002). Historical geographic and genetic evidence – along with the effects of song learning – all seem to support rapid speciation in this genus, most likely under sympatric conditions.

Specifications of the System and the Implications of Learning:

The brood parasitic indigobirds rely on a novel method to choose their parasitized host: they learn their song. Payne *et al.* (2004) describes this system in some detail and supports it with cross-foster experiments (Payne et al., 1998, 2000). The most simplistic description of this host-parasite relationship is as follows: adult females of *Vidua* lay their eggs in the nests of several other finch species in West and Central Africa. They choose which species to parasitize based upon the male calls of that species: the call of their host father. Their young, subsequently, imprint upon the host species' song: females learn to respond to it and males learn to produce it. The females, then, choose their conspecfic mates based on the song of their heterospecific host parents. The cycle then repeats, when these now pregnant females choose where to lay their eggs based on the learned calls (Payne *et al.*, 2004). To date, this type of behavior has been observed in the indigobirds of *Vidua*, with most having specific hosts in Estrildidae (Sorenson *et al.*, 2004). Importantly, the observed morphological differences amongst indigobirds of *Vidua* appears to be a recent adaptation that helps their orphaned young better exploit their specific host species; mouth markings differ significantly, resembling those of the offspring of the parasitized host (Sorenson *et al.*, 2003). To counter act these markings some host species have gotten better and better at determining which mouths belong to their own species. However, Payne *et al.* (2001) suggest that this mechanism is not very efficient, and depends on many variables – such the number and type of young present and in the nest (type meaning heterospecific, conspecific, or mixed nest mates).

Support for this song learning behavior is twofold: first, [1] cross foster experiments with non-traditional hosts supports the imprinting practice (Payne *et al.*, 1998, 2000); secondly, [2] in some described host-parasite complexes, their appears to be recent parasite switches, where the same species in sympatry have created two mutually exclusive breading pools by singing the songs of different host species – this would be the beginning of a speciation event (Payne *et al.*, 2002, 2005). These sympatric populations show little morphological differences, suggesting that these changes occur after the colonization of a new host species.

Payne *et al.* conducted their first cross foster experiment in 1998, where they showed that male finches will learn the calls of their typical[1] host, the red-billed firefinch (*Lagonosticta senegala*), or a stand-in non-normal host parent, the Bengalese finch (*Lonchura striata*). They conducted a second experiment in 2000 to test the extent of female imprinting and further strengthen previous observations for the 1998 study. Their experiment was designed principally to test three hypotheses: an H_0 of no preferential selection of host-nest by female indigobirds; an H_{a1} of innate selection of normal parasitized hosts; and an H_{a2} of a learned preferential selection of host-nest by females. Payne and his colleges performed the experiment with *Vidua chalybeata*, the village indigobird; again, it's normal host, the red-billed firefinch, and the experimental foster species, the Bengalese, finch were used.

In the cross-foster experiments captive-reared indigobirds were raised by either the Bengalese finch or the red-billed finch, as adults they were tested for preferences in mate and nest choice. In the support of their H_{a2}, Payne *et al.* (2000) find that captive females raised by Bengalese finches both respond to males who sing the Bengalese song and choose to parasitize the nests of the Bengalese finch, over those of their normal host. Implicit here is also the finding that male

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[1] The village indigobird also sometimes uses *L. nitidula* as host species, though infrequently (Sorenson *et al.*, 2004).

indigos raised by Bengalese parents produce the calls of their heterospecific parents (Payne *et al.*, 1998). Additionally, the captives raised by the normal host species respond in predictable manners: choosing to mate with indigos who produced a red-billed finch song and exploiting the nests of these heterospecifics. Furthermore, the experimenters found that later exposure to non-parental type songs had no effect on mate choice or nest chosen for brood parasitism; suggesting a critical period for song acquisition and imprinting sometime before fledging – this finding is also consistent with Payne *et al.* (1998).

When compared with other brood parasitizing bird species, these results are unique to the *Vidua*. Cowbirds, for example, are host generalists; both genetic and behavioral evidence suggest no pattern of consistent host selection (Payne *et al.*, 2000). Also, while there is some evidence of host specific preferences by females in the brood parasitic Cuckoo species (*Cuculus* spp.), male behaviors facilitate large quantities of gene flow between the female 'types', preventing the evolution of host-specific species. Male Cuckoos[2] will mate with different females with different host preferences – meaning that any possibility of speciation is hindered by the male lineages (Payne *et al.*, 2000).

Given that indigobirds can learn the call of a new host species in captivity, Payne *et al.* (2002, 2005) suggest that recent demographic changes may have forced a host switch in at least two separate *Vidua* species (*V. chalybeata* (2002) and *V. camerunensis* (2005)) – implying that this experimental data is supported by observational studies. The repercussions of these switches will be explored later; however, it is important to note here that both captive and wild indigobirds can and do occasionally learn songs of a novel host.

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[2] Experiments were done on the Common cuckoo (*Cuculus canorus*).

The observation that host switching does occur in the indigobird species is the first step in showing that sympatric speciation is possible under the correct ecological conditions. Beltman *et al.* (2003, 2004) explore some of the general theoretical consequences that learning can have on a speciation event. Arguments against the creation of new species under sympatry often question the amount of gene flow that could occur between two recently divergent populations and the ability for a new colonizing type to find conspecific mates (White, 1978; Coyne & Orr, 2004). Beltman *et al.* (2004) show rather convincingly, however, that the novel nature of this host-parasite interaction where both the male and the female 'mutants' will assortatively mate can facilitate speciation via a cultural trait. They suggest that, since indigobirds have low error rates in egg laying (≤1%) and the tendency to mate only within your cultural group is so great – both males and females have mechanisms of imprinting – initial assortative mating based only on learned traits could eventually lead to genetically isolated species. Furthermore, the observed mechanisms used by the host species to counter act the parasitism, may force genetic changes that will later make possible a genetically based form of isolation (Beltman *et al.* 2004).

However, they caution that the balance between low error rates and finding a conspecific mate create many difficulties; when colonization does occur the cost of finding a mate that knows the same song as you may be too high to make the colonization viable. Therefore, they assume that many colonization events probably occurred – only to fail many times – in the indigobird species before being successful (Beltman *et al.,* 2004). Conclusively showing that the observed diversification in indigos is due only to a learned song was beyond the scope of their paper; however, this theoretical work only supports the genetic evidence.

Evidence for Divergence in Sympatry:

Theoretical, verbal, and mathematical models can only go so far – descriptive and exhaustive field research is essential in showing what is actually happening. To this end, Sorenson and Payne have devoted a large portion of their fieldwork to genetics (Sorenson & Payne, 2001, 2002; Sorenson *et al.* 2003, 2004). Their research efforts have focused on the creation of an accurate phylogeny based upon genetic data – obvious arguments against this methodology and its application have been raised by many (see Coyne & Orr, 2004); however, their conclusions seem valid (Sorenson *et al.* 2003; Sefc *et al.* 2005). In any case, the many academic problems raised by this method will be discussed later. To best establish the evidence for sympatric divergence we will explore the work done by Payne, Sorenson, and their colleagues in the context of the eight criteria set down by Coyne & Orr (please see appendix, **table 1**). Thus, the following discussion will mirror the structure of Coyne & Orr, thereby, substantiating the presumed sympatric speciation of the indigobirds.

The first criterion is simply met by these birds: their ranges *do* overlap largely and nearly completely - though the birds have been described in two geographic distributions: the West African indigos (seven species) and the Southern African indigos (four species, *V. chalybeata* is present in both populations). Comprehensive field descriptions of the species distributions have been done by Payne. Of interest is Payne's 1982 publication; in this particular case, Payne described, among other things, the ranges of five species of *Vidua*[3] and their hosts' ranges[4]. All species were found to be sympatric in the range studied[5].

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[3] *V. chaybeata*, *V. larvaticola*, *V. raricola*, *V. funereal*, and *V. wilsoni*

[4] Respectively, *Lagonosticta senegala*, *L. larvata*, *L. rara*, *L. rhodopareia* and *L. rubricata,* and *L. rufopicta*

[5] See appendix for range map (**figure 1**)

In addition, this data set supports the second tenet of Coyne & Orr: it shows that these species do parasitize specific hosts – though, occasionally, they do make mistakes (Sefc *et al.*, 2005; Payne & Sorenson, 2004). Sorenson *et al.* (2004) clearly establishes the host-parasite relationship in a phylogenic reconstruction (see appendix **figure 2**); this data suggests that some *Vidua* parasitize multiple hosts occasionally (dotted lines), while others are very host-specific. In addition, this data illustrates the complexity of the speciation events occurring: the *Vidua* do not simply mirror the speciation events of their hosts – they radiated much later[6]. This is unlike many host-parasite speciation relationships, where a geographic separation of host populations caused a speciation event in both the host and parasite populations.

The third tenet, and perhaps one of the most challenging to meet, states that the parasites must be sister taxa – implying the necessity of clear phylogenic relationships. Coyne & Orr caution that a genetically based phylogeny may show inaccurate relationships and divergence rates – since interspecific hybridization probably occurs, tainting the gene pool. Exhaustive phylogenetic work, however, (mostly mtDNA) supports a sister taxa relationship (Sorenson et al., 2002, 2004; Sorenson & Payne, 2001, 2002). The data of Sorenson et al. (2002) presents the clearest image of these relationships; summarized in **figure 3** of the appendix, are is this phylogeny of both Viduidae and Estrildidae. While this work is genetic in nature, theoretically mathematical models (see Sefc *et al.*, 2005) on these particular relationships demonstrate its validity. Sefc *et al.* argues that, though the hybridization does occur, it is not often enough to significantly skew the data sets. In addition, this study established that the indigobirds meet the fourth criterion: reproductive isolation. Sefc *et al.* shows that the species are distinct and genetically isolated; importantly, however, this is not genetically based isolation – it is learned. Further direct obser-

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[6] Importantly, the absolute divergences dates are estimates only. However, the relative time lag between the hosts' radiations and the indigos' radiations is accurate, since the same regions were used (Sorenson *et al.*, 2003).

vational data of hybridization can be found in Payne & Sorenson (2004); here the authors observed hybridization between *V. paradisaea* and *V. chalybeata* – this hybridization was established by genetic tests (mtDNA). Thus far, the *Vidua* seem to conform to the first four tenets of Coyne & Orr.

Clearly, the fifth criterion of Coyne & Orr has already been well established: assortative mating does occur. Undeniably, Payne and Sorenson have shown countless times that the indigos preferentially choose conspecifics based on a learned call. This evidence has already been presented earlier, thus, will not be repeated. Allowing us then, to focus on the six and seventh criteria; it is best to take these two in tandem, since they represent very similar principles. First, as explained above the indigobird's young have developed specific mouth markings to deceive host parents; these markings represent both a genetic adaptation to a specific host and a means by which fitness is increased with the normative host (Payne *et al.*, 2001). Essentially, this evidence is used to forward a true species distinction in the face of introgression, and demonstrates that each species has adapted to their respective host. Coyne & Orr argue that a species definition based solely on a cultural trait, may be meaningless (2004:221-222). However, since these markings establish differences outside of simple maternal mitochondrial lineages, it is safe to conclude a true species distinction.

Outside of the descriptive studies, which demonstrate these differences (Payne, 1982), Payne *et al.* (2001) has done cross-foster experiments indicating a fitness advantage to the normative host based on the mouth markings. Their study focused mainly upon *V. chalybeata*, and interestingly showed that, while fitness advantages are present they are not great enough to prevent colonization of new hosts. This suggests that the indigobirds exist in a very narrow adaptive peak, where colonization advantages are only partially restrained by host specificity. Once a new

new niche is realized, it is best to evolve host-distinct features, when the peculiarity conveys fitness advantages.

Finally then, we are left with the eighth, and last tenet, of Coyne & Orr: "the biogeographic and evolutionary history of the taxa makes an allopatric phase *very unlikely*" (emphasis theirs, 158). While conforming to this criterion is difficult, both direct and indirect evidence seem to imply no allopatric phase (Payne, 1982; Payne *et al.*, 2002, 2005). Direct evidence comes from the geography of Africa; currently, the populations are sympatric and there seems to be no geographic barrier – past or present – to gene flow (Payne, 1982). Additionally, and more interestingly, there appears to observable sympatric speciation currently occurring in some *Vidua* populations; this evidence indirectly supports past sympatric speciation – since it supports the hypothetical possibility of this speciation mode (Payne *et al.*, 2002, 2005).

In their work done in 2002, Payne and his colleagues describe a system apparently limited to a population of indigos living on the Zambezi River. The populations consists of *V. chalybeata*, its normal host, *L. senegala*, and a novel host, *L. nitidula*. Genetic evidence suggests a recent switch of *V. chalybeata* from *L. senegala* to *L. nitidula*; this switch occurred in sympatry. Importantly, morphological features seem to have lagged behind this behavioral switch – aside from song no diagnostic technique can distinguish the two 'cultural morphs'. More interesting still are the kinship implications derived from mtDNA microsatellite analysis. There is a high incidences of relatedness between the *L. nitidula* parasites; specifically, the genes suggest that the host switch occurred four specific times, representing four matrilines. Essentially, it appears that the first steps toward speciation have occurred – in fact the *L. nitidula* morph was even once mistakenly describe as a new species (*V. incognita* by Nicolai (1972)). Payne *et al.* (2002) does not speculate on why the switch occurred; however, in a similar system described with *V. camerun-*

ensis environmental changes by humans may account for the host switch – they cite the concurrent introduction of wheat to the region (circa 0 A.D.)(Payne *et al.*, 2005).

Conclusion:

With the advancement of genetic technology, a vast quantity of data is being generated in the field of evolutionary biology. This new information has been applied by many to determine the nature of the biological systems observed, and has generated a resurgence of interest in sympatric speciation (Via, 2004). It remains unclear, however, if this new data will decisively end this debate; nonetheless, it has visibly altered the way we think about speciation. Apparently, Payne, Sorenson, and their colleagues, have described a system that has the general trappings of sympatric speciation; it meets all the criteria set down by Coyne & Orr and, also, relies upon a novel system to promote assortative mating: song learning. With further evidence and advancements in methodology, we may soon be able to demonstrate a more complex model for this speciation event, further supporting a hypothesis of sympatric speciation. As of now, it appears that 'cultural' traits can, in this instance, serve as the initial step towards speciation. Concerning this particular case, Coyne & Orr have written "this constitutes one of the few plausible cases of sympatric speciation" (222); and, given their usual staunch skepticism toward sympatric speciation, this is a clear stamp of approval. Hopefully, further systems will support these conclusions.

Appendix:

TABLE 1: COYNE AND ORR'S CRITERIA FOR SYMPATRIC SPECIATION VIA HOST-SWITCHING:

1. Range overlap, complete or nearly
2. Differential host exploitation
3. Establishment of sister taxa, by determining a fine phylogenetic relationship
4. Partial reproductive isolation, substantial but not total
5. Assortative mating
6. Genetic adaptations for specific host
7. Fitness advantages associated with specific host.
8. A very unlikely period of allopatry

summarized from Coyne & Orr (2004:158)

FIGURE 1: RANGE MAP SYNTHESIZED FROM PAYNE (1982)

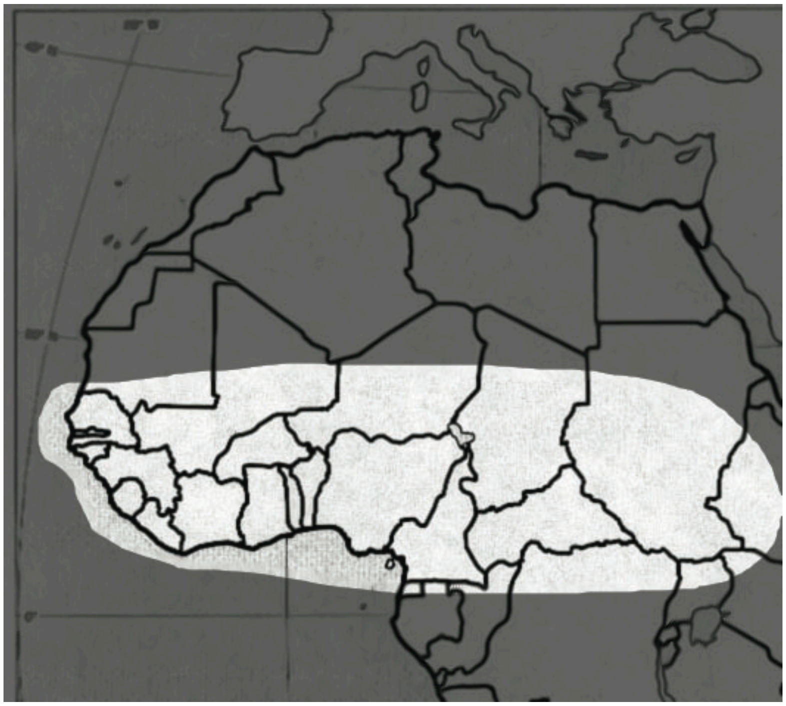

FIGURE 1: This figure represents the areas of sympatry for five *Vidua* species (*V. chaybeata*, *V. larvaticola*, *V. raricola*, *V. funereal*, and *V. wilsoni*) observed by Payne and synthesized from figures 5, 16, 21, 25, 49, 58 (in Payne 1982). It does not represent the entire range of the species; for example, *V. chaybeata* has a much larger range.

FIGURE 2: PHYLOGENETIC RECONSTRUCTION OF VIDUIDAE AND ESTRILDIDAE POPULATIONS REPRESENTING THE SPECIFIC HOST-PARASITE PAIR(S)

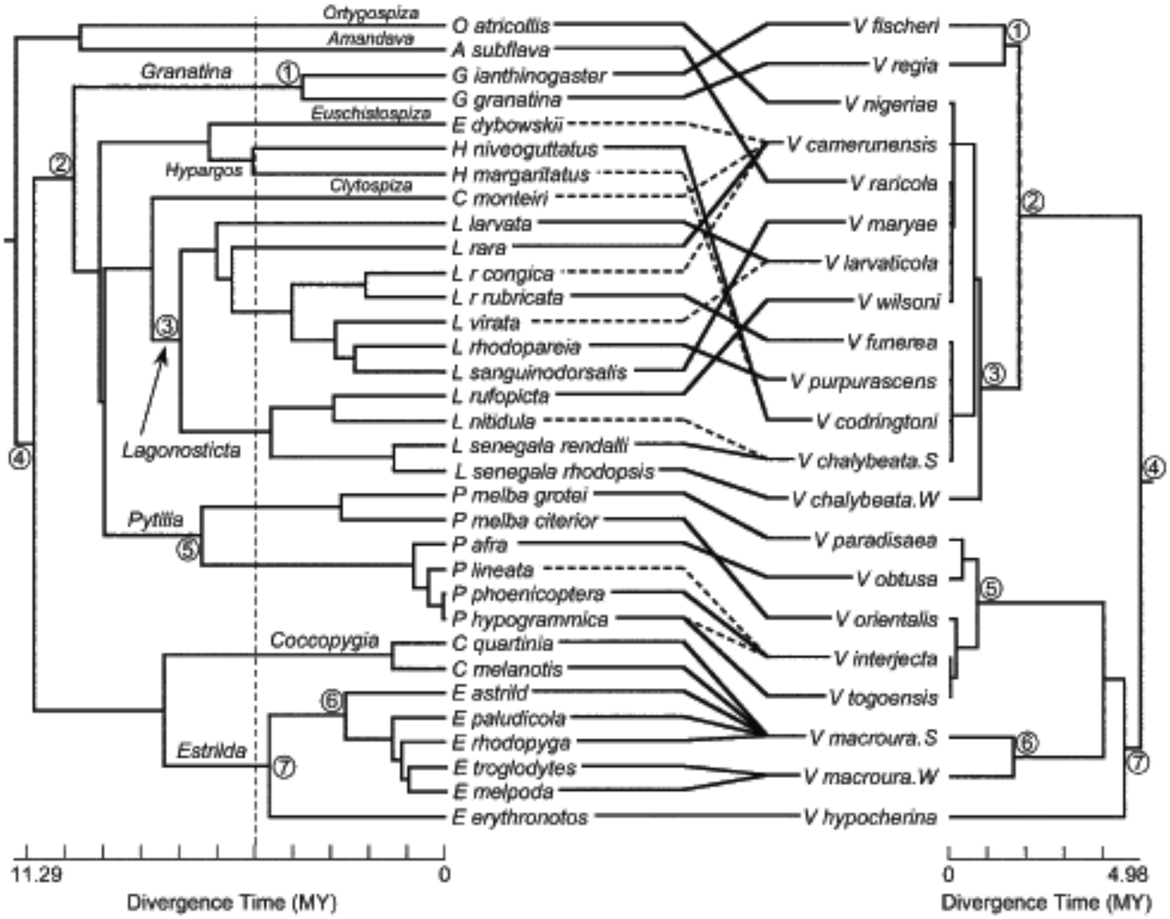

FIGURE 2: "Comparison of phylogenies for estrildid finch host species (left) and brood parasitic Vidua (right), with well-documented associations between hosts and parasites indicated. The primary host for each parasitic species is indicated by a solid line; other hosts are indicated with dashed lines except for V. macroura, which is a host generalist. Trees are drawn to the same scale with branch lengths proportional to divergence times (MY = million years) as estimated in a single analysis with both hosts and parasites in the same tree. Seven possible cospeciation events corresponding to data points in Figure 5 are numbered. The selected comparisons represent only a subset of all possible cospeciation events, are not necessarily mutually compatible in a single historical reconstruction, and are suggested by comparison of tree topologies only. The vertical dashed line indicates the time depth of the parasite tree. Note that nodes in both trees were rotated to maximize the appearance of congruence between the two trees." (reproduced in its entirety from Sorenson *et al.* (2004:147))

FIGURE 3: PARTIAL PHYLOGENY OF BOTH OF VIDUIDAE AND ESTRILDIDAE

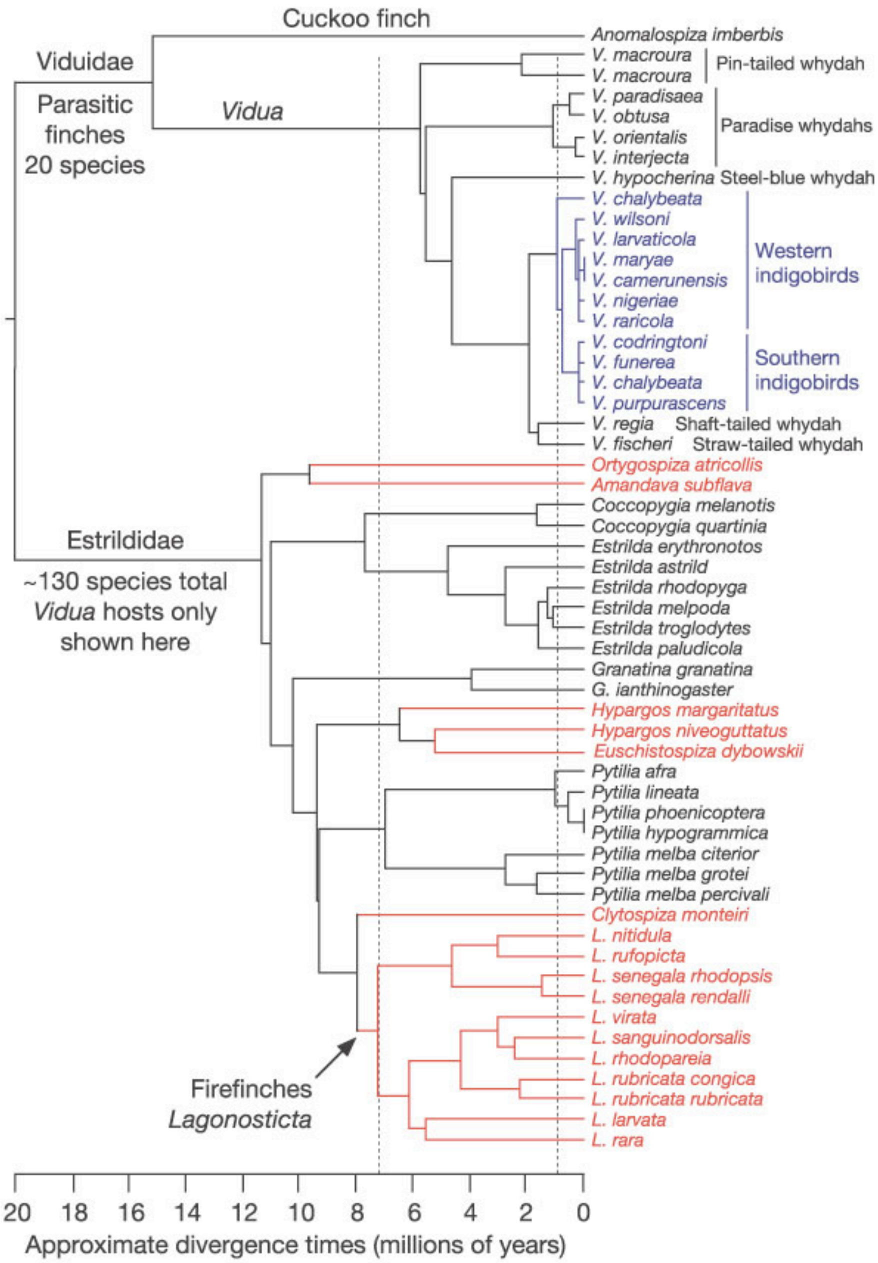

FIGURE 3: "mtDNA phylogeny of brood parasitic finches and their estrildid finch host species. (The cuckoo finch is a parasite of several more distantly related warblers.) Indigobirds are shown in blue [gray]; firefinches and other indigobird hosts are shown in red [gray]. Other estrildids shown are hosts of the various whydahs. Dotted lines indicate the most recent mtDNA ancestor for indigobirds and firefinches, respectively. Absolute values of divergence times should be viewed as rough approximations at best, but relative times are directly comparable between host and parasitic lineages." (reproduced in its entirety from Sorenson *et al.* (2003:929))

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