Trait Evolution in Estrildidae: Drivers of Variation in Female Song and Dance

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ABSTRACT

The estrildid finches (family Estrildidae) are a large family of songbirds of high ecological and conservation significance. The roughly 140 species that comprise the family are well-suited for evolutionary studies due to their extensive interspecific variation in plumage and courtship behavior. Although most estrildids are monogamous, many species exhibit sex-specific variation in courtship displays and parental care (e.g., nest-building). Using the most up-to-date phylogeny for the Estrildidae family, I performed ancestral state reconstruction for six life history traits: female dance, female song, coloniality, sexual dimorphism, brood parasitism, and nest-building sex. I used phylogenetic regression to test for correlations between female courtship behaviors and life history traits. The results of this study show that female song is not ancestral in Estrildidae, while the ancestral state of female dance is ambiguous. Female courtship is not correlated with other life history traits, suggesting that female song and courtship are evolving independently. I discuss alternative explanations for drivers of female courtship evolution, such as ecological factors, that may be explored in future work. These results clarify previous studies on female song and courtship in Estrildidae.

KEYWORDS

phylogenetics, breeding biology, finch, waxbills, firefinches

INTRODUCTION

Estrildidae are a family of gregarious, seed-eating passerine finches distributed in habitats ranging from desert to mountains throughout Asia, Australia, and Africa (Winkler et al. 2020). This family of ca. 140 species includes the Zebra Finch (*Taeniopygia guttata*), a model organism for a variety of biological research including animal behavior, sexual selection, and genomics (Warren et al. 2010). From an evolutionary perspective, the Estrildidae are of significance due to the extensive interspecific variation in breeding biology within the family (Gomes et al. 2017), as well as the ecological importance and conservation threat of many species (Winkler et al. 2020). Despite their evolutionarily importance, few comparative studies on breeding behavior in Estrildidae have been published. Studying the evolution of breeding behavior of this group would contribute to the understanding of sexual selection in passerines, a topic which currently has largely focused on male attributes.

The role of females in sexual selection is of particular interest in Estrildidae. Females of some species perform courtship dances, either in sync with male partners or individually (Ota et al. 2015); several species (16 ssp., 12 genera) in Estrildidae also exhibit female song. One scenario is that female dance and female song may act together as multimodal signaling (i.e.,type of signaling involving two or more senses). As no comparative studies examining female courtship in passerines exist, clarifying drivers of female courtship in Estrildidae and if female song and dance evolve in conjunction would expand this unknown topic.

Importantly, estrildids are monogamous and nonmigratory (Winkler et al. 2020). Mating system and migratory behavior have previously been shown to be predictors of female song loss, perhaps due to differences in stability between male-female bonds (Price 2009). Estrildidae pose a system in which these variables are controlled and further factors related to female song loss may be elucidated. Additionally, if monogamy is associated with female dance, the estrildids provide a study system in which monogamy is controlled for. By performing a comparative study on female song and dance in Estrildidae, drivers of these traits unrelated to monogamy or migratory behavior can be found.

A previous study of female song and dance evolution in the Estrildidae was conducted by Soma and Garamszegi (2015), who found no correlation between the two character traits, as well as no correlation between the presence of the two traits with other life history traits such as

interspecific brood parasitism and plumage color. However, Soma and Garamszegi (2015) based their analyses on a phylogenetic tree of the Estrildidae by Jetz et al. (2012) that has since been found to be problematic for trait-based comparative analyses due to its use of birth-death polytomy resolvers to account for missing genomic data, resulting in a number of incorrectly reconstructed phylogenetic relationships (Rabosky 2015). A more recent tree for the Estrildidae was constructed by Olsson and Alström (2020) based on genomic data from mitochondrial and nuclear genes, providing greater resolution for many of the interspecific relationships within Estrildidae.

In this study, I performed an analysis of drivers in the evolution of female courtship and song. I assessed the ancestral state for six life history characters to infer the ancestral condition for each trait and their evolutionary histories, including times these traits were gained and lost within the family. I performed phylogenetic logistic regression between female song and dance and other estrildid life history traits. Finally, I calculated the phylogenetic signal for several life history traits to assess their evolutionary lability.I used the most recent phylogeny by Olsson and Alström (2020) for each analysis. Additionally, I included nest-building sex as a trait, which Soma and Garamszegi (2015) excluded. Nest-building sex is often overlooked in comparative studies on breeding behavior despite potentially being a sexually selected trait relating to parental investment (Soler et al. 1998).

METHODS

Phylogenetic tree reconstruction

To build the phylogenetic tree, I used author-provided alignments from the most recent phylogeny by Olsson and Alström (2020). These alignments included seven mitochondrial and nuclear genes (ND2, cyt-b, G3P, ODC, TGF, fib-5 and myoglobin) and covered 105 estrildid species representing all estrildid genera and major clades. In addition, the alignment included 55 outgroup taxa from 33 families with 1-10 species per family. Using Geneious 2022.1, I concatenated the individual gene alignments into a single alignment. which I then inputted into IQ-TREE v2.2.0, which uses a maximum likelihood approach to search for the best-scoring tree (Nguyen et al. 2015). For the alignment partitioning scheme, I used the algorithms found in

PartitionFinder 2 to select the best model for each individual gene (Lanfear et al. 2017). Finally, I performed bootstrapping at 1000 iterations to calculate support values at each node.

Comparative analyses

Ancestral state reconstruction (ASR) is a method of approximating the character states at each node in the tree. It requires inputting a character matrix and an ultrametric phylogenetic tree, and can be run using either likelihood or Bayesian statistical methods (Joy et al. 2016). For my ancestral state reconstruction, I gathered life history data from Winkler et al. (2020), Goodwin (1982), and Restall (1997) for six characters: female song, female dance, coloniality, sexual dimorphism, and nest-building sex; traits were scored as discrete, numerical characters (Table 1). I included trait scores for outgroups from the families *Vidua*, *Ploceidae*, *Chloropsis*, *Dicaeum*, *Irena*, *Nectarinia*, *Peucedramus*, and *Urocynchramus* based on their close phylogenetic relationship to Estrildidae. To perform the ASR, character matrices and the ultrametric phylogeny were input into the R package ape 5.0 (Paradis and Schliep 2019). I performed both likelihood analyses and Bayesian stochastic character mapping for each trait.

Table 1. **Scoring of traits for ancestral state reconstruction.** Scoring criteria for each of the six life history traits I included in ancestral state reconstruction.

Trait	Scoring	Scoring Criteria	Primary Sources
Female song	1 - Female song absent 2 - Female song present	**Female song absent**: No description of female song recorded or available, despite sizable amount of life history information. **Female song present:** Female song description available	Goodwin (1982), Restall (1997), Winkler et al. (2020)
Female dance	1 - Female courtship dance absent 2 - Female courtship dance present 3 - Female courtship dance absent, greeting dance present	**Female courtship absent**: No description of female courtship recorded or available, despite sizable amount of life history information. **Female courtship present:** Female courtship description available	Goodwin (1982), Restall (1997), Winkler et al. (2020)

|			
Coloniality	1 - Noncolonial 2 - Colonial	**Noncolonial**: No description of birds nesting close together, despite sizable amount of life history information. **Colonial:** Described as colonial, semi-colonial, or nesting in close proximity to each other.	Goodwin (1982), Winkler et al. (2020)
Brood parasitism	0 - Brood parasitism absent 1 - Brood parasitism present	**Brood parasitism absent**: No description or evidence of brood parasites. **Brood parasitism present:** Brood parasites recorded or presumed based on *Vidua* mimicry.	Winkler et al. (2020)
Sexual dimorphism	1 - Sexes alike 2 - Sexes similar 3 - Sexes different	**Sexes alike**: No easily distinguishable differences between female and male. **Sexes similar:** Few differences between female and male. **Sexes different**: Male and female appear dramatically different.	Winkler et al. (2020)
Nest-building sex	1 - Male builds nest 2 - Female and male build nest 3 - Female builds nest 4- Appropriates nest	**Male builds nest**: Male is described as the primary builder of the nest. **Female and male build nest:** Male and female described as both contributing to the nest. **Female builds nest:** Female is described as the primary builder of the nest. **Appropriates nest:** Species is described as usually appropriating the nest of another species.	Goodwin (1982), Restall (1997)

I used phylogenetic logistic regressions (PLR) to test for the correlation between traits. Phylogenetic logistic regression is appropriate for binary, categorical, and continuous data as predictor variables, and binary data as the response variable. It replaces normal logistic regression when the confounding effect of phylogeny must be taken into account (Ives and Garland 2010). Using the R package phylolm (Ho and Ané 2014), I ran PLR for the binary characters of female song and dance, using coloniality, nest-building sex, brood parasitism, sexual dimorphism, and either song or dance as categorical, nominal predictors. Because of the statistical power of binary data, I performed PLR with only one independent variable at a time,

rather than performing a multivariate analysis; additionally, I did not perform a test of multicollinearity to check if independent variables were correlated, which is a requirement for multivariate analysis.

Finally, I calculated the measure of phylogenetic signal (Dst), a metric that represents how phylogenetically constrained a trait is. D typically ranges between values close to 0 and values close to 1, with values closer to 0 indicating stronger phylogenetic signal. I first converted female dance, nest-building sex, and sexual dimorphism into binary data. I then input the binary data and my phylogeny into the R package caper, which calculates Dst based on simulations that assume a model of Brownian evolution (Fritz and Purvis 2010).

RESULTS

There were no major conflicts between the tree I generated and the Olsson and Alström (2020) tree. On the other hand, my phylogeny differs significantly from the one used in Soma and Garamszegi (2015). The cladistic arrangements of the Jetz (2012) phylogeny used by Soma and Garamszegi are fundamentally different from the current 2020 phylogeny. In the Jetz (2012) tree, multiple clades are nested in each other, while the Olsson and Alström (2020) tree supports many of these clades being sister to each other. For example, in the Jetz (2012) tree, *Estrilda* is nested within the clades containing *Orytogospiza* and *Lagonosticta* (Figure 1, E and F), whereas in the updated tree, *Estrilda* is in a clade sister to the E and F. Other differences include the basal-most placement of *Neochmia temporalis* in the Jetz (2012) tree and the differential placement of *Erythrura*.
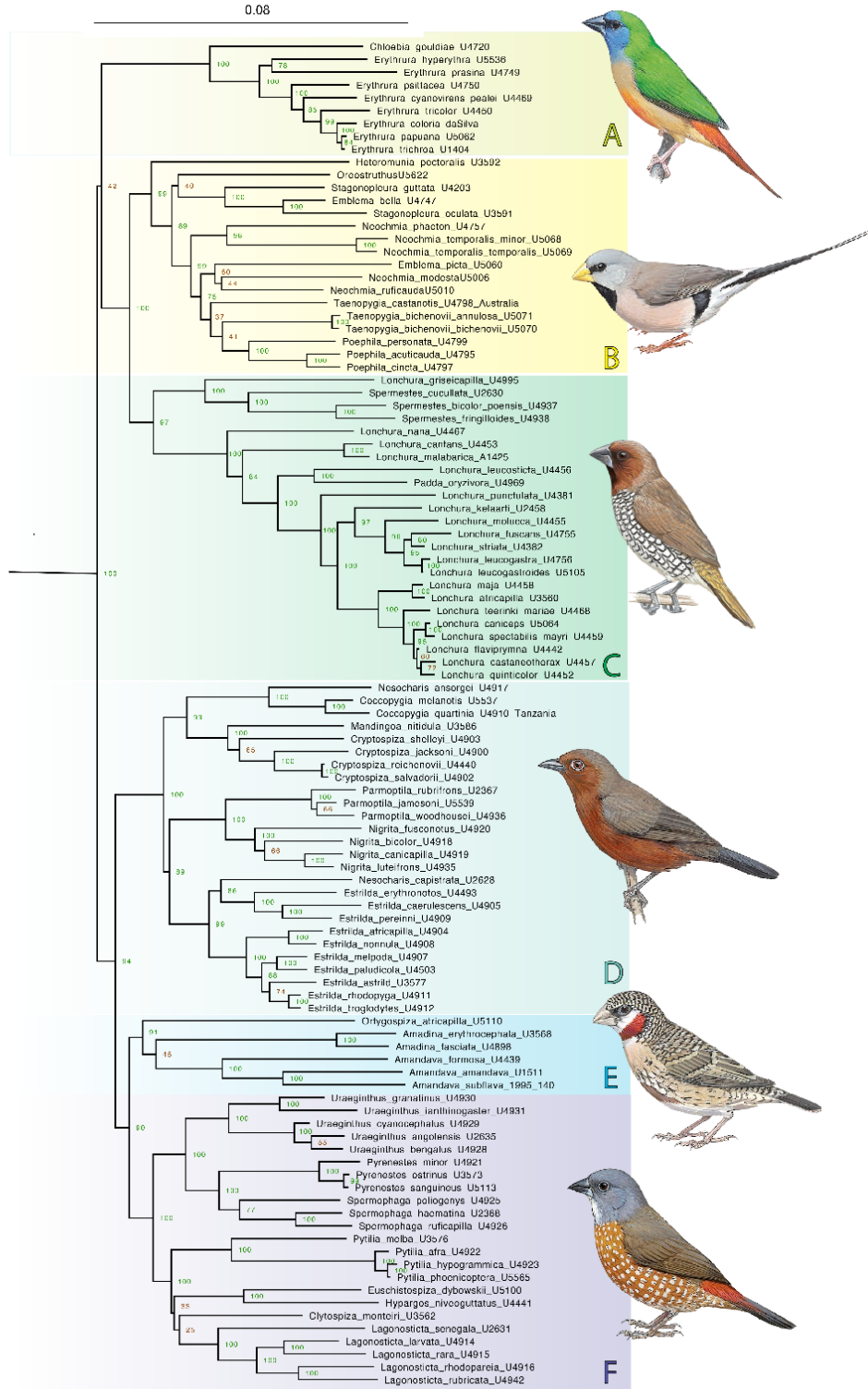
Figure 1. Updated phylogeny of Estrildidae. Maximum likelihood phylogram of the Estrildidae generated using concatenated mtDNA and nuclear gene alignments from Olsson and Alström (2020). Major clades are labeled A through F. Bootstrap values are provided for major nodes; bootstrap values < 70 are labeled in red. Illustrations: Winkler et al. 2020

Ancestral state reconstruction

Ancestral state reconstruction (ASR) performed on female song, female dance, coloniality, sexual dimorphism, and nest-building sex showed the evolutionary history of each trait. The ancestor of Estrildidae likely did not express female song, and it was only gained in the common ancestor of clades D, E and F, where it was lost independently several times and most commonly in clade D (Figure 2). In other clades, no female song was ancestral and only two species (*Estrilda nonnula*, *Neochmia temporalis*) independently gained female song. Unlike female song, it is ambiguous whether the ancestor of Estrildidae expressed female dance or not (Figure 3). Female dance occurs in all major clades. *Stagonopleura*, several *Spermestes* and *Lonchura* species, and various other species have reverted back to no female dance from a common ancestor that expressed female dance.

Coloniality has evolved in Estrildidae independently multiple times from a noncolonial common ancestor (Figure 4). The transition from noncoloniality to coloniality occurs late in the tree, with several colonial species only evolving coloniality since their most recent divergence (*Uraeginthus angolensis, Spermests cucullata, Stagonopleura guttata, Neochmia ruficauda*). The major transitions from non coloniality to coloniality are for genus *Lonchura* (clade C) and for clade B, which includes *Taeniopygia* and *Poephila*.

Sexual dimorphism showed 80 transitions on average, higher than any other trait in which ASR was performed. The common ancestor of Estrildidae was either strongly or weakly sexually dimorphic (Figure 5). This trait then became more pronounced in Clade D, E and F, which is composed of a highly sexually dimorphic ancestor and descendants. On the other hand, strong sexual dimorphism was lost in clades A, B, and C.

Nest-building sex showed frequent gains and reversals (Figure 6). The ancestral state of Estrildidae was female-built nests. This character shifted largely to male-building and both-sex-building in Clades D, E, and F (*Estrilda* to *Uraeginthus*), with only two species expressing female-building. Clades A, B, and C, on the other hand, had more species that had either female-building or both-sex-building. However, female-building was lost independently twice in *Neochmia* and *Lonchura*; it was gained again in *Lonchura*. Finally, brood parasitism is mostly present in clades D, E, and F.

Phylogenetic regression

As a result of the phylogenetic regression, there were no statistically significant correlations between female song and the other five characters (Table 2). Additionally, there was no statistically significant correlation between female dance and the other five characters (Table 3).

Phylogenetic signal

For phylogenetic signal, which I performed only on binary traits or traits easily converted to binary values, female dance had the highest value and weakest phylogenetic signal with a D-value of 0.575 (Table 4). Nest-building sex had the second-highest value of 0.202. Coloniality and female song had the highest phylogenetic signal and the lowest D-values of 0.067 and 0.068 respectively.

Table 2. Phylogenetic regression between female song and life history traits. Phylogenetic logistic regression testing for correlation between female song and other life history variables.

	Logistic coefficient	SE	Z-value	LowerCI	UpperCI	P-Val
Coloniality (Intercept)	-1.460	0.608	-2.399	-2.537	0.155	0.016
Colonial	-0.843	0.840	-1.003	-2.284	0.377	0.316
Brood parasitism (Intercept)	-2.304	0.880	-2.618	-3.714	-0.593	0.009
Presence of brood parasitism	1.344	0.825	1.629	0.111	2.998	0.103
Sexual dimorphism (Intercept)	-0.915	1.704	-0.537	-1.573	1.697	0.591
Sexes identical	0.055	1.540	0.036	-2.650	1.401	0.971
Sexes similar	-0.781	1.555	-0.502	-3.079	0.149	0.616
Sexes different	0.811	1.612	0.503	-1.832	2.292	0.615
Nest (Intercept)	-1.972	2.936	-0.672	-1.428	1.181	0.502
Male builds	0.847	2.907	0.291	-3.177	1.084	0.771
Male and female build	1.405	2.924	0.480	-1.456	1.710	0.631
Female builds	0.621	2.959	0.210	-2.037	1.036	0.834
Appropriates nests	-0.119	3.575	-0.033	-2.059	1.201	0.973
Female Dance (Intercept)	-1.720	0.762	-2.259	-2.371	0.131	0.024
Courtship dance	0.343	0.582	0.590	-0.631	1.333	0.555
Greeting dance only	-0.197	1.280	-0.154	-1.407	1.452	0.878
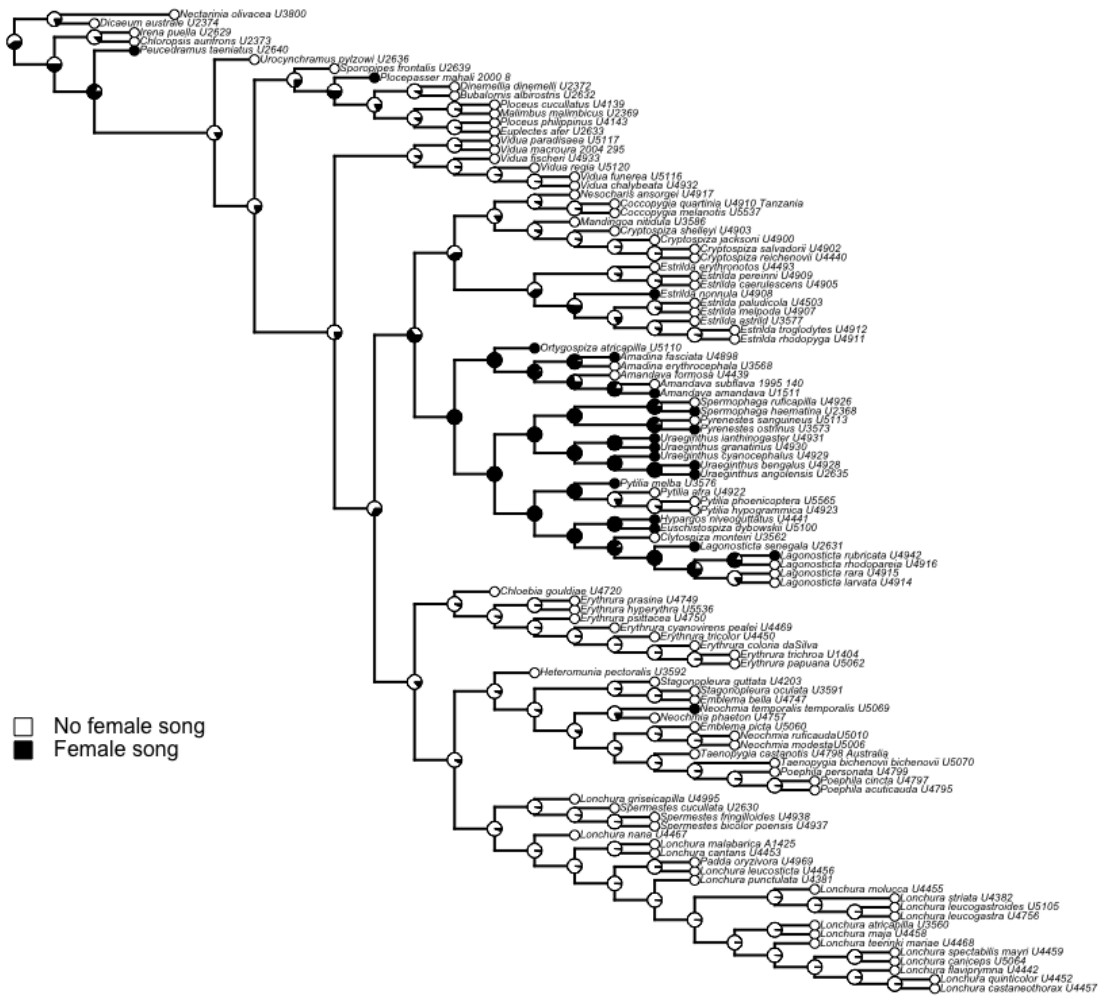
Figure 2. Evolution of female song in Estrildidae. Maximum-likelihood ancestral state reconstruction for female song. Circles represent maximum likelihood probability of either ancestral state at each node.
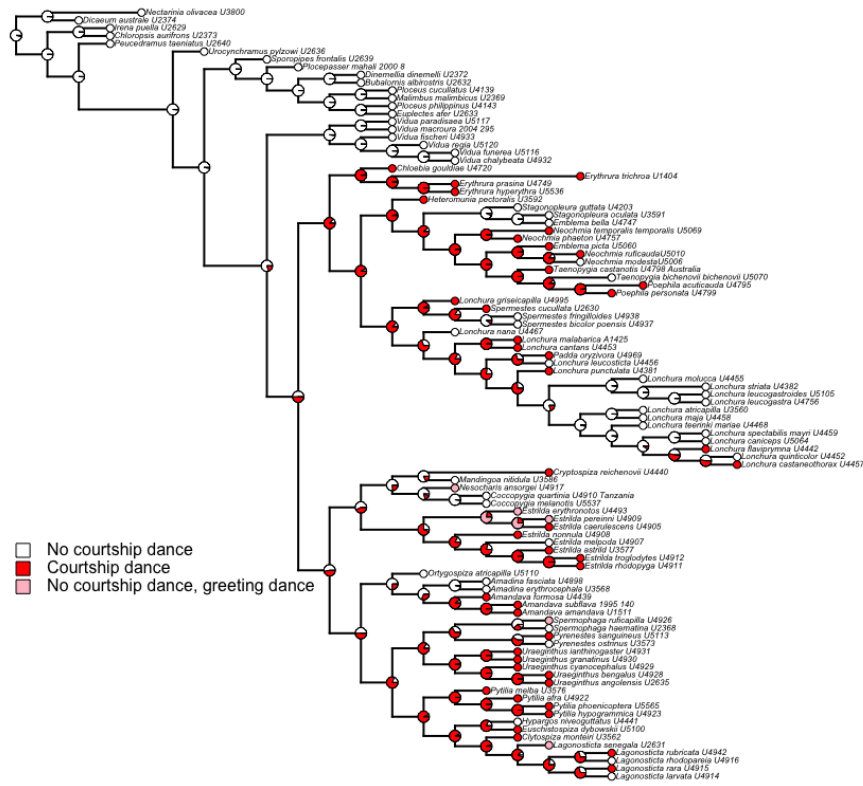
Figure 3. Evolution of courtship dance in Estrildidae. Maximum-likelihood ancestral state reconstruction for female courtship dance. Circles represent maximum likelihood probability of ancestral states at each node.

Table 3. Phylogenetic regression between female dance and life history traits. Phylogenetic logistic regression testing for correlation between female dance and other life history variables.

|	Logistic coefficient	SE	Z-value	LowerCI	UpperCI	P-Val
Coloniality (Intercept)	0.321	0.346	0.929	-0.263	0.887	0.353
Colonial	0.002	0.534	0.004	-0.874	1.076	0.997
Brood parasitism (Intercept)	-0.085	0.356	0.238	-0.823	0.597	0.812
Presence of brood parasitism	0.750	0.566	1.324	-0.446	1.926	0.186
Sexual dimorphism (Intercept)	-1.727	2.014	-0.857	-1.896	1.158	0.391
Sexes identical	1.848	2.063	0.895	-0.975	2.638	0.371
Sexes similar	2.106	2.044	1.030	-0.787	2.829	0.303
Sexes different	1.860	2.067	0.900	-1.210	2.742	0.368
Nest (intercept)	1.017	2.251	0.452	-1.163	1.282	0.652
Male builds	0.046	2.309	0.020	-0.627	3.140	0.984
Male and female build	-0.426	2.314	-0.184	-1.220	2.563	0.854
Female builds	-1.038	2.329	-0.445	-2.104	1.635	0.656
Appropriates nests	-2.310	2.821	-0.819	-2.918	1.329	0.413
Female Song (Intercept)	0.113	0.322	0.352	-0.544	0.785	0.725
Presence of female song	0.257	0.583	0.440	-0.889	1.548	0.660

Figure 4. Evolution of coloniality in Estrildidae. Maximum-likelihood ancestral state reconstruction for coloniality. Circles represent maximum likelihood probability of either ancestral state at each node.

Table 4. Phylogenetic signal of life history traits. Phylogenetic signal (Dst) values for coloniality, female song, and female dance. Only binary traits or traits easily converted to binary data are included.

	Counts of states (0=absence,1=presence)	Estimated D	Prob. E(D) from no phylogenetic structure
Coloniality	0=68, 1=25	0.067	0.000
Female song	0=72, 1=17	0.068	0.000
Female dance	0=36, 1=43	0.575	0.009
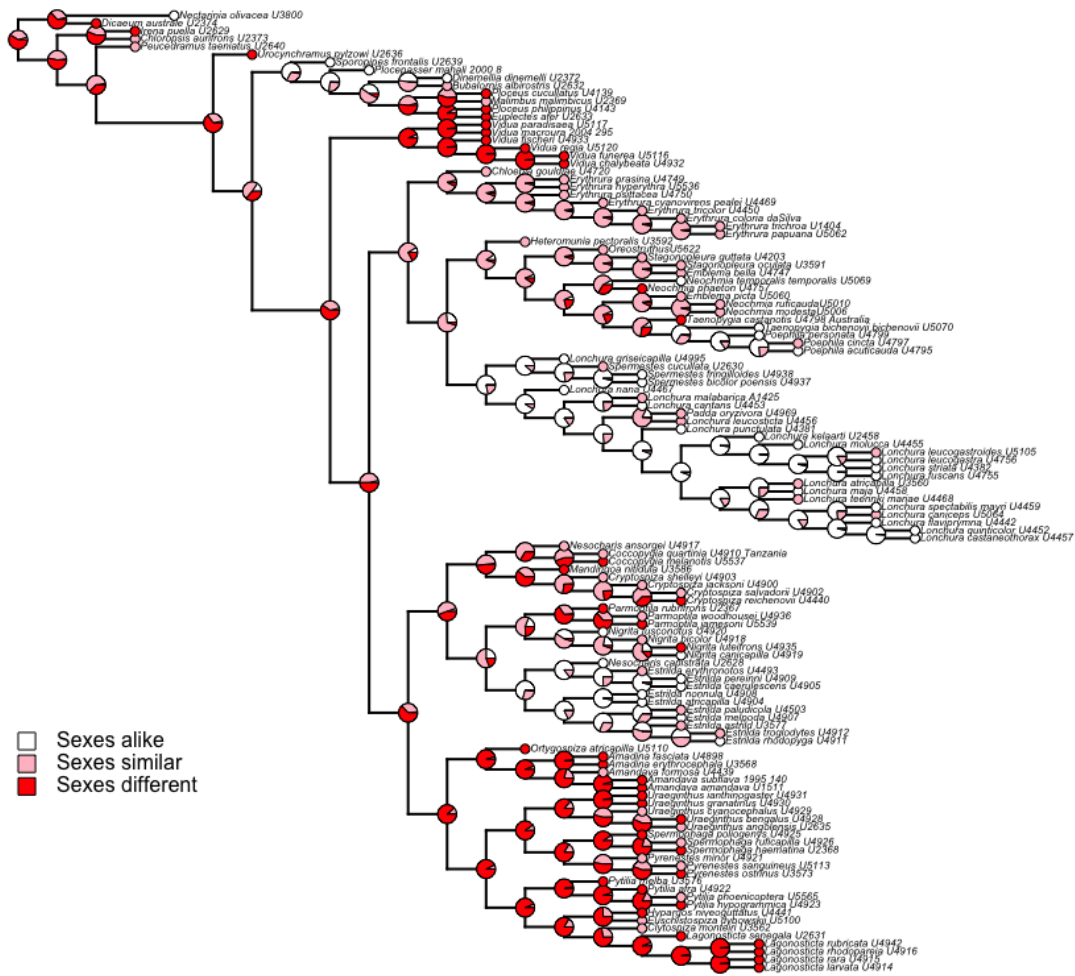
Figure 5. Evolution of sexual dimorphism in Estrildidae Maximum-likelihood ancestral state reconstruction for sexual dimorphism. Circles represent maximum likelihood probability of ancestral states at each node.
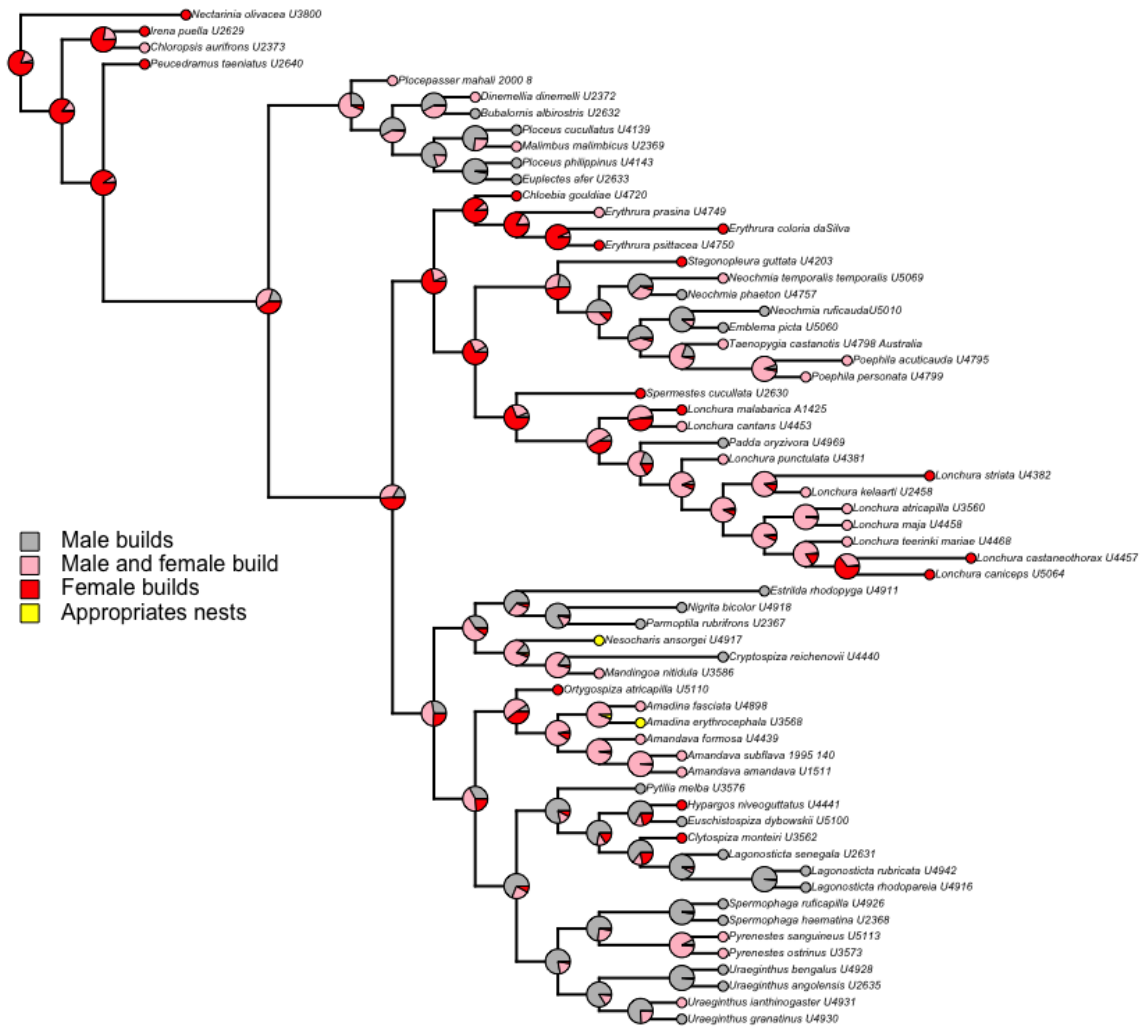
Figure 6. Evolution of nest-building sex in Estrildidae. Maximum-likelihood ancestral state reconstruction for nest-building sex. Circles represent maximum likelihood probability of ancestral states at each node.

DISCUSSION

To further understanding of female courtship in passerines, I studied the evolution of female song and dance in Estrildidae. I performed ancestral state reconstruction for female song and dance and found different evolutionary patterns than prior reconstructions. By testing for correlations between female song and dance with other life history traits, I found that female song and dance are evolving independently from each other and coloniality, brood parasitism, sexual dimorphism, and nest-building sex. These results suggest future studies should incorporate ecological variables as potential drivers of female song and dance. Finally,

comparative studies on female dance in passerines are needed for broader resolution of female courtship and breeding behavior.

Evolution of female song and dance

There were major differences between Soma and Garamszegi (2015) and my study in our ancestral state reconstructions of female song and dance. My ASRs support a vastly different amount of gains and losses at different points in the tree. The reconstruction of female song by Soma and Garamszegi (2015) supports a model in which an ancestor of a major clade gained female song and was subsequently lost in the later ancestor of clades nested within the larger clade. On the other hand, this ASR supports one gain of female song and no major subsequent loss within that clade, with most species' song losses occurring since their most recent divergences, suggesting loss of female song was relatively recent for many species. For female dance, this ASR suggests more independent transitions than the Soma and Garamszegi (2015). This shows potential convergent evolution of female dance across clades. The difference in our findings underscores the importance of phylogeny for comparative trait analyses.

Despite a fundamentally different phylogeny, the ASR and logistic regression I performed confirms results by Soma and Garamszegi (2015) that female song and dance in Estrildidae are evolving independently. Overall, female song and dance showed vastly different patterns of evolution. Female song was only prevalent in one clade (Figure 2). On the other hand, female dance was ubiquitous in all major estrildid clades, involving independently four times (Figure 3). The lack of correlation between female song and dance does not support an overarching model of multimodal signaling in which the evolution of female song or dance inevitably leads to the evolution of the other.

One possible hypothesis for the evolution of female courtship signals that female dance may be a mechanism to strengthen monogamous pair-bonds between males and females, or signal mutual interest to the male (Griffith 2019). In instances where the male is investing heavily in courtship signals such as plumage color, dance, and song, a reciprocal signal by the female may prevent unnecessary energy expenditure. A study finding that Java Sparrow (*Padda oryzivora*) mating success is highest when males and females dance together suggests a potential role in which female dance may act as a signal to the male (Soma and Iwama 2017). To further

understand the relationship between male and female courtship, it is necessary to examine the strength of courtship signal between male and female estrildids. Soma and Garamszegi (2015) found that the size of male dance repertoire was correlated with the size of female dance repertoire. Additionally, male plumage was correlated with female plumage, although the drivers influencing evolution of bright plumage were different between the sexes (Soma and Garamszegi 2015). Overall, the current lack of literature on female dance means that a larger comparative study of female dance in passerines is necessary to find a link between monogamy and female dance. If monogamy and female dance are strongly correlated in the Passeriformes, this supports the hypothesis that female dance is used to strengthen monogamous pair-bonds.

Drivers of trait evolution

The results of this ASR and phylogenetic regression shows that female song and dance are evolving independently from the life history traits of coloniality, brood parasitism, nest-building sex, or sexual dimorphism. Recent studies in ornithology reveal female song is more prevalent than once thought and is the ancestral state in multiple families (Odom and Benedict 2018). The presence of female song of Estrildidae has presented a mystery to scientists; many traditional drivers of female song loss, such as polygyny and migration, are nonfactors in the estrildids, a monogamous, largely nonmigratory group (Soma and Garamszegi 2015). These results suggest that ecological factors may be correlated with the evolution of female song and dance in Estrildidae instead.

A study on blackbirds by Price (2019) found colonial breeding and brood parasitism to be correlated with female song loss. However, I found no significant correlations between female song in Estrildidae with coloniality and brood parasitism. Female song was not the ancestral state in Estrildidae and only evolved to be widespread in one clade. Thus, the lack of correlation between female song loss and coloniality is perhaps partly due to the inherent rarity of female song in estrildids. These results suggest that other factors are driving the evolution of female song in Estrildidae. Ecological factors are major drivers of mating systems and sexual selection in avian species (Owens and Bennett 1997). Thus, traits relating to resources, habitat, and breeding season may be correlated with female song and dance.

Traditionally, sexual dimorphism is thought to be driven by female sexual selection. Plumage sexual dimorphism has generally been found to be correlated to parental care and extra-bond paternity to be factors (Owens and Hartley 1998). Few of these are viable factors in Estrildidae, as the family is monogamous, nonmigratory, both the female and male incubate, and both sexes feed offspring. In my analyses, there was no correlation between sexual dimorphism and female dance or song, showing that there is no evidence either of these factors leads to increased or decreased sexual dimorphism. However, the results of the ancestral state reconstruction showed a visual association between increased sexual dimorphism and male nest-building (Clades D, E, and F), suggesting that testing for correlation between these two traits may be worthwhile. Additionally, these clades have the highest proportion of brood parasitism, suggesting that a relationship between brood parasitism, nest-building sex, and sexual dimorphism may exist.

Finally, though nest-building sex has been hypothesized to represent parental investment and act as a sexually selected trait, it evolves independently of female song and dance in the Estrildidae (Soler et al. 1998). Previous studies investigating parental investments to nest-building have found that this trait correlates with environmental factors such as duration of breeding season and latitude (Mainwaring et al. 2021). Further analysis of this trait in Estrildidae should include factors such as habitat, altitude, and breeding season.

Limitations

A large quantity of missing data on life history traits complicates the precision and accuracy of my comparative analyses. For most characters, up to more than half of taxa were dropped from the tree due to missing data. One major limitation I ran into was the scoring of female song. Optimally, I would have categorized female song based on whether it is uttered during courtship or not. However, because of limited data and descriptions of female song, I lumped female song into a simple "absence" or "presence" score (see Table 1 for scoring details). Additionally, correlation tests between traits suffered from low statistical power of binary data, meaning that there may have been statistically significant correlations that were not detected (Ives and Garland 2010). This was especially a problem for traits with a large amount of

missing data, such as nest-building sex. Larger sample sizes would increase statistical power; this would require more complete life history data to reduce the amount of missing data.

Future directions

The next step of this project will involve implementing whole genome sequencing to refine the phylogeny and clarify placements of weakly supported clades such as *Erythrura*. Currently, I have sequenced 33 whole genome sequences for this purpose. Clarifying the phylogeny is important because analyses such as ancestral state reconstruction, phylogenetic logistic regression, and phylogenetic signal are influenced by phylogeny (Rabosky 2015). Secondly, I will be implementing ecological factors into my ancestral state reconstruction. Some of the factors I will look at are habitat, diet, gregariousness, breeding season duration, and nomadic behavior. Additionally, I will be scoring the level of courtship signal for male and female estrildids and testing for an association between the two to examine whether the strength of male and female sexual selection tend to be correlated. Finally, a comparative study on female dance in passerines is necessary to test for a link between monogamy and the presence of female courtship.

Broader Implications

Comparative analyses on life history traits in Estrildidae revealed noteworthy patterns of evolution in this family. Ancestral state reconstructions performed on female song and dance showed different patterns of evolution than previously thought, with potentially more independent transitions for female dance and a different pattern of gains and losses for female song; these results emphasize the importance of phylogeny for comparative studies.

The lack of a correlation between female song and female dance, as well as the lack of a correlation between female song and dance with life history factors such as coloniality, nest-building sex, and sexual dimorphism suggests none of the traits I examined evolve in conjunction. This corroborates previous results found by Soma and Garamszegi (2015), who use a vastly different phylogeny, and disproves female multimodal song-dance signaling as an ubiquitous signal in Estrildidae. One possibility is that other ecological factors, which influence

both male and female sexual selection, are potentially major drivers of female song and dance. Another possibility is that female courtship dance evolved as a mechanism to reinforce monogamous pair-bonds. Further study of drivers in female song and dance must examine factors such as diet, habitat, nomadic behavior, and breeding season duration, as well as look at passerines more broadly. The results of my study suggest that ecological factors, which are easily overlooked, may be important to include in comparative studies on breeding biology.

Sexual selection in ornithology is currently undergoing a paradigm shift. New research suggests that traditional views of breeding behavior, which focus on models of sexual selection where the female is a passive actor, are incorrect (Griffith 2019). Only now are many overlooked aspects of female behavior being studied in ornithology. My research adds to a growing body of literature suggesting a greater need for studying female roles in sexual selection. For example, my study highlights an urgent need for a broader comparative study on female dance in passerines.

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