ORIGINAL ARTICLE

Male-male competition and repeated evolution of terrestrial breeding in Atlantic Coastal Forest frogs

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Terrestrial breeding is a derived condition in frogs, with multiple transitions from an aquatic ancestor. Shifts in reproductive mode often involve changes in habitat use, and these are typically associated with diversification in body plans, with repeated transitions imposing similar selective pressures. We examine the diversification of reproductive modes, male and female body sizes, and sexual size dimorphism (SSD) in the Neotropical frog genera *Cycloramphus* and *Zachaenus*, both endemic to the Atlantic rainforest of Brazil. Species in this clade either breed in rocky streams (saxicolous) or in terrestrial environments, allowing us to investigate reproductive habitat shifts. We constructed a multilocus molecular phylogeny and inferred evolutionary histories of reproductive habitats, body sizes, and SSD. The common ancestor was small, saxicolous, and had low SSD. Terrestrial breeding evolved independently three times and we found a significant association between reproductive habitat and SSD, with shifts to terrestrial breeding evolving in correlation with decreases in male body size, but not female body size. Terrestrial breeding increases the availability of breeding sites and results in concealment of amplexus, egg-laying, and parental care, therefore reducing male-male competition at all stages of reproduction. We conclude that correlated evolution of terrestrial reproduction and small males is due to release from intense male-male competition that is typical of exposed saxicolous breeding.

KEY WORDS: Correlated evolution, *Cycloramphus*, reproductive mode, sexual selection, sexual size dimorphism, *Zachaenus*.

Diversification involving shifts in habitat use is often associated with phenotypic changes that optimize performance in new environments (Fleagle and Mittermeier 1980; Glor et al. 2003; Streelman and Danley 2003; Bell et al. 2010). Invasion of new habitats imposes new selective pressures, often requires adaptive evolution, and thus plays a fundamental role in shaping diversity (Losos et al. 1997). Similar environments impose similar selective pressures, which can drive adaptive convergence (McCracken et al. 1999; Ben-Moshe et al. 2001; Webster and Dawson 2004).

Phenotypic convergences due to independent shifts toward similar habitats are especially common when species are members of the same monophyletic group (Schluter 2000; Losos 2011).

Tetrapods have evolved recurrent shifts between aquatic and terrestrial breeding habitats throughout their evolutionary history (Vermeij and Dudley 2000; Sander 2012; Kelley and Pyenson 2015). Invasion of new habitats for reproduction can be advantageous in which it opens new competition-free environments for offspring, and in some cases can trigger higher rates of

evolutionary diversification (Wagner 2001; Sahney et al. 2010; Crump 2015). Living amphibians have diversified in almost all habitats on the planet (Wells 2010), with multiple independent shifts between aquatic and terrestrial breeding modes (Chippindale et al. 2004; Wei et al. 2009; San Mauro et al. 2014). For frogs, these evolutionary transitions are primarily associated with egg deposition sites and tadpole development sites (Haddad and Prado 2005; Zamudio et al. 2016); however, adults also experience new selective pressures as they move to terrestrial habitats for breeding. The prevailing hypothesis for frogs is that the selective advantage of escaping aquatic predators during early life stages, coupled with suitable climatic conditions (humidity and temperature), promotes the evolution of terrestrial breeding (Goin and Goin 1962; Wells 2010; Gomez-Mestre et al. 2012). An alternative hypothesis posits that terrestrial breeding decreases male-male competition that is typical of high-density aquatic breeding habitats (Zamudio et al. 2016). Terrestrial breeding reduces the need for costly behaviors associated with male defense of territories and females, and also reduces the potential for fitness loss due to polyandry that can occur in breeding aggregations where males directly compete for females (Zamudio et al. 2016).

Across all frogs, terrestrial breeding is a derived condition from an aquatic-breeding ancestor (Gao and Wang 2001; Wells 2010; Gomez-Mestre et al. 2012). Trends toward terrestrial breeding include increased independence from waterbodies for courting and breeding adults, for egg deposition, and for larval development (Duellman and Trueb 1994). The African *Phrynobatrachus* species (Zimkus et al. 2012), the Afro-Asian rhacophorids (Meegaskumbura et al. 2015), and the afrobatrachians (Portik and Blackburn 2016) all have aquatic basal lineages shifting toward more derived terrestrially reproducing species. In contrast, the South American *Pleurodema* and Leptodactylidae have evolved terrestrial breeding, but with reversals to more aquatic breeding modes (Heyer 1969; Faivovich et al. 2012; Pereira et al. 2015). Clearly, the overall trend toward terrestrial breeding across all anurans hides substantial diversity in the transitions between aquatic and terrestrial breeding in different frog lineages (Gomez-Mestre et al. 2012; Zamudio et al. 2016).

The South American species in the family Cycloramphidae have two reproductive modes. Saxicolous species in this clade breed and lay eggs in rock or root crevices at the margins of fast-flowing streams, commonly next to waterfalls (Giaretta and Cardoso 1995; Giaretta and Facure 2003). Males of saxicolous species are highly territorial; they mate within their territories and guard egg clutches that develop into semiterrestrial exotrophic tadpoles (Haddad and Sazima 1989; Giaretta and Cardoso 1995; Giaretta and Facure 2003; Verdade 2005). In contrast, terrestrial species mate and lay eggs under trunks or inside constructed burrows in leaf-litter of forest floors. Therefore, mating and oviposition for terrestrial species is concealed, and males and females

tend the eggs, which hatch into terrestrial endotrophic tadpoles that complete development on land (Heyer and Crombie 1979; McDiarmid and Altig 1999; Verdade 2005; Brasileiro et al. 2007; Zocca et al. 2014).

Previous phylogenetic studies have found that the 30 species in the genera *Cycloramphus* and *Zachaenus* are monophyletic (family Cycloramphidae; Verdade 2005; Fouquet et al. 2013; Faivovich et al. 2014; Grant et al. 2017). As in other clades, cycloramphid species with different reproductive modes have different body shapes and sizes (Verdade 2005; Blackburn et al. 2013), yet we do not know whether the specific selective forces acting on these traits are driven by natural selection imposed by new environments, sexual selection on one or both sexes, or both. Shifts in reproductive habitat include changes in environmental conditions, which might select directly for differences in body size. For example, the increased risk of desiccation could select for larger body sizes for water conservation (Nevo 1973; Gouveia and Correia 2016; Gouveia et al. 2019) or locomotion and exploitation of leaf-litter habitats could select for smaller body sizes (Lehr and Coloma 2008; Lehr and Catenazzi 2009; Kraus 2010, 2011). These selective pressures should be similar for males and females, thus we predict that if these mechanisms are at work, size will vary equally in both sexes. In contrast, intraspecific social interactions also potentially act as strong selective forces, shaping behaviors and morphology (West-Eberhard 1983). Males of saxicolous species benefit from large sizes due to the need to defend resources and exclude competing males in exposed environments (Lutz 1947; Giaretta and Cardoso 1995; Giaretta and Facure 2003). Terrestrially breeding male frogs will likely experience less male-male competition, primarily because breeding sites in leaf-litter are broadly available, and terrestrial breeding conceals mating behaviors, amplexus, and egg-laying (Verdade 2005; Zamudio et al. 2016). Thus, if sexual selection favors smaller males in terrestrially breeding species, we expect stronger sex-specific selection resulting in smaller males, more change in body size in males than in females, and an increase in sexual size dimorphism (SSD).

Here, we reconstructed the evolutionary history of reproductive mode, male and female body size, and SSD in the *Cycloramphus-Zachaenus* frog clade. We inferred a multilocus molecular phylogeny and used it to map reproductive and body size traits. We used comparative analyses to test hypotheses about the evolutionary forces behind this reproductive diversification, and explored the potential selective drivers for the evolution of terrestriality. Specifically, we tested three hypotheses: (1) terrestriality evolved only once in this clade, as indicated by an earlier morphological phylogeny (Verdade 2005); (2) both males and females vary in overall sizes according to reproductive habitats (Nevo 1973; Lehr and Coloma 2008; Lehr and Catenazzi 2009; Kraus 2010; Kraus 2011; Gouveia and Correia 2016; Gouveia

et al. 2019); and (3) males, but not females, decrease in size in terrestrial species because shifts to terrestriality impose lower sexual selection for large body sizes due to lower levels of male-male competition (Zamudio et al. 2016), and this in turn results in larger SSD in terrestrial species.

Materials and Methods
FOCAL TAXA AND SAMPLING
We gathered 86 tissue samples, including one to seven representatives of 25 of the 28 known *Cycloramphus* species and both of the *Zachaenus* species, totaling 90% of the currently recognized diversity in the clade. The completeness of our dataset is possible because of samples collected during expeditions in Brazil in the 1970s and 1980s; among them are samples from type localities and surroundings for a number of species that are currently declined or disappeared (Eterovick et al. 2005). Our genetic matrix only lacks *Cycloramphus catarinensis*, *Cycloramphus diringshofeni*, and *Cycloramphus duseni* for which tissues are unavailable in collections (Andersson 1914; Bokermann 1957; Heyer 1983; Lingnau et al. 2008). Based on previous studies (Frost et al. 2006; Grant et al. 2006; Fouquet et al. 2013; Jetz and Pyron 2018; Sabbag et al. 2018), we selected as out-groups *Thoropa lutzi* and *Thoropa taophora* (from the sister genus of the *Cycloramphus-Zachaenus* clade) and one species each from the genera *Crossodactylus*, *Hylodes*, and *Megaelosia* (family Hylodidae). We rooted our trees on *Paratelmatobius poecilogaster* (family Leptodactylidae). To ensure accurate taxonomic assignments for all species in our tree, whenever possible we selected representatives from type localities or their vicinity and checked external morphology of all vouchers (Table S1). Field research was approved by the committee on animal care use at Universidade Estadual Paulista, Rio Claro, Brazil.

MOLECULAR PROCEDURES
We extracted whole genomic DNA from ethanol-preserved tissues using a DNeasy Blood & Tissue kit (Qiagen Inc., Valencia, CA, USA) and following the manufacturer's protocol. Using published primers (Table 1), we PCR-amplified and sequenced three mitochondrial (*16S* [593 base pairs, bp], *Cytochrome-b* [635 bp], and *ND1* [1401 bp]) and four nuclear (α-*fibrinogen* [531 bp], *Cmyc* [410 bp], β-*crystallin* [475 bp], and β-*fibrinogen* [520 bp]) gene fragments. All PCRs were carried out in a final volume of 25 μL, each containing 1–10 ng DNA template, $1\times$ PCR Buffer (with 1.5–3 mM $MgCl_2$), $1\times$ BSA, 0.4 μM of forward and reverse primers, 0.76 mM dNTPs, and 0.625 units of Taq polymerase (Roche Diagnostics, Indianapolis, IN, USA). Amplification conditions included an initial denaturation at 94°C for 5 min, followed by 35–40 cycles of denaturation at 94°C for 1 min, annealing at

primer-specific temperatures from 48 to 60°C for 1 min (Table 1), extension at 72°C for 1 min, followed by a final extension at 72°C for 5–10 min. For all α-*fibrinogen* PCR amplicons (which have indels), and for any weak amplicons of *Cytochrome-b*, *ND1*, *Cmyc*, β-*crystallin*, and β-*fibrinogen*, we cloned PCR products using the TOPO TA cloning kit with PCR 2.1-TOPO TA vector (Life Technologies, Camarillo, CA, USA). We picked and amplified up to as many as 10 positive clones per amplicon using universal M13 primers and the same PCR conditions as above, but with an annealing time of 45 s (Table 1). We purified all final PCR amplicons using a cocktail of $1\times$ SAP buffer, SAP enzyme (1 unit; Life Technologies), and exonuclease I (10 units; Life Technologies). We sequenced the purified PCR products in both directions using BigDye terminator cycle sequencing (Applied Biosystems, Foster City, CA, USA) on an ABI 3730xl Genetic Analyzer (Applied Biosystems).

PHYLOGENETIC ANALYSES
We assembled all forward and reverse DNA sequences using Sequencher version 5 (Gene Codes Corporation, Ann Arbor, MI, USA) and aligned them using Clustal W implemented in Mega version 7 (Kumar et al. 2016). We coded all single polymorphic sites in heterozygous individuals with IUPAC ambiguity codes, and translated coding sequences to ensure reading frame conservation. We phased haplotypes via the probabilistic Bayesian algorithm PHASE (Stephens et al. 2001; Stephens and Donnelly 2003), implemented in DnaSP version 5 (Librado and Rozas 2009). We ran PHASE five times for each nuclear gene using distinct random seeds to check for consistency of haplotype reconstructions across runs. All specimens included in our phylogenetic analyses along with GenBank sequence accession numbers are listed in Table S1.

We determined the best partitions and the best models for each partition subset using the Akaike information criterion (AIC) in PartitionFinder version 2 (Lanfear et al. 2017). To check for stability of tree topologies, we performed maximum likelihood analyses in RAxML version 8 (Stamatakis 2014) testing distinct partitioning search algorithms (*greedy* and *rcluster*) and compared analyses obtained with only concatenated mitochondrial genes, with each nuclear gene separately, and with the final dataset combining all mitochondrial and nuclear genes. We inferred our final topology of species-level phylogenetic relationships within *Cycloramphus-Zachaenus* with Bayesian analysis and all genes concatenated. We used MrBayes version 3.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012) to perform two parallel runs with four chains each, adopting the Markov Chain Monte Carlo approach (MCMC). We ran analyses for 10,000,000 generations with sampling every 1,000 generations, resulting in 10,000 trees. We evaluated runs to ensure that all parameters had reached stationarity

Table 1. Mitochondrial and nuclear genes sequenced in this study with primer names, primer sequences, and specific PCR annealing temperatures.

Gene	Primer name	Sequence (5′–3′)	Annealing	Reference
16S	16Sa-L	CGCCTGTTTATCAAAAACAT	53°C	Palumbi et al. (1991)
	16Sb-H	CCGGTCTGAACTCAGATCACGT		Palumbi et al. (1991)
Cytochrome-b	MVZ15	GAACTAATGGCCCACACWWTACGNAA	48°C	Moritz et al. (1992)
	MVZ16	AAATAGGAARTATCAYTCTGGTTTRAT		Moritz et al. (1992)
ND1	16S-frog	TTACCCTRGGGATAACAGCGCAA	60°C	Wiens et al. (2005)
	16Sf (L2507)	CCCCGCCTGTTTACCAAAAA		Macey et al. (2001)
	ND1-int-ACA	ACGTGATCTGAGTTCAGACCG		Robertson and Zamudio (2009)
	tMet-frog	TTGGGGTATGGGCCCAAAAGCT		Wiens et al. (2005)
α-fibrinogen	MVZ47	AGTGAAAGATACAGTCACAGTGCTAGG	49–59°C	Bell et al. (2011)
	MVZ48	GGAGGATATCAGCACAGTCTAAAAAG		Bell et al. (2011)
Cmyc	cmyc1U	GAGGACATCTGGAARAARTT	57°C	Crawford (2003)
	Cmyc-ex2d R	TCATTCAATGGGTAAGGGAAGACC		Wiens et al. (2005)
β-crystallin	Cryb1Ls	CGCCTGATGTCTTTCCGCC	55°C	Dolman and Phillips (2004)
	Cryb2Ls	CCAATGAAGTTCTCTTTCTCAA		Dolman and Phillips (2004)
β-fibrinogen	Fib-b17U	GGAGAAAACAGGACAATGACAATTCAC	53°C	Prychitko and Moore (1997)
	Fib-b17L	TCCCCAGTAGTATCTGCCATTAGGGTT		Prychitko and Moore (1997)
M13	M13F	GTAAAACGACGGCCAG	54°C	Messing (1983)
	M13R	CAGGAAACAGCTATGAC		Messing (1983)

(average SD of split frequencies = 0.005585; average potential scale reduction factor (PSRF) = 1.000; maximum PSRF = 1.013). We discarded the first 25% of generations as burn-in and calculated a 50% majority rule consensus tree (Holder et al. 2008; Lamsdell et al. 2017) from the combined remaining trees from both runs. We checked for the SD of split frequencies between two runs (<0.01) and the effective sample size (ESS) in Tracer version 1.5 (Drummond and Rambaut 2007). We edited the tree using FigTree version 1.4 (Rambaut 2014).

PRUNING THE PHYLOGENETIC TREE

For phylogenetic signal, ancestral reconstruction, and correlated evolution analyses, we kept *Thoropa taophora*, but pruned all other out-groups from the final Bayesian tree. To select terminals retained in the pruned tree, we used currently recognized taxa. We selected one terminal per species or deeply divergent species lineages. When species included well-supported divergent lineages that were geographically separated (potentially indicative of cryptic or undescribed species), we retained independent lineages and collected morphological data specifically for those intraspecific lineages. In one particular case of a paraphyletic species (*Cycloramphus eleutherodactylus* relative to *Cycloramphus faustoi*), we opted to keep *C. faustoi* as a sister taxon of one lineage of *C. eleutherodactylus* because it is an insular species, and thus may show interesting patterns of body size evolution. We used the pruned phylogeny as the starting point for all downstream analyses.

ECOLOGICAL AND MORPHOLOGICAL TRAITS

To complete our phenotypic matrix, we supplemented our own collections of cycloramphid species in the field with data from museum collections. We visited six institutions: Célio F. B. Haddad amphibian collection, Universidade Estadual Paulista, Rio Claro, São Paulo (CFBH); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso," Campinas, São Paulo (ZUEC); Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (ZUFRJ); and National Museum of Natural History, Smithsonian Institute, Washington, DC (USNM). We measured the majority of cycloramphid material currently available in scientific collections. Our phenotypic matrix included data from a total of 960 specimens from 40 *Cycloramphus-Zachaenus* and one out-group species (*Thoropa taophora*). The only species missing in our morphological dataset was *Zachaenus carvalhoi*, for which we obtained body size measurements from the literature (Neto et al. 2016). For each specimen, we measured snout-vent length (SVL) of males and females, defined as the distance between the tip of the snout and the cloaca. We determined sex by checking for external inguinal macroglands present only in adult males and oocytes that are often visible through the skin in adult females. Because all species in the *Cycloramphus-Zachaenus* clade have female-biased SSD, we used a size dimorphism index that was the ratio of female to male body size (SDI: [female SVL/male SVL] – 1; Lovich and Gibbons 1992). Our final phenotypic data

matrix included reproductive habitat use (Verdade 2005), male and female body sizes, and SDI (Table S2).

ASSESSMENT OF PHYLOGENETIC SIGNAL

We investigated the extent to which our traits show phylogenetic signal in R version 3.3 (R Core Team 2016). We estimated phylogenetic signal by testing whether our data exhibit a significant tendency for related species to resemble each other under predictions of the Brownian motion model (Blomberg et al. 2003). For reproductive habitat (discrete trait: saxicolous or terrestrial), we used the R function *phylo.signal.disc* previously developed (Supporting Information 1), which corresponds to the "fixed tree, character randomly reshuffled" model (Maddison and Slatkin 1991). This algorithm estimates the minimum number of trait state transitions at each node assuming maximum parsimony, and compares those with median distributions from a randomized tip dataset. Observed transitions that are significantly less than the randomized median indicate significant phylogenetic signal in the data. For male and female body sizes, and SDI (continuous traits), we estimated Pagel's (1999) lambda and Blomberg's K (Blomberg et al. 2003) in PHYTOOLS (function *phylosig*; Ives et al. 2007; Revell 2012). Lambda varies from 0, indicating no phylogenetic signal, to 1, indicating strong phylogenetic signal. To evaluate whether lambda was significantly different than 0, we used a likelihood ratio test (LRT) using the R package NLME (functions *gls* and *pchisq*; Posten and Hallahan 1989; Pagel 1997; Pinheiro and Bates 2000; Freckleton et al. 2002). Values of Blomberg's K close to 1 suggest an evolutionary process under the Brownian motion model of evolution, indicating that trait similarity is proportional to divergence. A value of K > 1 indicates that traits are more similar and K < 1 indicates that traits are more different than expected by phylogenetic distance under a Brownian motion model.

ANCESTRAL STATE RECONSTRUCTIONS

To test hypotheses about the evolution of terrestriality in the *Cycloramphus-Zachaenus* clade, we reconstructed ancestral states for reproductive habitat (saxicolous or terrestrial), male and female body sizes, and SDI on our phylogeny.

For reproductive habitat, we first used the R package PHYTOOLS to reconstruct marginal ancestral states (functions *rerootingMethod* and *fitMk*; Paradis et al. 2004; Revell 2012), which consists of finding the maximum likelihood estimate at each node and integrating it over all other nodes (Yang et al. 1995). We ran this discrete state reconstruction under three distinct models: equal rates (ER), symmetrical rates, and all rates different model. Using LRT and AIC, ancestral reconstructions did not differ significantly among the three models (similar values), thus we selected ER as the simplest model for our data. Using stochastic character mapping (Bollback 2006), we estimated ancestral reproductive habitat states generating the probabilities of each node

with 1,000 iterations on our tree from the Bayesian phylogenetic reconstruction (function *make.simmap*; Huelsenbeck et al. 2003; Paradis et al. 2004; Bollback 2006; Revell 2012). To account for phylogenetic uncertainty, we repeated this final analysis step across 500 randomly selected trees from the posterior distribution.

For continuous traits (body sizes and SDI), we used different solutions for missing data. First, we removed the tips with missing morphological values from our tree (Portik and Blackburn 2016; Sauquet et al. 2017). Second, we kept our original tree and used the ancestral value for each missing taxon, assuming parsimonious change. Both analyses resulted in similar estimates; therefore, we report results of reconstructed ancestral states in the R package PHYTOOLS (function *anc.Bayes*; Revell 2012), removing tips with missing values, running an MCMC with 1,000,000 generations, and jointly finding the set of states at internal nodes. The first 200,000 generations were discarded as burn-in. For final character mapping of ancestral states on the phylogeny (model *fastAnc* implemented in function *contMap*; Felsenstein 1985; Revell 2012, 2013), we inferred tips with missing values, so that all taxa or lineages analyzed were represented.

PHYLOGENETIC COMPARATIVE ANALYSES

To test the hypotheses that body size traits in the *Cycloramphus-Zachaenus* clade are associated with saxicolous or terrestrial adult habitat use and to understand the directionality of evolution in these traits, we conducted phylogenetic comparative analyses. We implemented BayesTraits version 3 to document correlated evolutionary transitions of discrete traits (Pagel, 1994, 1999; Pagel et al. 2004; Pagel and Meade 2006). Because this analysis only tests for correlated evolution in pairs of dichotomous traits, we transformed continuous traits into categorical classes (Sauquet et al. 2017) using the midpoint for each body size or SDI range across all species. The midpoint of an interval is the lowest range plus the highest range divided by two. We classified species as "small" (when below the midpoint value for all tips) or "large" (when above the midpoint value for all tips). Likewise, we classified each SDI trait as "low" or "high" with a break at the midpoint for SDI values across all species. The thresholds for size class categories were 42.4 mm for species SVL; 44.1 mm for female SVL; 39.3 mm for male SVL; and 0.17 for SDI. We kept our original tree and for each missing taxon we used the ancestral value. For each pair of binary traits, there are four possible states and eight rate parameters (q_{ij}) that quantify the rate of change in traits, assuming that only a single change in one trait may occur instantaneously. The q_{ij} statistic represents the divergence between the observed and expected association of states i and j. The expected association is the product of the marginal probabilities of finding these states (i and j) at the same phylogenetic node (Huelsenbeck et al. 2003).

To control for phylogenetic uncertainty, we assessed transitions on 800 randomly selected trees from the Bayesian phylogeny. To test alternative evolutionary scenarios and describe how binary traits coevolved, we used reversible-jump MCMC (Pagel and Meade 2006), with independent, dependent, and covarion models (Tuffley and Steel 1998). For each model, we ran two independent chains of 1,000,000 generations, sampling every 1,000 generations. For calculating marginal likelihoods, we used stepping-stone sampling with 100 samples and 1,000 iterations per sample. We assessed convergence and verified that ESSs for all parameters were greater than 200 in Tracer version 1.5 (Drummond and Rambaut 2007). We also determined that acceptance rate values fell between 20% and 40%, which is expected under convergence. We compared marginal likelihoods to obtain the relative performance of the distinct models via Bayes factors (BF), using BF > 2 as positive evidence and BF > 5 as strong evidence, following the manual for BayesTraits version 3. For traits with evidence for the dependent models of evolution, we discarded the first 10,000 generations as burn-in and calculated mean rates of transition among trait states. We calculated the z-scores of trait transitions, expressed as percentage, from the proportion of occurrences of a value of zero estimated for relevant transition parameters (Pagel and Meade 2006). High z-scores indicate unlikely paths for evolutionarily correlated trait pairs.

First, we tested whether transitions between saxicolous and terrestrial breeding were correlated with changes in overall species body size (pooling females and males). We coded each species or lineage as "saxicolous" or "terrestrial" and transformed SVLs to the binary states of "small" or "large." Second, we repeated the test above separating each species or lineage by sex, separately coding females and males for each trait. When separated by sex, we considered phylogenies with all individuals included (inferring values for missing data). In the sex-specific analyses, we tested whether transition rates between small and large body sizes differed between saxicolous and terrestrial species, or vice versa, and whether those correlations were similar for both sexes. Finally, we coded each species or lineage as "saxicolous" or "terrestrial" and with low or high SDI to assess whether transitions in reproductive habitat were correlated with changes in SSD.

Results
PHYLOGENETIC RELATIONSHIPS
The concatenated multilocus matrix included all mitochondrial (*16S*, *Cytochrome-b*, and *ND1*) and nuclear genes (α-*fibrinogen*, *Cmyc*, β-*crystallin*, and β-*fibrinogen*). PartitionFinder selected 18 partitions across all mitochondrial and nuclear genes (Table S3). Our combined Bayesian tree recovered a monophyletic *Cycloramphus-Zachaenus* clade with high support for the majority of nodes. Our topology indicated that *Cycloramphus*

is paraphyletic and includes the genus *Zachaenus*, and thus *Zachaenus* should not be a separate genus (Fig. 1). We retain the original generic names, but taxonomic revision of this group is clearly necessary. Phylogenetic analyses of mitochondrial and nuclear genes independently yielded highly congruent topologies (Figs. S1–S5).

ASSESSMENT OF PHYLOGENETIC SIGNAL
Using our Bayesian phylogeny, excluding tips lacking trait data, we confirmed phylogenetic signal for most of our traits with high significance, indicating that it is necessary to consider phylogenetic relationships in our trait analyses (Revell 2010). We also performed the same analyses using the phylogenetic tree with inferred missing tip values and the results did not vary, thus we report results here using the fullest tree possible for each trait. For reproductive habitats, the observed transitions were significantly lower (= 3) than the randomized median transitions (= 14), indicating strong phylogenetic signal. For our continuous traits, we obtained values as follows: for overall species SVL, lambda = 0.99, LRT = 0.44, and K = 2.14; for female SVL, lambda = 0.99, LRT = 0.24, and K = 1.07; for male SVL, lambda = 0.99, LRT = 1, and K = 3.21; and for SDI, lambda = 0.96, LRT = 1, and K = 1.62. All lambda values suggest strong phylogenetic signal, but LRTs indicate that female SVL and overall species SVL follow a Brownian model of evolution. Blomberg's K results were >1 for all traits, indicating that closely related species and lineages are more similar than expected for all continuous traits, but male SVL had the largest K (3.21) and female SVL the smallest (1.07).

ANCESTRAL RECONSTRUCTIONS OF SPECIES HABITATS AND TRAITS
Our results show that reproductive modes are clustered, with terrestrial species grouping in several distinct clades that are derived from two saxicolous ancestral monophyletic groups. The reconstructed ancestor for the clade was saxicolous with overall relatively small body size (estimated overall species SVL = 31.23 mm), and very little difference between male and female body sizes (estimated female SVL = 43.39 mm, estimated male SVL = 43.71 mm, and estimated SDI = 0.095). From the saxicolous *Cycloramphus* ancestor, terrestriality evolved independently three times (Fig. 2) and male and female body sizes and SSD have increased and decreased in distinct lineages (Figs. 3–5).

EVOLUTIONARY CORRELATIONS BETWEEN SPECIES HABITATS AND TRAITS
We tested for correlated evolution in reproductive habitats and body sizes across all species using our phylogeny. For the three analyses of correlated trait evolution, we considered models that showed positive BF values, and at least one transition rate with
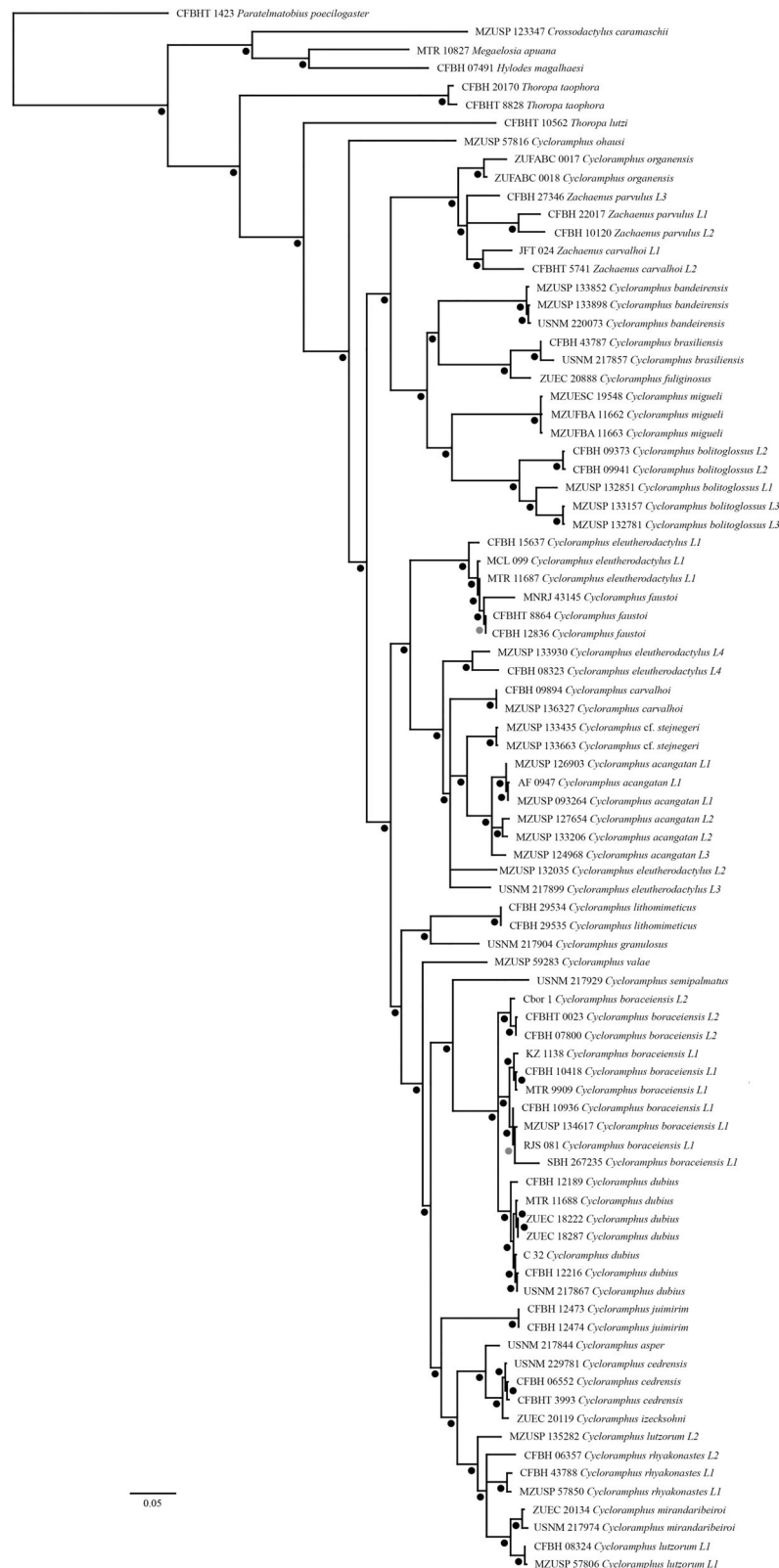
Figure 1. Bayesian multilocus-based phylogeny for 46 species or lineages of *Cycloramphus* and *Zachaenus* (40 study species and six outgroup species). *L1*, *L2*, *L3*, and *L4* indicate deeply divergent species lineages. Dots next to each node indicate Bayesian posterior probabilities (*PP*), with black dots indicating clades supported with *PP* > 90 and with gray dots indicating clades recovered with *PP* > 70. Nodes with *PP* < 50 are collapsed. This phylogeny was pruned to include named species and deeply divergent lineages for downstream comparative analyses.
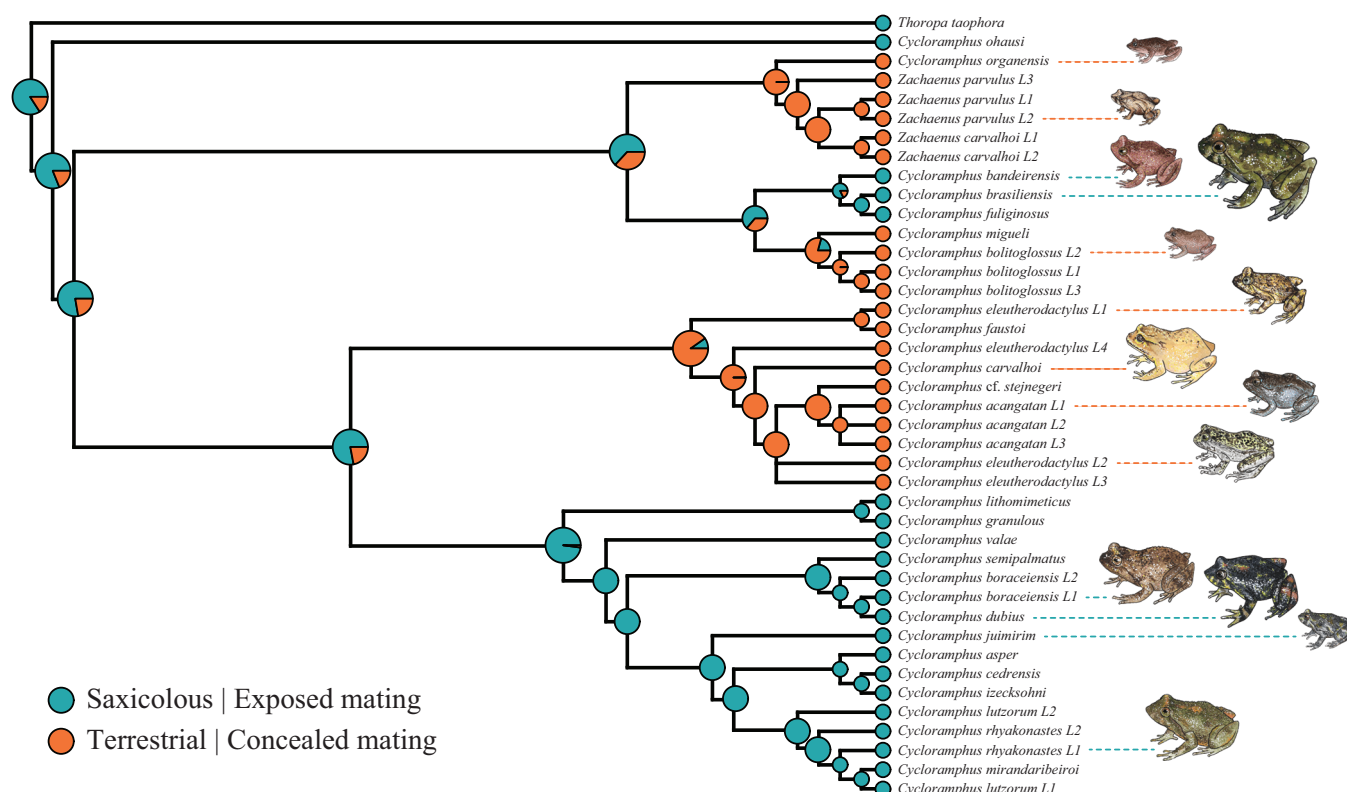
Figure 2. Reconstructed evolution of reproductive habitat in *Cycloramphus-Zachaenus* frogs. Saxicolous habitats are associated with exposed mating and terrestrial habitats are associated with concealed mating. *L1*, *L2*, *L3*, and *L4* indicate deeply divergent species lineages. This phylogeny was used as a starting point for all downstream comparative analyses.

a *z*-score <0.10, indicating that fewer than 10% of the iterations from the MCMC were assigned to zero for at least one transition rate. We found positive support for the dependent evolutionary model for all three body size traits (mean overall species, male, and female sizes) and for SDI with respect to reproductive mode (Table 2).

The results from dependent models of correlated evolution between overall species size (Fig. 6A), female size (Fig. 6B), and male size (Fig. 6C) showed different correlated transition rates with reproductive habitat. The pattern was the same for overall mean species size and female size. Significant transitions between body size and reproductive habitat only occurred in saxicolous species, and the transitions for those correlated phenotypes were approximately equal in both directions. For male body size, in addition to significantly higher transition rates in saxicolous species, we found an asymmetrically significant transition rate between terrestrial reproductive habitats and small size (Fig. 6C). These results indicate that in saxicolous species changes in male and female body sizes occur symmetrically, although the rates of change in males seem to be higher than in females (Fig. 6B, C). In contrast, in terrestrial species only changes in male size are significant, and evolved asymmetrically, toward smaller males. Finally, in the analyses of SDI and reproductive habitat (Fig. 6D),

we found significant evolutionary correlations for SDI and reproductive habitat across saxicolous and terrestrial species in the phylogeny. From the ancestral state (saxicolous and with low SDI), we found significant transitions in the evolutionary progression of these two correlated traits. Saxicolous species vary significantly in SDI, with a much higher transition rate toward lower SDI (males increasing in size and becoming closer to females in size). High SDI (when males are much smaller than females) is significantly correlated with transitions to terrestrial habitats ($q24$). Terrestrial species vary significantly in SDI with equal rates in both directions (low and high SDI). Combined, the analyses of body size and SDI show that SDI changes in a correlated manner with reproductive habitat, but that it is changes in male size that are primarily contributing to differences in sexual dimorphism.

Discussion
REPEATED EVOLUTION OF TERRESTRIALITY IN CYCLORAMPHIDS

Our phylogenetic reconstruction recovered several independent shifts to terrestrial breeding in the *Cycloramphus-Zachaenus* clade. This result rejects the hypothesis that terrestrial breeding evolved once (Verdade 2005) and lends support to adaptive
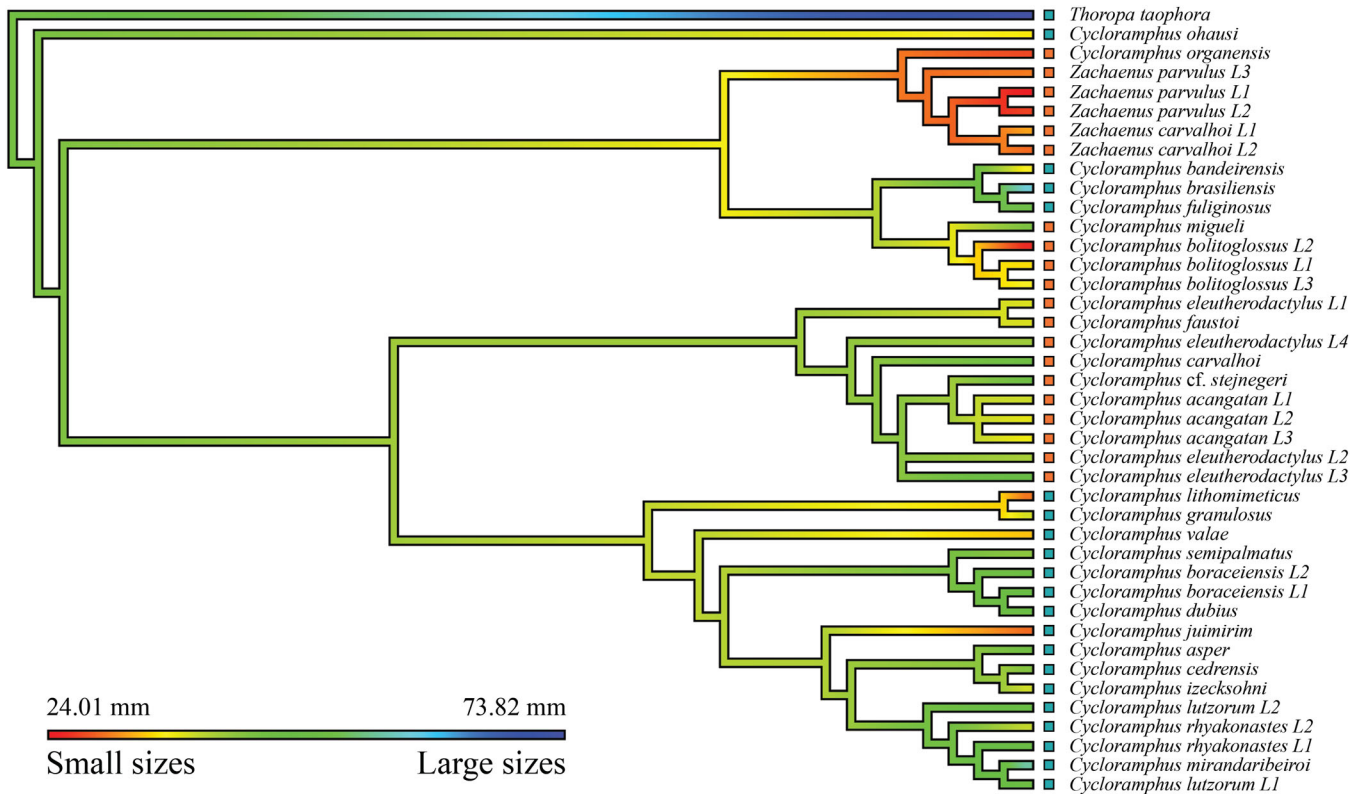
Figure 3. Reconstructed evolution of overall species body sizes in *Cycloramphus-Zachaenus* frogs. Blue squares and orange squares indicate saxicolous habitats (exposed mating) and terrestrial habitats (concealed mating), respectively. *L1*, *L2*, *L3*, and *L4* indicate deeply divergent species lineages.
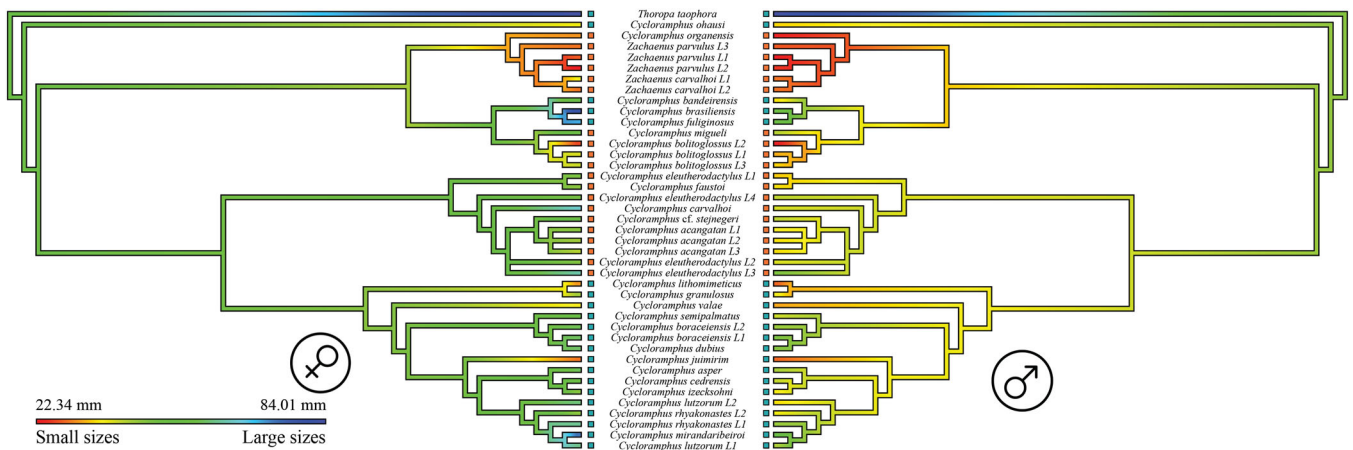

Figure 4. Reconstructed evolution of female (♀) and male (♂) body sizes in *Cycloramphus-Zachaenus* frogs. Blue squares and orange squares indicate saxicolous habitats (exposed mating) and terrestrial habitats (concealed mating), respectively. *L1*, *L2*, *L3*, and *L4* indicate deeply divergent species lineages.

convergence as a mechanism for phenotypic similarities among distinct terrestrial species groups. Novel environments increase both niche availability (which allows for persistence of invading populations) and niche discordance (which generates diversified selection) and thus provide ecological opportunity (sensu Wellborn and Langerhans 2015) for diversifying species and lineages. The rocky fast-flowing streams within forested habitats that are recovered as the ancestral habitat for cycloramphids are surrounded by thick and highly humid leaf-litter on the forest floors, which is an abundant and available niche with ideal conditions for terrestrial egg deposition (Lutz 1947; Zocca et al. 2014). Our data show that this ecological opportunity has
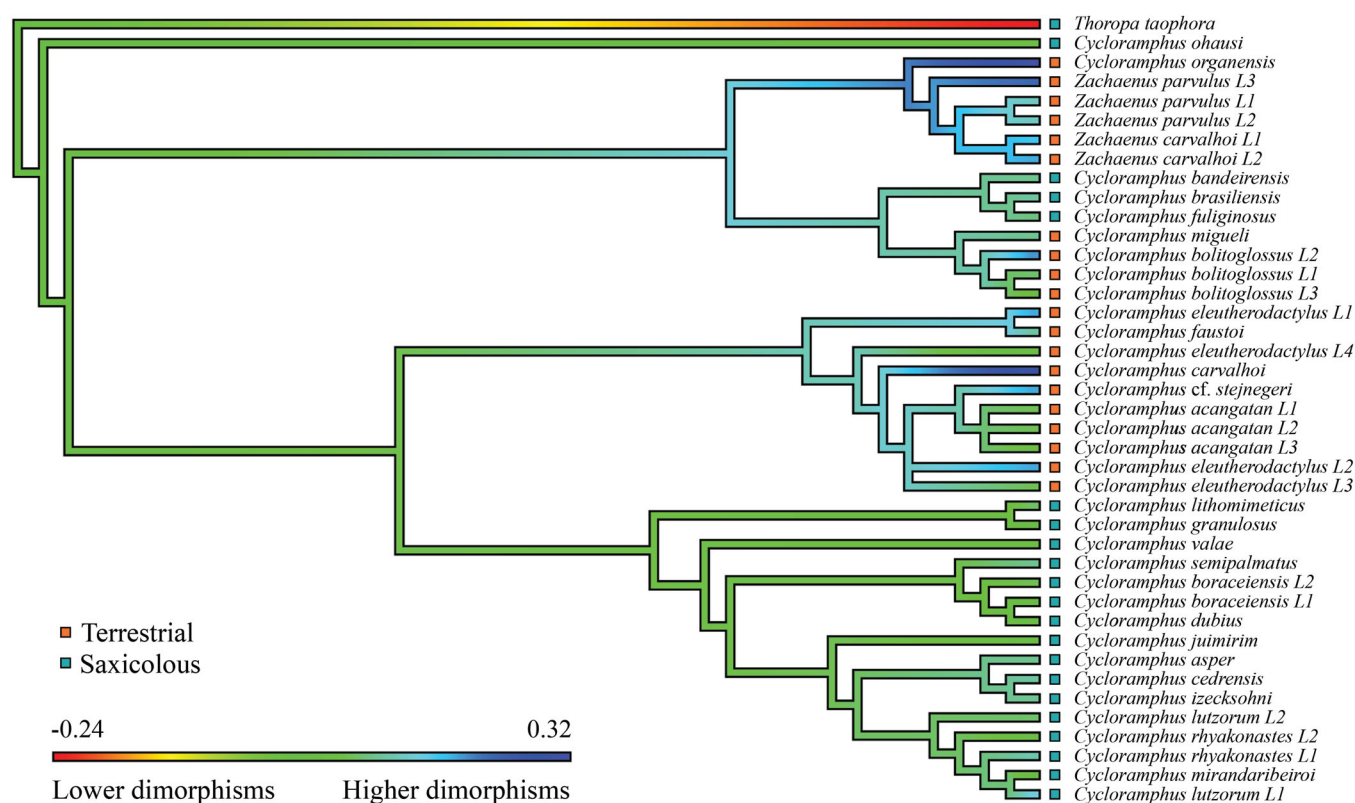
Figure 5. Reconstructed evolution of sexual size dimorphism (SSD) in *Cycloramphus-Zachaenus* frogs on the pruned tree. Blue squares and orange squares indicate saxicolous habitats (exposed mating) and terrestrial habitats (concealed mating), respectively. SSD was quantified by the sexual dimorphism index (SDI) with lower and higher indices indicating lower and higher divergences in sizes between conspecific males and females. *L1*, *L2*, *L3*, and *L4* indicate deeply divergent species lineages.

repeatably stimulated divergence, with the invasion of terrestrial habitats resulting in coordinated changes in phenotypes (Losos et al. 1997; McCracken et al. 1999; Ben-Moshe et al. 2001; Webster and Dawson 2004; Wellborn and Langerhans 2015). These repeated habitat invasions allow us to explore the mode of selection on the species in each of those invasions and whether those targets were the same in each case.

SIZE DIMORPHISM AND HABITAT TRANSITIONS IN CYCLORAMPHIDS

For cycloramphids, overall species body sizes are not clustered by reproductive mode, as both saxicolous and terrestrial species show high variances in male and female body sizes (Table S2; Figs. 3 and 4). This result rejects the hypothesis that both males and females vary in overall sizes according to reproductive habitats purely due to natural selection on both sexes imposed by environmental factors. The alternative explanation for changes in SSD with reproductive mode is that the sexes are under independent selection for body sizes, and that the selective mechanisms are sex specific. All species in the clade show female-biased SSD. The predominant explanation for female-biased SSD in frogs is strong fecundity selection with larger females having fitness

advantages due to larger clutch sizes (Shine 1979; Lüddecke 2002; Pupin et al. 2010). This selective advantage likely underlies the consistently larger sizes in cycloramphid females (Table S2). In contrast, we found more evolutionary change in males than in females with transitions to novel reproductive habitats, specifically, males become smaller with transitions to terrestrial breeding. These different changes in male and female body sizes result in consistent changes in SSD, with the largest differences in body sizes between the sexes always associated with terrestrial habitats (Fig. 5). Our analyses of correlated evolution confirm that evolutionary patterns for males and females are distinct. First, saxicolous males transition between small and large sizes in both directions at approximately doubled rates (compared to saxicolous females, Fig. 6B, C). Second, we found that terrestriality is correlated with smaller body sizes in males, but not females. Last, correlations between SSD and reproductive mode show that shifts from saxicolous toward terrestrial niches are associated with increases in SSD, primarily due to decreases in male sizes in terrestrially breeding species. Combined, trait mapping, phylogenetic signal, and correlated trait evolution analyses validate our hypothesis that males are the sex that primarily changes size with the shifts in reproductive modes. Given the biology of our focal

Table 2. Transition rate models and marginal likelihoods (estimated in BayesTraits and expressed on a natural log scale) were used to select models with stronger support for trait correlations based on Bayes factors.

Traits correlation, model	Independent	Dependent	Covarion
Reproductive mode vs. SVL	–42.859	–41.741[†]	–40.046
Reproductive mode vs. female SVL	–42.892	–41.529[†]	–39.952
Reproductive mode vs. male SVL	–43.943	–42.859[†]	–41.177
Reproductive mode vs. SDI	–40.708	–37.130[‡]	–36.114

SVL=snout-vent length.

[†]Best models for trait correlations, with positive evidence based on Bayes factors (BF > 2).

[‡]Best model for trait correlations, with strong evidence based on Bayes factors (BF > 5).

species, we propose that sexual selection, specifically male-male competition, is driving larger male body sizes in saxicolous species and that selection for large body size is relaxed with transitions to terrestrial breeding, when males no longer maintain territories.

BREEDING RESOURCES AND MALE-MALE COMPETITION IN CYCLORAMPHIDS

Body size is an important trait for intrasexual competition among male frogs, with larger individuals commonly having fitness advantages due to enhanced capacity for territorial defense and in some cases protection of offspring (Wilbur et al. 1978; Bateson 1983; Bourne et al. 2001; Ospina-L. et al. 2017). Typically, limited availability of breeding resources and the degree to which they are monopolizable result in mating systems that rely on male competition and higher degrees of intrasexual aggression (Emlen and Oring 1977; Howard 1978; Vonk and Shakelford 2017). Thus, sex-specific responses to the characteristics of the habitat can promote sexually dimorphic traits, with distinct reproductive roles yielding distinct selective regimes for each sex (Fairbairn 1997; Blanckenhorn 2000; Fairbairn et al. 2007).

Data on behavior and natural history for *Cycloramphus* and *Zachaenus* are difficult to obtain, especially for the terrestrial species that are cryptic and conceal mating behaviors in nests (Verdade 2005; Lingnau et al. 2008; Weber et al. 2011; Nunes-de-Almeida et al. 2016). Overall, we know that saxicolous males are highly territorial, discouraging intruders by emitting aggres-

sive calls, and repelling conspecific males that invade their breeding sites by biting and pushing them away (Lutz 1947; Giaretta and Cardoso 1995; Giaretta and Facure 2003). In some saxicolous species, males guard clutches (Giaretta and Cardoso 1995; Giaretta and Facure 2003). Terrestrially breeding males also show aggressive behaviors toward conspecifics and allospecifics (Neto et al. 2016), and we know that in some terrestrial species both males and females guard their clutches against intruders (Heyer and Crombie 1979; Verdade 2005; Brasileiro et al. 2007; Zocca et al. 2014). However, territorial and guarding behaviors between saxicolous and terrestrial cycloramphids are very different, primarily due to the degree of exposure of their breeding sites.

Saxicolous *Cycloramphus* have eggs, larvae, and mating behaviors that are exposed to conspecific male competitors (Giaretta and Cardoso 1995; Giaretta and Facure 2003; Verdade 2005; Maia-Carneiro et al. 2012), a condition that was likely shared by their common ancestor. Saxicolous environments are not only more exposed but offer limited suitable egg-laying sites in splash zones in the vicinity of waterfalls (Haddad and Sazima 1989; Giaretta and Cardoso 1995; Lima et al. 2010; Silva and Ouvernay 2012). This resource limitation leads to intense competition for egg-laying sites and presumably favors larger males that have an advantage in antagonistic interactions. In the saxicolous genus *Thoropa*, the sister taxon of the *Cycloramphus* clade (Frost et al. 2006; Grant et al. 2006; Fouquet et al. 2013; Jetz and Pyron 2018; Sabbag et al. 2018), the intensity of male-male competition has been well characterized. *Thoropa taophora* has a polygynous mating system associated with scarce breeding seeps and high levels of male-male competition (Muralidhar et al. 2014), and monopolist males exhibit paternal care of eggs and protect them against cannibalism by conspecific males (Giaretta and Facure 2004; Consolmagno et al. 2016). They discourage intruders using many of the same behaviors known for saxicolous *Cycloramphus* and use spines on their thumbs in male-male agonistic interactions (Bokermann 1965; Giaretta and Facure 2004; Muralidhar et al. 2014). In cases of extreme limitation in breeding resources, we expect intense selection for larger males, and consequently a decrease in dimorphism. Moreover, elevated levels of aggression in species where males defend territories often also select for sexual dimorphism in weaponry (Emlen 2008), which is observed in males of all *Thoropa* species as enlarged forearms and thumb spines (Bokermann 1965; Caramaschi and Sazima 1984; Cocroft and Heyer 1988; Feio et al. 2006). Similar weaponry is present in males and females of *Cycloramphus ohausi* (Heyer 1983), a species that has intermediate female-biased SSD and is the first species to diverge in the *Cycloramphus* clade. Jaw adductor musculature is also more developed in males and females of the terrestrial *Cycloramphus bolitoglossus* species group (Heyer 1983; Verdade and Rodrigues 2003) and might be associated
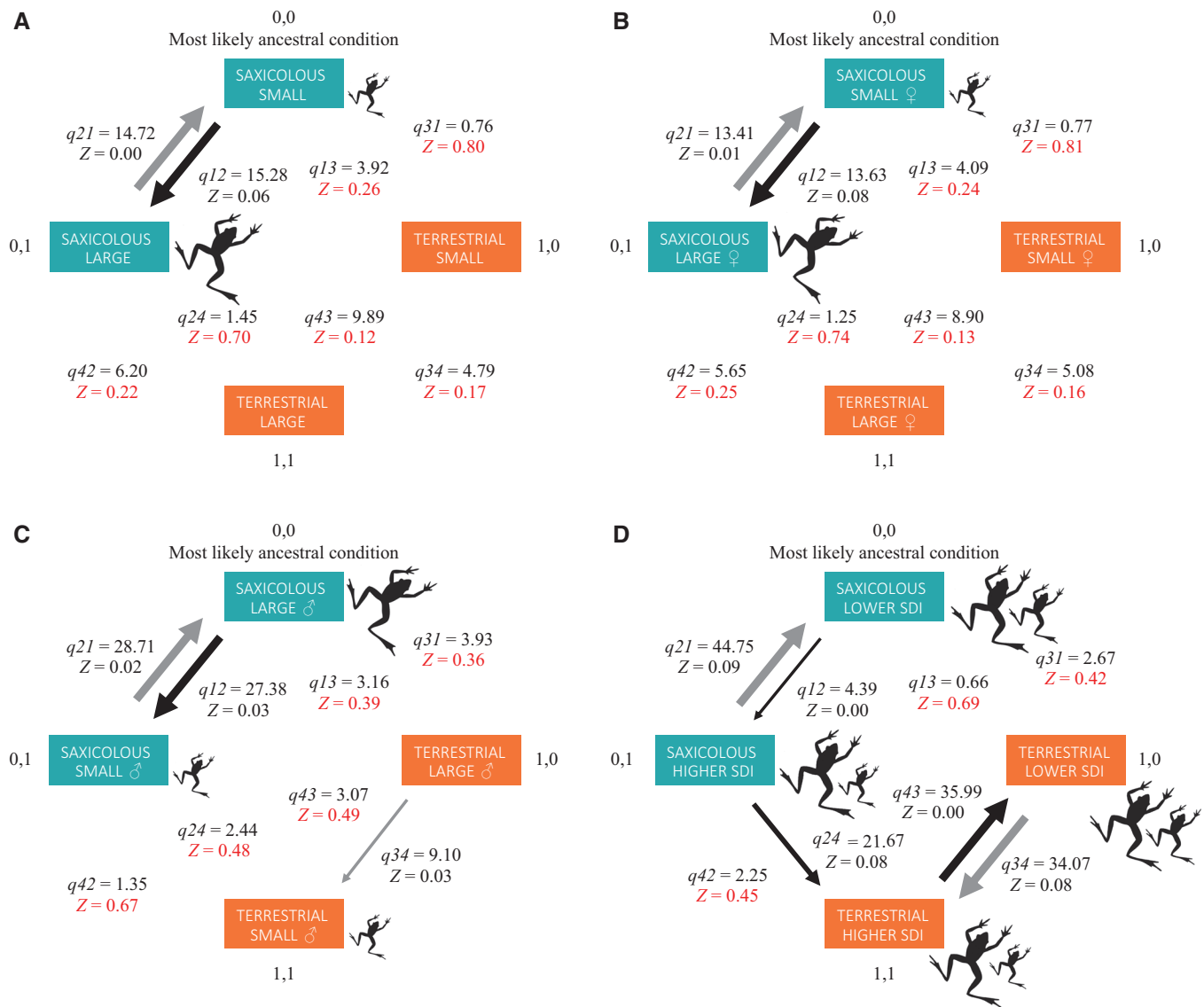
Figure 6. Evolutionary transitions across *Cycloramphus* and *Zachaenus* frog species. BayesTraits transitions for species reproductive habitats (saxicolous or terrestrial) and (A) overall species body sizes, (B) female body sizes, (C) male body sizes, and (D) sexual size dimorphism (SSD). SSD was quantified by the sexual dimorphism index (SDI), with lower and higher indices indicating lower and higher divergences in sizes between conspecific males and females. Arrow thickness is proportional to each transition rate between trait states. For each transition, we reported a *q*-value, representing the mean transition parameter, and a *Z*-value, the proportion of iterations that were assigned to zero (i.e., unlikely transitions). Low *Z*-values indicate more likely evolutionary transitions. Transitions are considered possible when $Z < 0.10$ (10% of the iterations are assigned to zero) or when the nonsignificant transition parameter (*q* value) is higher than that of the lowest parameter that yielded a significant transition. *Z*-values for nonsignificant transitions are shown in red.

to aggressive behaviors such as biting. Unfortunately, we lack natural history information for *Cycloramphus ohausi* and *Cycloramphus bolitoglossus* species, and specifically how these spines and jaw adductor musculature enhance male and female fitness. Spines are absent and jaw adductor musculature are less developed in males or females of all other cycloramphids, but variation in male-male competition associated with limited breeding resources has clearly been present over much of their evolutionary history.

Terrestrial *Cycloramphus* and *Zachaenus* lay eggs under trunks or inside constructed burrows in the leaf-litter on forest floors. They hatch endotrophic terrestrial tadpoles in advanced stages that use yolk to complete the development inside the nest; thus, terrestrial species have eggs, larvae, and mating behaviors that are concealed from conspecifics (Lutz 1947; Heyer and Crombie 1979; McDiarmid and Altig 1999; Verdade 2005; Brasileiro et al. 2007; Zocca et al. 2014). The leaf-litter environment not only allows concealment but also offers abundant suitable egg-laying

sites in humid forest floors. The broad availability of breeding sites likely reduces competition and agonistic male-male interactions among terrestrial cycloramphids.

SEXUAL SELECTION AND SEXUAL DIMORPHISM ACROSS FROGS

SSD is a composite character resulting from different selective pressures on the sexes (Carranza 2009). Many factors can affect male and female body sizes, making the analysis of SSD across larger taxonomic groups difficult (Fleagle and Mittermeier 1980; Fairbairn 1997; Blanckenhorn 2000; Fairbairn et al. 2007; Ospina-L. et al. 2017; Gouveia et al. 2019). Our data confirm some of the predictions from broader studies of SSD across all frogs and also provide information about the environmental and behavioral contexts that might explain the high variance and size dependence in selection on male and female sizes across mating systems (Nali et al. 2014). Across all frogs, the main selective pressure driving the predominance of female-biased SSD is female-fecundity (Shine 1979; Lüddecke 2002; Pupin et al. 2010), although the correlation between female size and SSD is most evident for species with smaller overall body size (Nali et al. 2014). Across all frogs, male size and SSD are also correlated, such that species with larger males show less-pronounced SSD, with males becoming closer to female sizes (Nali et al. 2014). However, the relationship between male size and SSD holds for both territorial and nonterritorial species, demonstrating that selection on territorial males does not contribute disproportionately to SSD, and that lineage-specific ecology and behavior could be masking the role of male size in studies of SSD evolution at larger phylogenetic scales (Nali et al. 2014). The lack of evidence for male-male competition as an important driver of SSD across all frogs is perhaps not surprising because male frogs have evolved a number of size-independent strategies that contribute to fitness. These include forearm thickness for male displacement, time at reproductive site, energy expenditure in calling activity, early sexual maturity, and alternative mating tactics (Howard and Kluge 1985; Haddad 1991; Howard et al. 1994; Prado and Haddad 2003; Vieites et al. 2004; Byrne 2008; Zhang and Lu 2013). Our analysis of the *Cycloramphus* clade allowed us to focus on social dynamics during breeding, which in our system are influenced by reproductive habitat. Analyses of a single clade with repeated reproductive transitions allowed us to examine how interactions during breeding impose selective mechanisms that differ between the sexes.

The importance of social dynamics during breeding has been highlighted in other taxa. Dale et al. (2007) argued that social mating system is a key life-history variable that predicts size allometry and SSD in birds because of differential selection on males and females. Likewise, habitat types have also influenced the evolution of male body size and SSD in turtles, in which terrestrial

males are proportionally larger than aquatic ones (Ceballos et al. 2013), likely because of territoriality and increased male-male interactions in terrestrial species. In *Cycloramphus*, the clear distinction between territorial defense in saxicolous males and lack thereof in terrestrial ones permits a lineage-specific comparison of species that repeatedly and consistently differ in ecology and behavior, and underscores the importance of habitat transitions for differential selection on males and females.

The long-standing hypothesis for transitions to terrestrial breeding in frogs is the "predator-avoidance" hypothesis, which posits that the selective advantage of moving eggs and/or larvae out of water bodies drives the evolution of more terrestrial reproductive modes, especially in tropical regions with adequate temperature and humidity conditions for the development of anamniote eggs on land (Goin and Goin 1962; Wells 2010; Gomez-Mestre et al. 2012). Our analyses indicate that predator avoidance may not be the only driver of the highly diverse reproductive modes observed in tropical frogs (Haddad and Prado 2005; Verdade 2005; Zamudio et al. 2016). Although avoidance of aquatic predators may be important in some cases, in lineages with high degrees of male-male competition and high costs of territoriality, an equally important selective force may be avoidance of those costs. The multiple transitions to terrestrial reproductive modes observed in frogs, and in amphibians more generally, likely also involve aspects of the social context in which breeding occurs, and the potential fitness benefits of avoiding the costs associated with intraspecific competition.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA ARCHIVING

GenBank accession numbers are provided in Table S1. All other data are avilable in the text and Supporting files.

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Supporting Information

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

Table S1. Specimens included in our phylogenetic analyses along with GenBank sequence accession numbers.

Table S2. Summary of phenotypic data matrix including female and male body sizes, sexual size dimorphism, reproductive habitat use, and sampled localities grouped by species and lineage.

Table S3. Models selected for the optimal partitioning strategy obtained across all mitochondrial and nuclear genes.

Figure S1. *Cycloramphus clade* maximum likelihood tree reconstructed with concatenated mitochondrial genes (*16S*, *Cytochrome-b*, and *ND1*).

Figure S2. *Cycloramphus* clade maximum likelihood tree reconstructed with the nuclear gene α-*fibrinogen*.

Figure S3. *Cycloramphus* clade maximum likelihood tree reconstructed with the nuclear gene *Cmyc*.

Figure S4. *Cycloramphus* clade maximum likelihood tree reconstructed with the nuclear gene β-*crystallin*.

Figure S5. *Cycloramphus* clade maximum likelihood tree reconstructed with the nuclear gene β-*fibrinogen*.