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NELSON RODRIGUES DA SILVA

Aspectos da biologia reprodutiva de *Dendropsophus haddadi* (Anura: Hylidae) e a influência dos locais de oviposição no dimorfismo sexual e fecundidade em anuros

Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, como requisito para obtenção do grau de Doutor em CIÊNCIAS BIOLÓGICAS com ênfase em Biodiversidade.

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Nelson Rodrigues da Silva

Modos reprodutivos em anuros: Modos arborícolas e suas implicações

Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Doutor em CIÊNCIAS BIOLÓGICAS na área da Biodiversidade.

Tese aprovada em 03 de junho de 2020.

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Junho/ 2020

DEDICATÓRIA

Dedico esta tese aos meus pais, Genésio Rodrigues da Silva e Olga Maria Rodrigues, aos meus irmãos Marcelo, Maurício, Márcio e Nilson, às minhas sobrinhas Clarinha. Mariana, Marcela, Flávia, Lívia, Milena e Gyovanna, e aos meus sobrinhos, Tales, Túlio, Vinicius e Benício. E a inspiradora Mary Jane (litle).

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RESUMO

Os anfíbios anuros apresentam uma grande diversidade de modos reprodutivos. Os comportamentos de ovipositar na água ou na terra envolvem diferentes adaptações e a terrestrialidade evoluiu no grupo de forma independente. Diferenças morfológicas entre machos e fêmeas e a fecundidade das fêmeas são características importantes ligadas aos modos reprodutivos. Porém, para muitas espécies não há dados básicos sobre biologia, dificultando estudos em ecologia e evolução de anuros. Deste modo, esta tese teve como objetivos estudar a biologia de uma espécie com modo reprodutivo arborícola, bem como investigar a inter-relação entre modos arborícolas, fecundidade e o dimorfismo sexual em anuros. No primeiro capítulo descrevemos a biologia reprodutiva de *Dendropsophus haddadi*, um anuro endêmico da Mata Atlântica. Duas populações foram estudadas em Maceió, Alagoas, nordeste do Brasil. Os indivíduos foram observados a uma altura média de 3-5 m na vegetação à beira de corpos d´água temporários. Os machos foram territoriais, emitiram cantos, sinais visuais e se envolveram em combates físicos. As desovas foram encontradas sobre troncos, folhas e galhos acima da água. O número de ovos correlacionou-se positivamente com o tamanho da desova e nossas observações sugerem que, na ausência de chuvas, as fêmeas podem proteger os ovos contra dessecação, juntando os ovos logo após a oviposição. Essa forma de cuidado parental é uma novidade para o gênero. O dimorfismo sexual em tamanho (SSD) resulta de pressões de seleção natural e sexual em ambos os sexos e a fecundidade é uma importante pressão seletiva sobre tamanho das fêmeas. Logo, no segundo capítulo, investigamos a influência dos diferentes locais de desova sobre o SSD e fecundidade das fêmeas em Anura e na família Hylidae. Analisamos 385 espécies de anuros (32 famílias) com desovas aquáticas (271), arborícolas (48), terrestres escondidas (35) e terrestres expostas (31). Para Hylidae, analisamos 221 espécies, sendo 175 com modos aquáticos, 30 arborícolas e 16 com desovas escondidas. O SSD médio não variou entre os locais de oviposição; em geral, os machos foram ca. 20% menores que as fêmeas, o que pode estar relacionado com a justaposição cloacal e o sucesso de fertilização. No entanto, em espécies com oviposição em locais escondidos, machos e fêmeas tenderam a ter tamanhos corporais semelhantes, o que poderia ser explicado por restrições ao tamanho das fêmeas devido à limitação de espaço para casais em amplexo. Também testamos a hipótese de que fêmeas com reprodução arborícola podem sofrer restrições ao aumento da fecundidade para compensar os custos impostos pelo transporte de machos em amplexo. No geral, a fecundidade foi menor nas espécies arborícolas comparada com a das aquáticas. No entanto, em hilídeos, a fecundidade tendeu a ser menor em espécies arborícolas quando comparada a todos os outros locais de oviposição, o que sugere que a arborealidade pode impor restrições à fecundidade. Nossos resultados para Anura e Hylidae mostraram a complexa interação entre locais de oviposição, fecundidade e SSD. Sugerimos que o microhabitat reprodutivo também possa influenciar o tamanho do corpo e a fecundidade das fêmeas. Portanto, o grau e a direção do SSD nos anuros pode ser o resultado dessa complexa combinação de processos evolutivos atuando em diferentes escalas evolutivas.

Palavras-chave: Amphibia, comportamento reprodutivo, Mata Atlântica, tamanho do corpo, seleção sexual, seleção natural.

ABSTRACT

Anuran amphibians exhibit a great diversity of reproductive modes. The behaviors of laying eggs in the water or on terrestrial habitats involve different adaptations and terrestriality evolved independently in the group. Morphological differences between males and females and female fecundity are important traits related to the reproductive modes. However, basic information on biology is not available for many species, hampering studies on ecology and evolution of anurans. Thus, the aims of this thesis were to study the biology of one species with arboreal reproductive mode and investigate the interplay among arboreal modes, fecundity and sexual dimorphism in anurans. In the first chapter, we describe the reproductive biology of *Dendropsophus haddadi*, a species endemic to the Atlantic forest. Two populations were studied in Maceió, Alagoas state, northeastern Brazil. Individuals were observed perched on the vegetation, approximately 3-5 m high, at the margins of temporary water bodies. Males were territorial, emitted calls, visual signs, and engaged in fights. Clutches were found on trunks, leaves and twigs above the water. Number of eggs was positively correlated with clutch size and our observations suggest that, in the absence of rains, females may protect the eggs against desiccation by joining them right after oviposition. This form of parental care is a novelty for the genus. Sexual size dimorphism (SSD) results from natural and sexual selection pressures on both sexes and fecundity is an important selective pressure on female size. Thus, in the second chapter, we investigated the influence of the oviposition site on SSD and female fecundity in Anura and in the Hylidae family. We analyzed 385 anuran species (32 families) exhibiting aquatic (271), arboreal (48), terrestrail hidden (35), and terrestrail exposed (31) clutches. For Hylidae, we analyzed 221 species with aquatic (175), arboreal (30) and hidden (16) clutches. Mean SSD did not vary among species with different oviposition sites; in general, males were ca. 20% smaller than females, what could be related to cloacal juxtaposition and fertilization success. Nonetheless, in species with hidden clutches, males and females tended to have similar body sizes, what could be explained by restrictions to female size increase because of space limitation to amplectant pairs. We also tested the hypothesis that females with arboreal clutches may suffer restrictions to fecundity increase to offset the costs of carrying amplectan males. In general, fecundity was smaller in arboreal breeders compared to that of aquatic breeders. However, in hylids, fecundity tended to be smaller in arboreal breeders compared to all other oviposition sites, what suggests that arboreality may restrict female fecundity increase. Our findings for Anura and Hylidae showed the complex relationship among oviposition site, fecundity and SSD in frogs, suggesting that the reproductive microhabitat may also influence female size and fecundity. Thus, degree and direction of SSD in anurans may result from complex mechanisms operating at different evolutionary scales.

Keywords: Amphibia, reproductive behaviour, Atlantic Forest, body size, sexual selection, natural selection.

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SUMÁRIO

1 APRESENTAÇÃO

Os anfíbios anuros apresentam uma diversidade ímpar de modos reprodutivos (~50 modos reprodutivos; e.g. HADDAD; PRADO, 2005; GURURAJA et al., 2014; ISKANDAR; EVANS; MCGUIRE, 2014; KUSRINI et al., 2015). A oviposição na água (considerado ancestral) ou em ambiente terrestre (estado derivado) são adaptações reprodutivas diferentes selecionadas ao longo da evolução que ocorreu de forma não linear (GOMEZ-MESTRE; PYRON; WIENS, 2012). Na desova aquática, geralmente são muitos ovos pequenos, com grande suscetibilidade a predadores aquáticos, porém sem o risco de dessecação (LUTZ, 1948; TOUCHON; WARKENTIM, 2008). No ambiente terrestre, por outro lado, os ovos são geralmente maiores e em menor número e apresentam uma camada protetora mais espessa para diminuir a dessecação (LUTZ, 1948). As adaptações para a oviposição terrestre ocorreram independentemente ao longo da história evolutiva dos anfíbios anuros e saber quais pressões e *trade-offs* estão envolvidos com este comportamento é um grande desafio (CRUMP, 2015; ZAMUDIO et al., 2016). A reconstrução filogenética de traços ancestrais, funcionalmente ligados ao desenvolvimento dos ovos aquáticos e terrestres auxilia no entendimento da evolução dos modos reprodutivos, mas geralmente estas análises são limitadas, pois há uma carência de dados sobre a biologia reprodutiva e de detalhes sobre os modos reprodutivos das espécies de anuros. De fato, atualmente, ainda faltam informações para um grande número de espécies.

A presente tese foi dividida em dois capítulos. O primeiro capítulo apresenta aspectos da biologia reprodutiva da perereca *Dendropsophus haddadi*, uma espécie endêmica da Mata Atlântica encontrada nos pequenos fragmentos florestais existentes nos estados de Alagoas, Bahia, Espírito Santo e Pernambuco (ARAÚJO-NETO et al., 2012). A grande maioria das 108 espécies do gênero *Dendropsophus* (FROST, 2020) possui modo reprodutivo aquático, mas algumas espécies depositam ovos em ambientes terrestres. Porém, detalhes da biologia reprodutiva são desconhecidos para muitas das espécies. Desta forma, informações sobre o comportamento reprodutivo de machos e fêmeas, locais da desova, número e tamanho de ovos e das desovas e tempo de desenvolvimento dos embriões foram obtidos para duas populações de Maceió, estado de Alagoas, Brasil, e são aqui descritos.

O segundo capítulo é uma análise de como os locais de oviposição (aquático, terrestre, arborícola, escondido) podem afetar o grau de dimorfismo sexual e a fecundidade em anuros, com especial enfoque nos modos reprodutivos arborícolas. As análises foram realizadas em duas escalas evolutivas: para Anura e para a família Hylidae. Dados sobre o local de oviposição, tamanho e número de ovos (fecundidade) e tamanho corporal de machos e fêmeas de anuros foram analisados utilizando uma abordagem filogenética comparativa.

2. REVISÃO DE LITERATURA

2.1 DA ÁGUA PARA O AMBIENTE TERRESTRE: DESAFIOS E OPORTUNIDADES

Os vertebrados iniciaram a saída da água para os ambientes terrestres há aproximadamente 385–359 m.a., no período Devoniano (DAESCHLER; SHUBIN; JENKINS, 2006). A saída dos animais da água para a terra está diretamente relacionada a fatores bióticos e abióticos. Restrições de oxigênio, superpopulação e altos riscos de predação nos ambientes aquáticos foram determinantes para a passagem dos vertebrados dos ambientes aquáticos para o terrestre (CARROLL, 2009; CLACK, 2012; CLOUDSLEY-THOMPSON, 2012). Nos ambientes terrestres, em contraste, havia maior disponibilidade de alimentos (e.g. primeiros artrópodes), ambientes livres de competidores e ausência de predadores terrestres (GRAY; SHEAR, 1992). Entretanto, a força da gravidade na terra e as menores densidades, viscosidade, condutividade de calor, e condutividade de eletricidade, quando comparada com a água, foram desafios a serem enfrentados (POUGH; HEISER; MCFARLAND, 2003). Mudanças morfofisiológicas, comportamentais e ecológicas foram mandatórias para estes animais (SELDEN; EDWARDS, 1989; PISANI et al., 2004), e tais modificações incluem atributos da história de vida como fecundidade, taxa de crescimento, período de reprodução, entre outras (BRADSHAW, 1986; NIELSEN, 2012).

Dentre os vertebrados, algumas linhagens de peixes ósseos sarcopterígeos sofreram modificações em suas características morfológicas, fisiológicas e comportamentais, que resultaram também em alterações e adaptações no sistema tegumentar, locomotor, respiratório e sensorial (CLARK, 2007). Tais alterações permitiram que algumas linhagens iniciassem a exploração dos ambientes terrestres. Com essas modificações e adaptações graduais, surgiram animais com características intermediárias, capazes de explorar tanto ambientes aquáticos quanto os ambientes terrestres, como o *Tiktaalik roseae*, bem como os primeiros tetrápodes conhecidos (e.g. *Ichthyostega*, *Acanthostega*), os quais, apesar de serem ainda organismos predominantemente aquáticos, já possuíam características mais adaptadas aos ambientes terrestres (CLARK, 2012). Posteriormente, surgem os Temnospondyli (batracomorfos), grupo mais diversificado e com maiores adaptações para ocuparem os ambientes terrestres (CASTROVIEJO-FISHER et al., 2015).

Acredita-se que linhagens de Temnospondyli tenham dado origem aos Lissamphibia, que inclui as três ordens dos anfíbios viventes: Gymnophiona, que compreende as cecílias; Caudata, que compreende as salamandras e tritões; e Anura, que compreende os sapos, rãs e pererecas (CASTROVIEJO-FISHER et al., 2015). Apesar da linhagem irmã dos anfíbios ter surgido há cerca de 365 milhões de anos e da maioria das espécies serem consideradas terrestres, todos os anfíbios atuais são sensíveis à baixa umidade (apresentam maior dessecação quando comparados a outros vertebrados terrestres). Os anfíbios possuem a pele nua e adaptada à respiração cutânea, sendo muito permeável (maior tendência à perda de água e absorção de calor). A maioria dos anfíbios continua dependente de ambientes aquáticos ou úmidos para sua sobrevivência e reprodução (DUELLMAN; TRUEB, 1994; CARROLL, 2009; CLARK, 2012).

Dentre as 8.156 espécies atuais de anfíbios, os anuros somam quase 90% da diversidade (FROST, 2020). Na maioria das espécies de anuros, o ciclo de vida inclui um macho vocalizando para atrair a fêmea. A fêmea é atraída, o casal entra em amplexo, há a liberação dos gametas e a fertilização dos ovócitos é externa. A desova geralmente é aquática. Ocorre o desenvolvimento dos embriões que eclodem em larvas chamadas de girinos (geralmente aquática), que sofrem modificações extremas na sua morfofisiologia durante a metamorfose. Estes animais recém metamorfoseados (imagos) apresentam morfofisiologia de um animal adulto (geralmente terrestres). Apesar deste padrão geral, a reprodução dos anuros é extremamente diversificada, incluindo variações morfológicas, fisiológicas e comportamentais, provavelmente devido à capacidade de explorar ambientes aquáticos, terrestres e intermediários (CALDWELL, 1992; DUELLMAN; TRUEB, 1994; POUGH; HEISER; MCFARLAND, 2003).

Nos anfíbios anuros, dentre as principais adaptações para a ocupação do meio terrestre podemos citar as mudanças nos modos reprodutivos (ANGELINI; GHIARA, 1984; HADDAD; PRADO, 2005; CRUMP, 2015). Como mencionado, na maioria das espécies, a fecundação é externa em meio aquático: o macho abraça a fêmea, em um ritual de acasalamento chamado amplexo, e suas cloacas se justapõe. Os ovócitos são fertilizados externamente no ambiente aquático, após os gametas serem eliminados pelas cloacas (DUELLMAN; TRUEB, 1994). O amplexo traz uma vantagem, pois permite que a fecundação possa ocorrer também fora da água, uma vez que não depende mais da água para carregar e/ou unir os gametas (CLOUDSLEY-THOMPSON, 2012). Entretanto, os zigotos e embriões não são totalmente adaptados a sobreviver fora da água e o risco de dessecação é um grande desafio (CLOUDSLEY-THOMPSON, 2012). A membrana protetora dos ovos protege contra a perda ou a absorção de água e também pode proteger contra ataques de predadores (FOX; CSEZAK, 2000; TOUCHON, 2012), ainda assim, as desovas terrestres são dependentes de ambientes úmidos (HADDAD; PRADO, 2005). A postura dos ovos fora da água pode ser vantajosa, pois melhora a respiração do embrião (já que é um ambiente mais rico em oxigênio), evita que o ovo seja levado pela correnteza e pode diminuir riscos de predação de ovos/larvas (MAGNUSSON; HERO, 1991; TOUCHON; WARKENTIM, 2008).

2.2 MODOS REPRODUTIVOS EM ANUROS: ESTADO DA ARTE

Estudos pioneiros sobre a reprodução em anfíbios datam de 1730 (TERRALL, 2011; CRUMP, 2015). O pesquisador René-Antoine Ferchault de Re'aumur, por volta de 1730, fazia as primeiras pesquisas para saber como um ovo de anfíbio era fecundado (TERRALL, 2011; CRUMP, 2015). Ele observou o amplexo e acreditou que a fertilização pudesse ocorrer de três possíveis formas: 1) os dedos dos machos poderiam, através de uma abertura no peito das fêmeas, inserir os espermatozoides e fecundar os ovócitos, ou 2) os machos poderiam inserir os espermatozoides através da pele das fêmeas, ou 3) as glândulas peitorais masculinas poderiam fertilizar as fêmeas (ver CRUMP, 2015). Para verificar como ocorria a fecundação dos ovócitos em sapos, ele colocou uma calça nos sapos machos com a intenção de isolar a parte da cloaca (CRUMP, 2015). Apesar do esforço, Re´aumur não teve sucesso e não conseguiu ver como os sapos se reproduziam. Entretanto, o italiano Lazzaro Spallanzani refez os experimentos e em 1768 concluiu que os sapos possuíam fecundação externa (TERRALL, 2011; CRUMP, 2015).

Até o ano de 1900, os dados sobre história natural ainda eram escassos, fragmentados e amplamente dispersos. Desta forma, era necessário um grande esforço e investimento de tempo em pesquisas para juntar esses dados (SAMPSON, 1900). Para contribuir com o conhecimento sobre os aspectos da história de vida dos anfíbios, Sampson (1900) reuniu e obteve algumas novas informações sobre reprodução para muitas espécies de anuros (e.g. *Hylodes*, *Rhacophorus*, *Phyllomedusa*, *Pipa*) de várias regiões do mundo, incluindo América Latina. O hemisfério Sul foi reconhecido como uma região com anuros de vários hábitos reprodutivos, inclusive com o desenvolvimento dos ovos e larvas extremamente variados (SAMPSON, 1900).

Também no sentido de tentar compreender melhor os modos reprodutivos, Noble (1925, 1927) trouxe algumas reflexões importantes sobre os modos reprodutivos: "(1) o modo de história de vida é um indicador muito melhor de relacionamento nos anfíbios do que o comumente utilizado; (2) especializações embrionárias ou larvais homólogas em diferentes gêneros de Amphibia podem ser tomadas como evidência da relação entre esses gêneros; (3) um modo muito especializado de história de vida ou estrutura larval que ocorre em dois tipos diferentes de anfíbios, geralmente, oferece algumas das melhores evidências de que essas formas estão relacionadas; (4) a posição filogenética de um anfíbio é melhor determinada pela comparação de seus hábitos e história de vida, bem como de sua estrutura, com os de seus parentes".

Posteriormente, Bertha Lutz foi extremamente importante nos estudos pioneiros dos modos reprodutivos, principalmente no Brasil (LUTZ 1947, 1948). Apresentou várias observações de história de vida resultantes de suas expedições ao Rio de Janeiro, juntamente com seu pai Adolpho Lutz, incluindo observações básicas ainda não registradas e/ou publicadas para muitos gêneros e espécies: *Hyla decipiens* (atualmente *Dendropsophus decipiens*), que possui ovos pequenos e em grande quantidade e desova nas pontas das folhas; *Phyllomedusa* oviposita sobre as folhas e, quando ocorre a desova, os adultos dobram as folhas com os pés e "colam" as pontas laterais das folhas com ovócitos; em *Gastrotheca*, a fêmea apresenta uma abertura ("bolsas") no dorso onde carrega os ovos (em algumas espécies, quando os embriões estão prontos para eclodir, a fêmea vai até a água e os libera; em outras, pode ocorrer o desenvolvimento completo dentro das bolsas). Bertha Lutz traz também informações para outros gêneros (e.g. *Pipa*, *Dendrobates*, *Phyllobates, Thoropa, Cyclorhamphus* e *Leptodactylus*) (LUTZ, 1947).

Lutz (1948) sugeriu que devido à grande diversidade de tipos de desenvolvimento das larvas, os anfíbios representam um grupo interessante para estudar a evolução molecular. Lutz (1948) também descreveu a tendência em direção a maior terrestrialidade. Ademais, a pesquisadora notou que tais modificações envolvem: modificações do comportamento reprodutivo, preferências de habitat e adaptações ecotópicas dos adultos, sendo a reserva de vitelo e a aceleração de desenvolvimento mudanças muito importantes. Lutz (1948) ainda observou que histórias de vida se repetiam em diferentes regiões do globo em condições ecológicas similares em grupos considerados filogeneticamente distintos (LUTZ, 1948) e que, quando ocorria ausência de evolução paralela ou convergente, isso poderia estar relacionado à falta de ecótonos similares.

Observações feitas por Jameson (1955) trouxeram dados de comportamento reprodutivo para várias espécies, incluindo 13 famílias de anuros (*Ascaphidae*, *Pipidae*, *Discoglossidae, Rhinophrynidae, Pelobatidae, Rhacophoridae, Ranidae, Microhylidae, Hylidae, Bufonidae, Leptodactylidae, Dendrobatidae* e *Atelopodidae*). Este trabalho teve como foco preencher muitas lacunas e procurou compreender tendências evolutivas e generalidades no comportamento reprodutivo. Jameson (1955) levantou uma importante questão: “a situação ambiental produz um impulso final para o ciclo hormonal no sentido fisiológico, ou serve como um estímulo passivo e mecânico para comportamento de reprodução?”. Em muitas espécies, as fêmeas não ovulam quando migram de um local para outro, outras não permitem o amplexo até a ovulação estar quase completa e outras não ovulam, exceto durante o amplexo (BRAGG, 1940). Desta forma, podemos ver que o acasalamento (amplexo), a ovulação e a oviposição são fatores independentes e fatores ambientais como temperatura, umidade do ar, precipitação e umidade do solo podem influenciar as etapas deste processo (CUMMINS, 1920; BARBOUR; WALTERS, 1941; BRAGG, 1940; JAMESON, 1955).

Em meados das décadas de 40-50, os modos reprodutivos eram conhecidos como “formas de história de vida”. Somente entre as décadas de 60-70 é que o termo “modo reprodutivo” começou a ser utilizado (LUTZ, 1947; CRUMP, 2015). Para os anfíbios, o conceito e definição de modos reprodutivos incluem uma combinação de fatores, tais como a fecundidade, tamanho e número dos ovos, tamanho das desovas, freqüência de oviposição, tempo de desenvolvimento dos embriões e dos estágios larvais, presença/ausência de estágios larvais, local de oviposição, local do desenvolvimento larval, tempo da primeira reprodução, duração da capacidade reprodutiva, esforço reprodutivo (incluindo cuidado parental) (SALTHE, 1969; SALTHE; DUELLMAN, 1973; DUELLMAN; TRUEB, 1994). Haddad e Prado (2005) revisaram os modos reprodutivos dos anuros, rearranjaram alguns modos já conhecidos e trouxeram informações novas para algumas famílias, gêneros e espécies. Nos últimos anos, maior esforço tem sido empregado em estudos sobre a evolução dos modos reprodutivos, tentando elucidar os fatores que poderiam explicar a grande diversidade de modos em anuros e a evolução dos modos terrestres, apresentados no item 2.5 (e.g. GOMEZ-MESTRE; PYRON; WIENS 2012; ZAMUDIO et al., 2016; VÁGI et al., 2019).

2.3 MODOS REPRODUTIVOS EM ANUROS: CLASSIFICAÇÃO E DIVERSIDADE

Uma das primeiras classificações dos modos reprodutivos, considerando o local de oviposição, estágio de eclosão das larvas e local de desenvolvimento das larvas, foi proposta por Lutz (1948). Quatro tipos principais de local de oviposição foram reconhecidos: aquáticos (desovas e girinos ocorrem em ambientes aquáticos), semi-terrestres (desovas terrestres com girinos aquáticos), terrestres (desovas e girinos terrestres ou arborícolas) e terrestres com desenvolvimento direto (ovo terrestre sem fase larval) (LUTZ, 1948; DUELLMAN; TRUEB, 1994; HADDAD; PRADO, 2005). Essa classificação foi revista, primeiramente, por Duellman e Trueb (1986) e, posteriormente, por Haddad e Prado (2005). Duellman e Trueb (1986) propuseram três categorias (ovos aquáticos, ovos terrestres ou arborícolas e ovos retidos nos ovidutos) e 29 modos reprodutivos para anuros.

Haddad e Prado (2005) revisaram os modos reprodutivos dos anuros. Nesta revisão, os autores adicionaram sete novos modos reprodutivos à lista anterior proposta por Duellman e Trueb (1986). Haddad e Prado (2005) reconheceram, mundialmente, 39 modos reprodutivos para anuros, sendo estes classificados em três categorias principais: ovos aquáticos (modos 1 a 16), ovos terrestres ou arborícolas (não aquáticos, modos 17 a 37), e ovos retidos nos ovidutos (modo 38 - ovoviviparidade, onde nutrição é fornecida pelo vitelo, e modo 39 - viviparidade, onde a nutrição é fornecida por secreções do oviduto) (Tabela 1, fonte HADDAD; PRADO, 2005). O modo 1 (Modo 1: Ovos e girinos exotróficos em água lêntica) foi considerado o mais basal e generalizado e os outros modos graus de especialização como respostas adaptativas a diferentes ambientes (HADDAD; PRADO, 2005).

A maioria dos anfíbios deposita seus ovos diretamente na água (HADDAD; PRADO, 2005). A reprodução não aquática pode ocorrer de duas formas: semi-terrestre ou terrestre (HADDAD; PRADO, 2005). Na reprodução semi-terrestre, as fêmeas podem depositar os ovos em folhas, galhos e troncos nos arredores dos corpos d’água e os girinos eclodem e caem na água onde terminam seu desenvolvimento (e.g. gêneros *Dendropsophus*, *Phyllomedusa*). Ou então, ainda considerada reprodução semi-terrestre, as fêmeas podem depositar seus ovos fora da água, mas utilizam rochas úmidas (e.g. gêneros *Thoropa*, *Cycloramphus*); nesses ambientes, ovos e girinos se desenvolvem em águas rasas na superfície das rochas (LUTZ, 1947; CARAMASCHI; SAZIMA, 1983; GIARETTA; FACUE, 2004). Geralmente, a reprodução terrestre pode ser definida como os casos em que a fêmea deposita os ovos diretamente sobre o solo, ou os transporta; em muitas espécies, do ovo já sai o juvenil formado (desenvolvimento direto; DUELLMAN; TRUEB, 1994; HADDAD; PRADO, 2005). Entretanto, na reprodução terrestre, existem casos em que mesmo a espécie possuindo desovas terrestres, não ocorre desenvolvimento direto (e.g. dendrobatídeos). Dos ovos eclodem girinos que são transportados até um corpo d´água (e.g. poças, fitotelmatas) e nesses ambientes terminam seu desenvolvimento (FURNESS; CAPELLINI, 2019). Aproximadamente 24% das espécies de anuros têm desenvolvimento direto (DUELLMAN, 2007; CRUMP, 2015).

Também podemos encontrar uma classificação dos ovos e modos de oviposição e uma terminologia padronizada tanto para estruturas que recobrem os ovos quanto para desovas. Altig e McDiarmid (2007) dividem os sítios/locais de oviposição em quatro categorias (associados aos pais, terrestres, semi-terrestres e aquáticos) e indicam que cada categoria pode ser subdividida com base em fatores biológicos e físicos. Esses autores também reconhecem cinco categorias de tipos de desova (desovas com ovos independentes, tridimensionais, desovas flutuantes, ninhos de espuma e desovas lineares). Por serem extremamente frágeis, os ovos dos anfíbios podem sofrer conseqüências de fatores físicos e biológicos. Tais fatores somados à disponibilidade de diferentes tipos de habitats podem ser responsáveis pelas diferentes formas e estruturas de desovas e ovos. Em resumo, os padrões de oviposição identificados refletem a morfologia dos ovos, ecologia, eventos pós-desova, condições bióticas e abióticas, local da desova e comportamento dos pais (ALTIG; MCDIARMID, 2007). Tais padrões podem ser entendidos por uma perspectiva filogenética e/ou ecológica (ALTIG; MCDIARMID, 2007).

Os anfíbios são conhecidos como o grupo com maior diversidade de modos reprodutivos entre os vertebrados tetrápodes (DUELLMAN; TRUEB, 1994), incluindo até fertilização interna. A fertilização interna aparece em apenas algumas espécies nos gêneros *Nectophrynoides* e *Nimbaphrynoides*, na extinta espécie *Eleutherodactylus jasperi* (ISKANDAR; EVANS; MCGUIRE, 2014), além do gênero *Ascaphus* (WELLS, 2007).

Novos modos reprodutivos, com relação à fecundação e desenvolvimento dos ovos e girinos, continuam a ser descobertos e descritos. Podemos citar, como exemplo, a espécie *Limnonectes larvaepartus* (de "larvae", plural de larva, a forma inicial de um animal e "partus", dar à luz) (ISKANDAR; EVANS; MCGUIRE, 2014). Os pesquisadores descobriram girinos nos ovidutos enquanto preparavam os espécimes. Ao eutanasiar as fêmeas, observaram movimentos na parte abdominal e ao fazer uma incisão, os girinos saíram vivos. Os pesquisadores observaram, também, a fêmea dar à luz a girinos no momento da captura e também deram à luz em sacos de coleta, enquanto eram transportadas. É provável que nesta espécie o desenvolvimento dos girinos até imagos ocorra no oviduto, com nascimento de sapos formados, como em *Eleutherodactylus jasperi*, *Nectophrynoides* e *Nimbaphrynoides* (ISKANDAR; EVANS; MCGUIRE, 2014). A fertilização de *L. larvaepartus* ocorre internamente. Entretanto, como ocorre à fertilização ainda não foi registrado, pois não há existência aparente de órgão intromitente para o transporte dos espermatozoides, o mesmo observado para *Eleutherodactylus jasperi*, *Nectophrynoides* e *Nimbaphrynoides* (WELLS, 2007). Não se sabe com certeza se a reprodução de *L. larvaepartus* sempre envolve o nascimento de girinos; se sim, é provável que eles sejam ovovivíparos (ISKANDAR; EVANS; MCGUIRE, 2014).

Em suma, atualmente, em torno de 50 modos reprodutivos são reconhecidos para anuros no mundo (e.g. HADDAD, PRADO, 2005; GURURAJA et al., 2014; ISKANDAR; EVANS; MCGUIRE, 2014; KUSRINI et al., 2015). Considerando a grande diversidade de espécies, diversidade na ocupação de habitats, bem como a escassez de informações sobre a biologia de muitas espécies, podemos supor que novos modos reprodutivos poderão vir a ser descobertos e descritos nos próximos anos.

Tabela 1 Os 39 modos reprodutivos conhecidos para anfíbios anuros (Adaptada de HADDAD; PRADO, 2005).

Ovos aquáticos		
	Ovos depositados na água	
		Modo 1: Ovos e girinos exotróficos em água lêntica
		Modo 2: Ovos e girinos exotróficos em água lótica
		Modo 3: Ovos e estágios iniciais das larvas em câmaras subaquáticas construídas; girinos exotróficos em riachos
		Modo 4: Ovos e estágios iniciais das larvas em cavidades naturais ou construídas; após inundações, girinos exotróficos em lagoas ou riachos .
		Modo 5: Ovos e estágios iniciais das larvas em ninhos subterrâneos construídos; após inundações, girinos exotróficos em lagoas ou riachos
		Modo 6: Ovos e girinos exotróficos na água em buracos de árvores ou fitotelmos
		Modo 7: Ovos e girinos endotróficos em depressões cheias de água.
		Modo 8: Ovos e girinos endotróficos na água em buracos de árvores ou fitotelmos
		Modo 9: Ovos depositados em um riacho e engolidos por fêmeas; ovos e girinos completam o desenvolvimento no estômago.

	Ovos em ninhos de bolhas na água	
		Modo 10: Ninho de bolhas flutuando na lagoa; girinos exotróficos em lagoas
	Ovos em ninho de espuma na água	
		Modo 11: Ninho de espuma flutuando na lagoa; girinos exotróficos em lagoas Modo 12: Ninho de espuma flutuando na lagoa; girinos exotróficos em riachos. Modo 13: Ninho de espuma flutuando na água acumulada em bacias construídas; girinos exotróficos em lagoas Modo 14: Ninho de espuma flutuando na água acumulada nas axilas das bromélias terrestres; girinos exotróficos em lagoas
	Ovos embutidos no dorso da fêmea (aquática)	
		Modo 15: Ovos eclodem em girinos exotróficos Modo 16: Ovos eclodem em sapos.
Ovos terrestres ou arborícolas (não na água)		

	Ovos no chão, em pedras ou em tocas	
		Modo 17: Ovos e girinos iniciais em ninhos escavados; após inundações, girinos exotróficos em lagoas ou córregos Modo 18: Ovos no chão ou pedras acima da água; após a eclosão, os girinos exotróficos movem-se para a água Modo 19: Ovos em rochas úmidas, em fendas rochosas ou em raízes de árvores acima da água; girinos semiterrestres exotróficos vivendo em rochas e fendas no filme da água ou na interface água-terra Modo 20: Ovos que dão origem a girinos exotróficos que são transportados para a água pelo adulto Modo 21: Ovos que dão origem a girinos endotróficos que completam seu desenvolvimento no ninho Modo 22: Ovos que dão origem a girinos endotróficos que completam seu desenvolvimento no dorso ou nas bolsas de adultos Modo 23. Desenvolvimento direto de ovos terrestres
	Ovos arborícolas	
		Modo 24: Ovos eclodem em girinos exotróficos que caem na água lêntica Modo 25: Ovos eclodem em girinos exotróficos que caem na água lótica

	Modo 26: Ovos eclodem em girinos exotróficos que se desenvolvem em cavidades cheias de água nas árvores Modo 27: Ovos eclodem em sapos (desenvolvimento direto).
Ovos em ninho de espuma (terrestre ou arborícola)	
	Modo 28: Ninho de espuma no chão úmido da floresta; após inundações, girinos exotróficos em lagoas Modo 29: Ninho de espuma com ovos e estágios iniciais das larvas nas depressões; após inundações, girinos exotróficos em lagoas ou córregos Modo 30: Ninho de espuma com ovos e estágios iniciais de larvas em ninhos subterrâneos construídos; após inundações, girinos exotróficos em lagoas Modo 31: Ninho de espuma com ovos e estágios iniciais de larvas em ninhos subterrâneos construídos; após inundações, girinos exotróficos em riachos Modo 32: Ninho de espuma em câmaras subterrâneas construídas; girinos endotróficos completam o desenvolvimento no ninho Modo 33: Ninho de espuma arborícola; girinos caem em lagoas ou córregos.
Ovos transportados por adulto	

	Modo 34: Ovos transportados nas pernas do macho; girinos exotróficos em lagoas. Modo 35: Ovos transportados em bolsa dorsal da fêmea; girinos exotróficos em lagoas. Modo 36: Ovos transportados no dorso ou em bolsa dorsal da fêmea; girinos endotróficos em bromélias ou bambus Modo 37: Ovos transportados no dorso ou em bolsa dorsal da fêmea; desenvolvimento direto
Ovos retidos nos ovidutos	
	Modo 38. Ovoviviparidade; nutrição fornecida pelo vitelo. Modo 39. Viviparidade; nutrição fornecida por secreções do oviduto.

2.4 MODOS REPRODUTIVOS: DIVERSIDADE NA FLORESTA ATLÂNTICA

A Floresta Atlântica, um *hotspot* mundial (MYERS et al., 2000), abriga uma grande diversidade de anuros. Mais da metade das 1.000 espécies de anuros, já registradas no Brasil, ocorre neste bioma, com elevadíssimo endemismo (80% dos anuros são endêmicos deste bioma, HADDAD et al., 2013; MELCHIOR; ROSSA-FERES; DA SILVA, 2017; DA SILVA et al., 2017). A complexa heterogeneidade do bioma proporcionou uma grande diversidade nos modos reprodutivos dos anuros (HADDAD; PRADO, 2005). De fato, dentre os 31 modos reprodutivos encontrados nos trópicos, 27 deles ocorrem na Floresta Atlântica e seis são endêmicos deste bioma (HADDAD; PRADO, 2005).

Especificamente para a Floresta Atlântica, podemos dividir os modos reprodutivos em dois grupos: associados à vegetação e associados ao solo (HADDAD; PRADO, 2005). Hylidae (pererecas) e Leptodactylidae (rãs) são as famílias mais ricas em espécies e diversas em modos reprodutivos (HADDAD; PRADO, 2005). Para Hylidae, foram registrados quatro modos associados à vegetação e três associados ao solo; para Leptodactylidae, três modos associados à vegetação e 10 ao solo (HADDAD; PRADO, 2005). A grande diversidade de modos reprodutivos encontrada na Floresta Atlântica pode ser o resultado de diversos fatores, como a topografia acidentada e com grande variação altitudinal em várias regiões do bioma, propiciando a ocorrência de uma ampla variedade de microhabitas, a sua grande extensão latitudianal e variação climática associada, bem como os altos índices de precipitação e alta umidade da floresta, o que diminui os riscos de dessecação dos ovos e favorece a ocorrência de modos reprodutivos mais terrestres (HADDAD; PRADO, 2005; DA SILVA et al., 2012; THOMÉ et al., 2020). Além disso, a longa história evolutiva de diferentes grupos filogenéticos e existência de pressões seletivas diversas (e.g. disponibilidade de microhabitats adequados, imprevisibilidade das chuvas, predação e competição intra-específica) podem, também, ter favorecido a diversificação dos modos reprodutivos de anuros na Floresta Atlântica (HADDAD; PRADO, 2005; HARTMANN; HARTMANN; HADDAD, 2010; THOMÉ et al., 2020).

2.5 MODOS REPRODUTIVOS EM ANUROS: EVOLUÇÃO

Classicamente, o modo reprodutivo considerado mais ancestral e generalizado entre os anfíbios anuros é o aquático (Ovos e girinos exotróficos em água lêntica) (DUELLMAN; TRUEB, 1994; HADDAD; PRADO, 2005). A partir do modo aquático, outros modos reprodutivos teriam surgido (e.g. semi-terrestre, terrestre, e terrestre com desenvolvimento direto). Tanto os modos mais ancestrais (e.g. ovos e girinos aquáticos), quanto os modos mais derivados (e.g. ovos semi-terrestres) mantêm, na maioria, girinos que se desenvolvem em ambientes aquáticos e isso é altamente difundido entre os anuros (CRUMP, 2015; TOUCHON; WORLEY, 2015; ZAMUDIO et al., 2016).

A evolução dos modos reprodutivos em uma seqüência gradual e ordenada (ovos e larvas aquáticas, ovos terrestres e larvas ainda aquáticas, ovos e larvas terrestres, e por fim, ovos terrestres com desenvolvimento direto) era hipotetizado (LUTZ, 1948; SALTHE; DUELLMAN, 1973; WELLS, 2007). Entretanto, Gomez-Mestre, Pyron e Wiens (2012), utilizando métodos filogenéticos comparativos para tentar entender a evolução dos modos reprodutivos em anuros, testaram se o desenvolvimento direto foi precedido por modos reprodutivos com ovos terrestres versus ovos aquáticos, larvas exotróficas versus endotróficas e ovos ou larvas aparentemente protegidos de predadores aquáticos. A partir da análise de 720 espécies de anuros com dados reprodutivos, os autores confirmaram o modo aquático como sendo ancestral. Além disso, recuperaram transições evolutivas entre espécies com ovos aquáticos para espécies com desenvolvimento direto, sem a existência de formas intermediárias, enfatizando a não linearidade na evolução dos modos reprodutivos. Na história evolutiva dos anfíbios, a reprodução terrestre evoluiu independentemente 48 vezes e o desenvolvimento direto evoluiu 19 vezes. Ademais, muitos padrões inesperados na seqüência de mudanças entre os modos reprodutivos foram recuperados: 1) ovos aquáticos dão origem ao desenvolvimento terrestre, igualmente aos ovos terrestres; 2) o desenvolvimento direto, geralmente, não tem origem a partir de modos com larvas endotróficas e, sim, de modos com larvas exotróficas; 3) modos em que ovos e larvas são protegidos têm origem, freqüentemente, de ovos e larvas desprotegidas e raramente dão origem ao desenvolvimento direto. Ademais, o estudo de Gomez-Mestre, Pyron e Wiens (2012) mostrou que o tamanho corporal, tamanho do ovo, tamanho da desova, cuidados parentais, distribuição climática (e.g. ambientes com alta precipitação) e cobertura vegetal (e.g. Floresta Atlântica) estão correlacionados com a evolução dos modos reprodutivos e podem explicar a persistência e freqüência dos modos aquáticos e as origens repetidas dos modos terrestres (GOMEZ-MESTRE; PYRON; WIENS, 2012). Outro resultado inesperado desse estudo foi que dentro das mudanças graduais esperadas em direção ao desenvolvimento terrestre, foram encontradas reversões de modos terrestres para modos considerados mais basais, incluindo a reversão aquática. Para que alguns anfíbios pudessem ter o início da vida fora da água, foi necessário o aumento do conteúdo do vitelo no ovo, levando ao aumento no tamanho dos ovos nas espécies com reprodução terrestre. Mas, em alguns casos, a quantidade de vitelo sofreu diminuição ou foi perdida secundariamente, com ressurgimento do girino aquático (GOMEZ-MESTRE; PYRON; WIENS, 2012).

Segundo Gomez-Mestre, Pyron e Wiens (2012), a explicação para as repetidas origens da reprodução terrestre e a diversidade geral dos modos reprodutivos seria a permanência do modo primitivo ao longo de centenas de milhões de anos entre as espécies (GOMEZ-MESTRE; PYRON; WIENS, 2012). A ocorrência e a permanência do modo reprodutivo aquático (considerado mais basal) há tantos milhões de anos podem ser evidências da existência de vantagens relacionadas a este modo (e.g. grandes tamanhos de desovas, grandes tamanhos corpóreos e capacidade de colonizar regiões mais secas) (GOMEZ-MESTRE; PYRON; WIENS, 2012). Mudanças da reprodução aquática para a terrestre podem ocorrer de forma relativamente rápida e muitos passos intermediários podem ser desnecessários. Os resultados desse trabalho sugerem, também, que essa mudança para a reprodução terrestre pode ter sido associada à redução do tamanho do corpo e da desova, aumento do tamanho dos ovos, cuidados parentais e ocorrência em climas com alta precipitação, densa cobertura vegetal e temperaturas anuais médias (GOMEZ-MESTRE; PYRON; WIENS, 2012).

Alguns trabalhos sugerem que a pressão exercida pela predação aquática sobre ovos e girinos (e.g. peixes, cobras, insetos, larvas) seria um fator importante para saída da água e colonização de habitats terrestres, levando a evolução de modos reprodutivos terrestres em anfíbios (LUTZ, 1947, 1948; MAGNUSSON; HERO, 1991; ALTIG; MCDIARMID, 2007; TOUCHON; WARKENTIM, 2008). Muitos são os estudos que mostram a importância dos predadores aquáticos e como influenciam no comportamanto dos anuros (BUXTON; SPERRY, 2017). Alguns anuros (e.g. *Hoplobatrachus occipitalis*) podem detectar diferenças sutis na quantidade e no tamanho das larvas predadoras, usando apenas pistas olfativas ou químicas. Outras espécies podem escolher locais com alta densidade de girinos da mesma espécie, e isso pode ser um indicador de boa qualidade da água, baixa predação e também de disponibilidade de alimentos (BUXTON; SPERRY, 2017). Também pode ocorrer a oviposição em locais com ovos e desovas de espécies diferentes que podem servir de futuro alimento para os futuros girinos. Podemos encontrar também espécies (e.g. *Ranitomeya variabilis*) que são capazes, ainda, de identificar predadores diferentes para ovos e desovas (BUXTON; SPERRY, 2017). Alterações sazonais também podem mudar o comportamento e influenciar na escolha do melhor local para colocar os ovos. Essa estratégia pode ser usada para aumentar as chances de sobrevivência da prole frente às alterações nos corpos d´água (BUXTON; SPERRY, 2017). A presença de ovos e girinos da mesma espécie em determinados locais pode ser uma indicação positiva ou negativa. Dependendo do local, áreas com alta densidade devem ser evitadas, pois podem dificultar a maximização da aptidão individual e, por outro lado, a presença de ovos e girinos da mesma espécie pode indicar bom local para reprodução e servir como parâmetro para escolha de local ideal (BUXTON; SPERRY, 2017). O papel da presença de predadores e fatores relacionados às escolhas de locais de postura dos ovos são extremamente complexos e muitos estudos devem ser feitos para melhorar a nossa compreensão (BUXTON; SPERRY, 2017).

Recentemente, procurando entender a evolução dos modos reprodutivos por uma nova perspectiva, foi testada a hipótese de que a seleção sexual teria favorecido a evolução de modos reprodutivos terrestres em anuros (ZAMUDIO et al., 2016). O mecanismo seletivo para origem de novos modos reprodutivos pode não estar somente relacionado à pressão de predação sobre ovos e girinos em ambientes aquáticos, mas também a reprodução em locais escondidos, como uma forma dos machos evitarem a poliandria, teria levado ao surgimento de modos terrestres (ZAMUDIO et al., 2016). Desta forma, o macho, ao tentar se livrar da competição com outros machos acaba explorando habitats mais seguros e livres de competidores para oviposição, contribuindo para uma maior diversidade no local de deposição de ovos. O risco de poliandria, portanto, seria menor em espécies com oviposição terrestre e deposição de ovos e comportamentos de acasalamento em locais que reduzem a exposição dos casais (e.g. bromélias, buracos de árvores ou câmaras subterrâneas). Usando análises comparativas filogenéticas, foram mapeados padrões de diversificação dos modos reprodutivos, analisando-se as principais causas que alteram locais de deposição de ovos e de desenvolvimento dos girinos em Hylidae e Leptodactylidae. O amplexo em locais escondidos apareceu 18 vezes em diferentes clados, todos em espécies tropicais. Para as duas famílias, foi encontrada uma relação entre deposição de ovos terrestres e amplexo escondido, sugerindo que a seleção intra-sexual, ou seja, estratégias dos machos para evitar a competição e poliandria pode desempenhar um papel importante na evolução para a deposição de ovos terrestres (ZAMUDIO et al., 2016).

E se a espécie puder escolher, dependendo das condições (e.g. precipitação, predadores), entre colocar os ovos na água ou na terra? A plasticidade reprodutiva consiste na capacidade comportamental e fisiológica em que, de alguma forma, os organismos percebem e escolhem os melhores locais ou momentos para maximizar o sucesso reprodutivo frente às diferentes condições ambientais (SOWA et al., 2015). Especificamente nos anfíbios, a plasticidade reprodutiva pode ser vista como a combinação da capacidade de reprodução e desenvolvimento aquático, com a capacidade de também realizar a desova e desenvolvimento em ambientes terrestres, podendo ser vista como um estágio intermediário aquático-terrestre, importante no contexto da evolução dos modos reprodutivos (TOUCHON; WARKENTIN, 2008). Foi descoberta, através de experimentos e observações na natureza, uma espécie de anuro (*Dendropsophus ebraccatus*) que tem plasticidade reprodutiva, ou seja, se reproduz tanto na água como em ambiente terrestre (TOUCHON; WARKENTIN, 2008). No estudo conduzido no Panamá, foi observado que o casal em amplexo pode colocar os ovos em ambiente aquático, na superfície da água ou totalmente submerso, mas também sobre folhas acima da água. Além disso, a escolha do local de oviposição é feita em resposta a fatores que afetam o risco de dessecação do ovo terrestre (TOUCHON; WARKENTIN, 2008). Este registro foi extremamente importante e revelou que, além da grande diversidade de modos reprodutivos em anfíbios, algumas espécies podem combinar modos diferentes dependendo das condições e pressões ambientais (plasticidade). Não se tinha o registro de um vertebrado que fosse capaz de ovipositar tanto na terra quanto na água, sendo este o primeiro registro (TOUCHON; WARKENTIN, 2008). Esta variação reflete respostas comportamentais plásticas dos anuros a diferentes contextos ambientais e não está ligada à variação genética ou polimorfismo (TOUCHON; WARKENTIN, 2008).

Entender a variação dos comportamentos de cuidado parental pode também nos ajudar na compreensão da origem e evolução dos diferentes modos reprodutivos em anuros (VÁGI et al., 2019). A diversidade do cuidado parental em anfíbios anuros é enorme e podemos encontrar cuidado parental realizado somente pelo macho ou somente pela fêmea, ou por ambos ao mesmo tempo. Isso ocorre de forma generalizada entre várias linhagens (VÁGI et al., 2019). O cuidado parental aumenta as chances dos filhotes sobreviverem, principalmente em ambientes hostis e imprevisíveis, e pode ter contribuído para a colonização de ambientes terrestres, assim como para origem e diversificação dos vertebrados terrestres (VÁGI et al., 2019). Desta forma, entender a origem e evolução das diferentes formas de cuidado parental pode nos ajudar a entender muito além deste cenário e pode nos trazer pistas importantes sobre a origem, inclusive, dos primeiros tetrápodes (VÁGI et al., 2019).

2.6 MODOS REPRODUTIVOS EM ANUROS: o gênero *Dendropsophus*

A família Hylidae representa 10% da diversidade de anuros e o gênero *Dendropsophus*, com 108 espécies em nove grupos reconhecidos, representa 15% da diversidade de Hylidae (FROST, 2020). Apesar da maioria das espécies do gênero apresentar reprodução aquática, sabe-se que a reprodução terrestre surgiu independente pelo menos quatro vezes (TOUCHON; WARKENTIN, 2008; CRUMP, 2015). No entanto, para mais de 50% das espécies de *Dendropsophus* não há informações sobre seus modos reprodutivos e é provável que ocorra oviposição terrestre entre essas espécies (TOUCHON; WARKENTIN, 2008; CRUMP, 2015). Ademais, algumas espécies, como *D. ebraccatus*, apresentam plasticidade reprodutiva, ou seja, dependendo das condições ambientais, a desova pode ser depositada na água ou sobre folhas em ambiente terrestre, como descrito acima (TOUCHON; WARKENTIN, 2008). Assim, estudos sobre biologia reprodutiva destas espécies podem alterar o entendimento sobre a evolução dos modos reprodutivos no gênero, principalmente com relação aos modos arborícolas.

No gênero *Dendropsophus,* o grupo *D. decipiens* inclui quatro espécies: *D. decipiens*, *D. berthalutzae, D. oliveirai* e *D. haddadi* (FAIVOVICH et al., 2005). Uma característica considerada como sinapomorfia para o grupo é o comportamento reprodutivo de suas espécies (FAIVOVICH et al., 2005). Essa sinapomorfia consiste na deposição dos ovos fora da água, na ponta das folhas de árvores e arbustos localizados nos arredores de corpos d´água, dos quais eclodem girinos que caem e se desenvolvem nos ambientes aquáticos (FAIVOVICH et al., 2005). Como faltam informações mais completas sobre o modo reprodutivo de espécies do grupo *D. decipiens*, é difícil saber se ocorre variação nos modos reprodutivos entre as espécies e entre populações da mesma espécie. Como pode ocorrer variação reprodutiva frente a diferentes condições ambientais (WORLEY, 2009), é provável que essas espécies possam apresentar comportamentos reprodutivos ainda não registrados.

2.7 DIMORFISMO SEXUAL EM TAMANHO EM ANUROS

Quando nos referimos às diferenças de tamanho entre machos e fêmeas, classicamente duas explicações são amplamente utilizadas, seleção sexual e seleção natural. A seleção sexual pode ser dividida em duas categorias: seleção intrasexual, quando ocorre a disputa direta entre indivíduos do mesmo sexo (e.g. competição entre machos por fêmeas ou defesa de territórios); e seleção intersexual, onde um sexo escolhe seu parceiro (a) (e.g. a escolha dos machos pelas fêmeas de anuros) (WELLS, 1979; TEJEDO, 1988; NALI et al., 2014). No caso da seleção natural, podemos citar a pressão para o aumento do tamanho/massa do corpo que favorece o aumento da fecundidade (e.g. número de ovos) (NALI et al., 2014). Entretanto, muitas outras pressões podem causar alterações morfológicas e resultar em diferenças de tamanho em machos e fêmeas como, por exemplo, o habitat em que a espécie ocorre (LIAO et al., 2014), disponibilidade de alimento (GIRISH; SAIDAPUR, 2000) e gradientes ou condições climáticos (GVOŽDÍK et al., 2008; GOLDBERG et al., 2018).

Alterações ou variações de tamanho do corpo também podem afetar a capacidade reprodutiva das espécies de anuros, uma vez o tamanho das fêmeas está positivamente correlacionado com número e tamanho dos ovos (PRADO & HADDAD, 2005). Além disso, nos anuros em que a fecundação é externa na maioria das espécies, a justaposição da cloaca é extremamente importante para uma fertilização mais eficiente dos ovócitos (ROBERTSON, 1990; BOURNE, 1993; BASTOS; HADDAD, 1996). Nos anfíbios anuros as fêmeas são maiores que os machos em 90% das espécies e estudos apontam que a pressão para o aumento do tamanho da fêmea esteja relacionada à vantagem do aumento da fecundidade (SHINE, 1979; KATSIKAROS; SHINE, 1997; NALI et al., 2014). No entanto, podemos encontrar grandes variações de tamanho em machos e fêmeas, conseqüentemente no grau de dimorfismo sexual em tamanho (NALI et al., 2014). Diferentes pressões, tais como disputas por territórios ou características ecológicas (e.g. variáveis ambientais, padrão reprodutivo) podem influenciar o tamanho dos anuros (NALI et al., 2014).

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3 CAPÍTULO 1: REPRODUCTIVE BIOLOGY OF *DENDROPSOPHUS HADDADI* (BASTOS AND POMBAL, 1994), A SMALL TREEFROG OF THE ATLANTIC FOREST

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Reproductive biology of *Dendropsophus haddadi* (Bastos and Pombal, 1994), a small treefrog of the Atlantic forest

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Abstract. Terrestrial reproduction has evolved at least 48 times in the evolutionary history of anurans. Most species in the genus *Dendropsophus* deposit eggs in water, but some, including *Dendropsophus haddadi*, lay terrestrial eggs. This species is restricted to the Atlantic forest in Brazil and herein, we describe its reproductive biology. Individuals were observed at a height of 3-5 meters on vegetation at the edge of temporary ponds. Males are territorial, emitted calls, visual signals, and engaged in physical combats. Clutches were found at the margins of temporary ponds on trunks, leaves and branches. The number of hatchlings correlated with clutch size and our observations suggest that females may protect the eggs against desiccation following oviposition in the absence of rain. This form of parental care is a novelty for the genus and future studies should detail and assess costs and benefits of this behaviour. The Atlantic forest harbours an extremely rich frog diversity, however information on species natural history is scarce, which may hamper studies on behavioural evolution, phylogeny, as well as conservation actions and decisions.

Keywords. Anura, courtship, eggs, embryo development, territoriality

3.1 INTRODUCTION

The reproductive modes of anurans are remarkably diverse, from aquatic to terrestrial eggs and larvae (Haddad and Prado, 2005; Crump, 2015). Egg development out of water has evolved at least 48 times in the evolutionary history of anurans (Gomez-Mestre, Pyron and Wiens, 2012). Such characteristic may have influenced the dependence of water sources and may have been a significant step towards terrestriality (Touchon and Worley, 2015). The evolution of terrestrial reproduction in amphibians is therefore of great interest to evolutionary biologists (Magnusson and Hero, 1991; Zamudio et al., 2016), but requires accurate baseline data to improve our understanding of the presumptive evolutionary pathway.

Regions characterized by altitudinal and latitudinal variation, rich floristic composition and high rainfall present greater complexity and, consequently, contribute to a greater diversity of reproductive modes in anurans (Silva et al., 2012). The Atlantic forest has complex and diverse characteristics in its horizontal and vertical structure, producing different microhabitats, and the species display various ways of exploring this mosaic (Carnaval et al., 2009; Ribeiro et al., 2009). Behavioural and natural history studies are scarce for the majority of the species described in this biome, which hampers testing hypotheses on ecology, phylogeny, and behavioural evolution (Haddad and Prado, 2005; Crump, 2015; Zamudio et al., 2016).

Approximately 100 species are known for the Neotropical genus *Dendropsophus* (Frost, 2019). The reproductive mode with aquatic eggs and tadpoles is present in nearly 80% of the species (Touchon and Warkentin, 2008; V.G.D. Orrico, pers. comm.). However, terrestrial eggs have been recorded for some species (e.g. *D. leucophyllatus*, *D. berthalutzae*, and *D. haddadi*; Crump, 1974; Hartmann, Hartmann and Haddad, 2010; Mageski, Silva-Soares and Ferreira, 2014), and others exhibit reproductive plasticity, with aquatic and terrestrial spawns (e.g. *D. ebraccatus* and *D. werneri*; Miranda et al., 2008; Touchon and Warkentin, 2008). One of the terrestrial breeders is *D. haddadi* (Bastos and Pombal, 1996), a small treefrog restricted to the Atlantic forest (Frost, 2019) described about 20 years ago. In all known localities, this species has generally been associated with the interior of fragments of the Atlantic forest (Bastos and Pombal, 1996; Araújo-Neto et al., 2012). This biome is constantly affected by anthropogenic actions that lead to the decrease and fragmentation of areas that were previously continuous (e.g. Becker et al., 2007). In this context, this species, as many others, may be negatively impacted by these alterations, including climate and environmental changes (Silva et al., 2012; Loyola et al., 2014). Some information has already been published on the morphology of adults, tadpoles and spawning of *D. haddadi*, however, its reproductive behaviour remains poorly known (Toledo et al., 2011; Lourenço de Moraes, Campos and Toledo, 2012; Mageski, Silva-Soares and Ferreira, 2014; De Abreu et al., 2013). In this way, our objective was to describe in more detail the reproductive biology of *D. haddadi* to contribute with future studies interested in phylogeny and the evolution of the reproductive behaviours in the genus.

3.2 MATERIAL AND METHODS

We carried out field work in the Municipal Park of Maceió (MP) (9.607778 S and 35.764167 W) and in the protected area of Catolé and Fernão Velho (CFV) (9.556112 S and 35.799722 W), Maceió, Alagoas, northeastern Brazil. Our active searches lasted from 17:00 to 23:00 PM (6 hours/person; n = 2 persons), from May to June, 2011, and June to September, 2016, the rainy season in the area, when the species is breeding. Our observations of *D. haddadi* adults occurred in a natural environment. Clutches were classified as terrestrial when fully in contact with air, semiaquatic when on the surface of water (water / air), and aquatic when fully submerged (see Touchon and Warkentin, 2008). For each clutch, information on type of substrate used (shrub, tree, trunk), oviposition site (pond, temporary, permanent pool) and the height of clutches were collected. The ImageJ program was used to count and measure egg and clutch diameters. Plastic containers filled with water from the sampling site were placed just beneath the clutches, until all embryos had hatched. To test for correlation between size of clutches and number of eggs, and number of hatchlings and number of eggs, we performed Pearson's correlation coefficient analysis. We used the R software environment for all analyses (R Development Core Team, 2009).

3.3 RESULTS

We observed adult males, gravid females and spawns of *D. haddadi* from May to September, the rainy season in the region. Females were larger in SVL (X = 20.96

mm ± 2.18; range = 17.00 - 23.75; N = 15) than males (X = 17.73 mm ± 0.94; range = 15.14 - 19.43; N = 58; t = 10.14; p = <0.001. All clutches were laid on the vegetation above lentic environments and exotrophic tadpoles fell into the water to complete development (mode 24 sensu Haddad and Prado, 2005). Males were observed emitting advertisement and aggressive calls. Moreover, two males were observed engaging in physical combat. The combat occurred when a male invaded the territory of a resident male. The resident male was emitting advertisement call and the invading male approached in silence. Before engaging in physical combat, we observed that the resident male, in the presence of an invading male, performed movements with the hind limbs raised and swinging them (foot-flagging, sensu Hödl and Amézquita, 2001) while emitting aggressive vocalizations (Fig. 1A). Two amplectant pairs were observed at the MP study site on July 30, 2016. During courtship, before amplexus, males performed similar movements with their hind limbs, as described above (foot-flagging, sensu Hödl and Amézquita, 2001). Following, during axillary amplexus (Fig.1B) males made discrete movements with their heads, pressing on top of female´s head. The females oviposited three times with the same male and each spawning was deposited in a different place; each amplexus lasted about 30 minutes until spawning occurred. Intervals between one amplexus and another were about 40 minutes (n = 3 amplexus of each pair). After spawning in the absence of rain, we observed one female joining the eggs with her hind limbs (Fig. 1C). Approximately 40 minutes later, the same pair amplexed again and following oviposition on another leaf, the female stayed on top of the spawn for about 24 minutes. With rain, females abandoned clutches immediately after spawning (n = 6 clutches). After each spawning, males jumped off immediately from the female's back, began calling (Fig. 1D) and performed movements with their limbs.

All clutches observed were associated with temporary ponds and were considered terrestrial. They were deposited on leaves above water bodies at a mean height of 1.28 m (SD = 0.74; n = 58 clutches). The mean number of eggs per clutch was 29.34 (SD = 11.38; n = 24 clutches), mean diameter of the eggs was 2.0 mm (SD = 1.0; n = 1,056 eggs), and mean diameter of clutches was 2.29 cm (SD = 1.91; n = 24). Larger clutches, i.e. with larger number of eggs, presented higher percentage of eggs developing until hatching (P < 0.001; r = 0.633; n = 24 clutches).

The mean time for embryos to hatch was 4.3 days (SD = 1.69; n = 500 embryos). From all clutches, 95% were deposited on the tip of the leaves of the dendê palm (*Elaeis guineensis*) (Fig. 2A), 4% on trunks (Fig. 2B), and 1% on branches (Fig. 2C).

Figure 1. (A) A male of *Dendropsophus haddadi* signaling with his left hind limb in the Catolé and Fernão Velho protected area. (B) Axillary amplexus. (C) A female joining the eggs with her hind limbs. (D) A male calling soon after spawning in the Municipal Park, Maceió, Alagoas, Brazil.

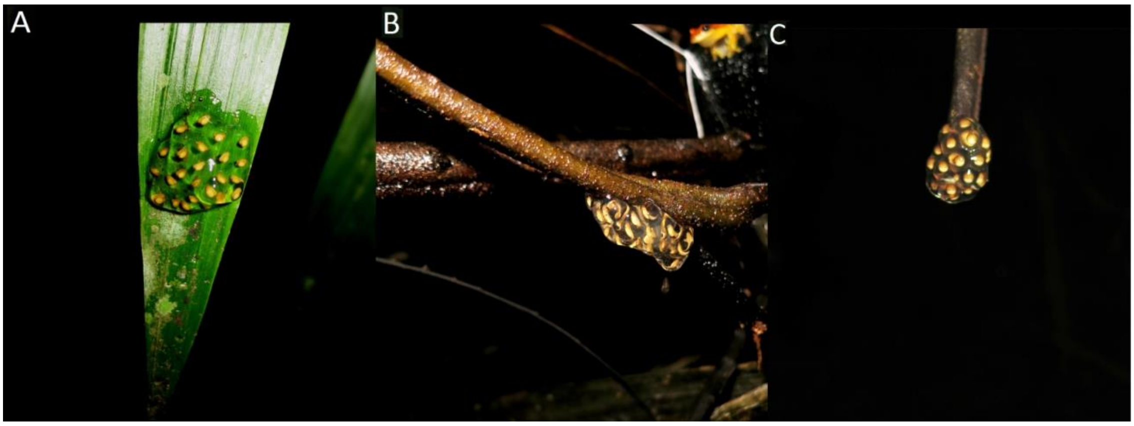

Figure 2. Clutches of *Dendropsophus haddadi* (A) deposited on the tip of *dendê* palm leaves (*Elaeis guineensis*), (B) on bole and (C) on a branch in the Municipal Park, Maceió, Alagoas, Brazil.

3.4 DISCUSSION

Individuals of *D. haddadi* reproduced from May to September, characterizing a prolonged reproductive pattern (sensu Wells, 1977). For *D. haddadi*, a previous study registered clutches on leaves of terrestrial bromeliads, however, authors did not record where tadpoles developed (Mageski, Silva-Soares and Ferreira, 2014). According to our observations, we conclude that all species of the *D. decipiens* clade (*D. decipiens*, *D. berthalutzae*, *D. oliveirai* and *D. haddadi*) (Faivovich et al., 2005) have the reproductive mode 24: terrestrial eggs on leaves above lentic environments and exotrophic tadpoles that fall and complete development in the water (Bokermann, 1962; Bokermann, 1963; Lutz, 1973; Bastos and Pombal, 1996; this study).

Anurans may employ, in addition to acoustic communication, visual signals as part of their courtship behaviour and territorial defence (Haddad and Giaretta, 1999) and male combat may occur when the above strategies do not work (Costa, Guimarães and Bastos, 2010; Miranda et al., 2008). Visual communication used to be more reported for diurnal species and was considered rare in nocturnal frogs, which was associated with habitat light availability (Haddad and Giaretta, 1999; Hartmann et al., 2005). However, studies reporting visual communication in nocturnal anurans of different families increased in the last years, including many hylid species (Hartmann et al., 2005; Toledo et al., 2007; Miranda et al., 2008). In the nocturnal hylid *D. parviceps*, males call from perches with high vegetation density, which may protect from predators but decrease sound propagation (Amézquita and Hödl, 2004). These males also perform visual signals, which may favour conspecific locatability in acoustic and visual complex habitats at low light conditions (Amézquita and Hödl, 2004). Our observations of *D. haddadi* support that this species also performs visual signals during aggressive and courtship interactions, similar to those observed for *D. werneri* in the Atlantic forest of south Brazil (Miranda et al., 2008). Future studies should detail the visual communication in *D. haddadi* and the evolution of this behaviour in a phylogenetic context.

We observed that the protective gelatine capsule surrounding the eggs of *D. haddadi* was generated soon after hydration by water. The eggs and gelatinous capsule need to be hydrated immediately after oviposition to perform its protective function (Touchon and Warkentin, 2008; Valencia-Aguilar, Castro-Herrera and

RamírezPinilla, 2012), otherwise development may be disrupted and embryos may die (Altig and McDiarmid, 2007; Warkentin, 2011). In anurans, the gelatinous capsule protects the eggs against predation, fungal infection and regulates gas exchange with the external environment, maintaining moisture and oxygenation (Warkentin, 2011). Furthermore, we found that hatching success was positively correlated with the number of eggs in the spawn, possibly due to the smaller ratio between surface area and volume, reducing dehydration (Zina, 2006). This might explain the behaviour of *D. haddadi* female that joined the spawn in the absence of rain and right after stayed on top of another spawn for more than 20 minutes. In addition, by dividing the spawn into multiple masses, *D. haddadi* females may increase offspring survival. Although rare (from 10-20% of species), anurans exhibit a great diversity of parental care behaviour (Wells, 2007) that evolved close related with terrestrial reproduction (Gomez-Mestre, Pyron and Wiens, 2012). In spite of this great diversity, we still lack information whether parental care is present in many groups and recent studies have shown that it is more common and diverse than previously thought (Delia, Bravo-Valencia and Warkentin, 2017). For instance, recently, short-term female care of eggs, only during the first night after oviposition, has been described for some centrolenids, which also deposit eggs on leaves above water (Delia, Bravo-Valencia and Warkentin, 2017). The behaviours of *D. haddadi* female, joining the eggs and sitting on the spawn, we described here have never been observed in other species of the genus and suggest some form of short-term maternal care of eggs. Further observations are needed to better describe the circumstances triggering these behaviours and their importance for offspring survival.

Toledo et al. (2011) described a spawn of *D. haddadi* on leaves above water, in Itacaré, Bahia state, northeastern Brazil, and observed that embryos were active on the fourth day and when they fell into the water they immediately started to swim. In our study, development took four days before tadpoles fell into the water. However, some tadpoles did not swim right on, probably because they were not fully developed. Tadpoles that fall into the water with the ability to swim are more likely to avoid predators and to be able to feed themselves (Warkentin et al., 2017). However, as described for *Agalychnis callidryas*, in cases of predator attack risks, embryos are able to hatch and fall earlier in the water and have a chance of surviving (Warkentin et al., 2017). We did not observe predators attacking spawns of *D. haddadi*, thus we could not confirm that embryos are able to hatch earlier.

At our study site, clutches of *D. haddadi* were mostly deposited on leaves of *Elaeis guineensis* (95% of observations), an exotic palm very common in this region present in great abundance surrounding all bodies of water. We also observed other anuran species (e.g., *Boana albomarginata* and *Hylomantis granulosus*) using *Elaeis guineensis* leaves as perches to vocalize. Other *Dendropsophus* species, such as *D. ebraccatus* and *D. microcephalus*, have also been observed associated with *Elaeis guineensis* in Costa Rica (Aranda et al., 2014). *Dendropsophus haddadi*, *D. microcephalus* and *D. ebraccatus* present the same reproductive mode (terrestrial eggs on leaves above lentic environments and exotrophic tadpoles that complete development in the water). Thus, the use of *Elaeis guineensis* by these species could be related with their similar reproductive biology and also due to the availability of this palm species commonly associated with humid environments.

Throughout the distribution of *D. haddadi*, in the Atlantic forest along the coast of Brazil, from the state of Pernambuco to the state of Rio de Janeiro (Bastos and Pombal 1996; De Abreu et al., 2013; Frost, 2019), populations face different rainy periods, habitat conditions and altitudes. We do not know how these variations can affect populations, but we can predict, through models indicating temperature increases (Lemes, Melo and Loyola, 2014) and forests' decrease and fragmentation (Ranta et al., 1998; Tabarelli et al., 2010), that they may suffer serious consequences, since they are associated with the few remaining areas of Atlantic forest. Amphibians are at serious risk of extinction in many regions of the world (da Silva et al., 2012; Vasconcelos, Nascimento and Prado, 2018). Studies using predictive models of climate change indicate that the extinction of 37 anuran species (10.57%) may occur in the Atlantic forest between 2050-2070 (Vasconcelos, Nascimento and Prado, 2018). The reasons for this scenario include global warming, rising temperatures, decreasing rainfall periods, spaced and torrential rains, habitat fragmentation, invasion of exotic species, diseases, use of pesticides, among many others (Young et al. 2005; Vasconcelos, Nascimento and Prado, 2018). For amphibians, decrease of forest area and fragmentation represent great threats when comparing with other impacts (Young et al., 2005). Thus, information about species´ ecology and behaviour serves not only to enhance our knowledge on their natural history, but are also extremely important to support conservation actions and policies (Loyola et al., 2008; da Silva et al., 2012).

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4 CAPÍTULO 2: EGG LAYING SITE, FECUNDITY AND DEGREE OF SEXUAL SIZE DIMORPHISM IN FROGS

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Egg laying site, fecundity and degree of sexual size dimorphism in frogs

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ABSTRACT

Female fecundity is an important selective force leading to female-biased sexual size dimorphism (SSD) in frogs. Because anurans exhibit diverse reproductive modes, we investigated whether variation in SSD and fecundity are correlated with oviposition site. Speciafically, we asked whether arboreal breeding species will show pronounced female-biased SSD and if, paradoxically, females will have lower fecundity because of the costs of carrying amplectant males. Conversely, we tested if species that deposit eggs in concealed terrestrial sites will show less pronounced SSD, because females do not carry males and space limitation may reduce fecundity and female size. Our results across all frogs and for hylids only showed that, in general, males were approximately 20% smaller than females. However, for hidden oviposition sites, males and females tended to have more similar body sizes, corroborating our hypothesis. Overall, fecundity was higher in aquatic breeders, as expected, but in hylids, fecundity was smaller in arboreal breeders, which suggests that arboreality may impose restrictions to fecundity. By analyzing SSD in a broader and more specific lineage, we found that the reproductive microhabitat may also influence female size and fecundity, playing an important role in the evolution of SSD in frogs at different evolutionary scales.

ADDITIONAL KEYWORDS: Anura, body size, costs of reproduction, female investment, Hylidae, reproductive mode

4.1 INTRODUCTION

Animals have undergone morphological, physiological, and behavioral adaptations in the transition from the aquatic to terrestrial habitats (Stearns, 1977; McInerney *et al*., 2011). Among these changes, the evolution and diversification of reproductive behaviors are highly related to environmental conditions and habitat types (Sadleir, 1973; Shine, 2005; Schoch, 2014; Pereira *et al*., 2015). Predation pressure by aquatic predators, water physico-chemical alterations, and terrestrial vacant niches have been considered as important selective factors leading to the evolution of terrestrial reproduction (Oparin, 1957; Magnusson & Hero, 1991; Touchon & Worley, 2015). More recently, sexual selection in the form of male-male competition (Zamudio *et al*., 2016) and parental care (Vági *et al*., 2019) have also been suggested as important pressures in the evolution of terrestrial reproduction in anuran amphibians. Among tetrapods, the extraordinary diversity of reproductive modes in frogs provides an opportunity to investigate hypotheses about the ecological and behavioral adaptations related to the aquatic-terrestrial transition (Grosjean *et al*., 2008; Crump, 2015; Zamudio *et al*., 2016; de Sá *et al*., 2019).

The most uptodate survey of anurans indicates that the group exhibits approximately 50 reproductive modes (e.g. Haddad & Prado, 2005; Gururaja *et al*., 2014; Iskandar *et al*., 2014; Kusrini *et al*., 2015) ranging from aquatic eggs to viviparity, and with great variation in egg deposition site, larval development site (if any), and type of parental care (Haddad & Prado, 2005; Wells, 2007; Furness & Capelini, 2019). Aquatic eggs and tadpoles are hypothesized as the ancestral mode in anurans and terrestrial modes evolved independently many times (Gomez-Mestre *et al*., 2012). Females of terrestrial breeding frogs tend to have small body sizes and deposit small clutches with large eggs (Salthe & Duellman, 1973; Pupin *et al*., 2010; Gomez-Mestre et al., 2012). In contrast, females of species with aquatic reproductive modes tend to be larger in body size and deposit a large number of small eggs (Salthe & Duellman, 1973; Crump, 1974; Gomez-Mestre *et al*., 2012). Because the reproductive output of females exerts a strong selective pressure on female body size, this can lead to differences in body sizes between the sexes, a phenomenon known as sexual size dimorphism (e.g. Shine, 1979; Nali *et al*., 2014).

Fecundity is positively correlated with female size (Hartmann *et al*., 2010; Gomez-Mestre *et al*., 2012; Torres-Cervantes *et al*., 2019) and the ‘fecundity advantage' hypothesis (Darwin, 1874; Shine, 1989; Nali *et al*., 2014) has been invoked as one of the main forces in the evolution of sexual size dimorphism (SSD) in frogs, where females are larger in nearly 90% of the species (Shine, 1979; Katsikaros & Shine, 1997; Nali *et al*., 2014). However, the degree of SSD is highly variable among species, indicating that males and females may suffer different selective pressures on body size (Han & Fu, 2013; Nali *et al*., 2014). Moreover, pressures are not linear, with stronger selective forces for fecundity increase being observed on females of smaller species (Nali *et al*., 2014). Costs of reproduction for females may also influence the evolution of sexual dimorphism (Shine *et al*., 1998). Although large females may have the advantage of higher fecundity, there might be constraints or trade-offs imposed by the costs of reproduction (Shine, 1992; Shine *et al*., 1998). Gravid females potentially have reduced survivorship due to decreases in locomotor ability, difficulties in using narrow shelters, and reduced predator escape capacity (Vitt, 1981; Shine *et al*., 1998). Moreover, interspecific differences in female fecundity may also be shaped by costs of reproduction associated to different habitat use and forms of locomotion, as reported for snakes and lizards (Gans, 1975; Shine, 1988; Shine *et al*., 1998). In frogs, females deposit eggs in a great variety of microhabitats, from water bodies to terrestrial humid sites, such as the surface of pendant leaves, rock crevices and tree holes (Haddad & Prado, 2005). Additionally, females need to choose suitable oviposition sites and sometimes escape from predators carrying amplectant males on their backs (Murphy, 2003; Wells, 2007). Thus, female size and fecundity, and consequently SSD, might be modulated by the habitat type used for oviposition.

Here, we used phylogenetic comparative methods to investigate the relationship among reproductive modes, degree of SSD, and fecundity in frogs. Aquatic, arboreal, exposed terrestrial, and concealed terrestrial (hereafter 'hidden') habitats encompass the majority of oviposition sites used by anuran species, and these habitats might impose different challenges for females and amplectant pairs. Therefore, we evaluated how SSD and fecundity varied among these reproductive site categories. We specifically tested the hypotheses that: (1) arboreal breeding species will show pronounced female-biased SSD (larger females and smaller males) because females need to move on the vegetation to deposit eggs carrying amplectant males on their back; (2) species that deposit eggs in concealed terrestrial sites (‘hidden sites’) will show less pronounced or absent SSD, because females do not carry males and space limitations to amplectant pairs may reduce female size and fecundity; and (3) species that deposit eggs in exposed sites (either aquatic or terrestrial) will follow the SSD pattern for frogs (females larger than males), but at an intermediate degree when compared to species breeding in arboreal and concealed sites. Because fecundity is an important selective force affecting female size and SSD in frogs, we also investigated clutch size variation (number of eggs) among different oviposition sites. We asked whether in arboreal species, female fecundity will be smaller compared to species that use other terrestrial oviposition sites (e.g. leaf litter, rock crevices, holes, subterranean chamber), because of the extra load that females have to carry in their abdomen. Thus, although we expect larger females in arboreal breeders, we paradoxically expect lower fecundity because of the transport cost for females.

4.2 MATERIALS AND METHODS

4.2.1 Data Collection and Phylogeny

We extracted from the literature data on average snout-vent length of males and females (SVL, standard measurement of body size), as well as clutch size (average number of eggs per clutch) and egg size (average diameter of eggs). In the absence of clutch and egg size, we complemented our dataset including average number of oocytes per gravid female and average oocyte diameter (see Nali *et al*., 2014). Based on literature description of reproductive modes (*sensu* Haddad and Prado, 2005), we classified the oviposition sites in four main categories: (1) arboreal (species with eggs deposited on leaves, twigs or trunks), (2) aquatic (species with eggs deposited directly in the water, both lentic and lotic), (3) terrestrial (species with eggs deposited directly on the soil or litter) and (4) hidden (species with eggs in concealed sites, including natural or constructed nests, such as burrows, tree holes, subterranean chambers, crevices, and phytotelmata).

We ran all phylogenetic comparative analyses (see below) using the amphibian topology proposed by Pyron *et al*. (2011) with original branch lengths. For each analysis, we pruned the original tree in the software Mesquite v. 3.51 (Maddison & Maddison, 2018) to contain only the species with available data.

4.2.2 Sexual Size Dimorphism and Oviposition Site

Each species was assigned a sexual size dimorphism index (SDI) based on a two-step ratio of male and female body sizes (Lovich & Gibbons, 1992; revised by Smith, 1999), a value that is symmetrical around one, when males and females have the same body sizes. For species in which male SVL ≥ female SVL, SDI = male SVL / female SVL. For species in which female SVL > male SVL, SDI = 2 - (female SVL / male SVL). Thus, species with female-biased sexual size dimorphism show SDI < 1, and those with male-biased sexual size dimorphism show SDI > 1. We then compared SDI among the different oviposition site categories using phylogenetic analyses of variance (phylogenetic ANOVAs), with pairwise post hoc tests under a thousand simulations yielding adjusted *P* values, according to Holm (1979). We conducted the analyses for all anuran species in our dataset and also separately only for species of Hylidae (*sensu* Faivovich *et al*. 2005), the most speciose family in our dataset that exhibits a great diversity of reproductive modes (Haddad & Prado, 2005). For Anura, all four oviposition site categories were used, but for hylids only three categories were used: aquatic, arboreal and hidden, because there were no exposed terrestrial breeding species in the hylid dataset. Because we had different sample sizes in our oviposition categories for both Anura and Hylidae, we ran additional analyses to check for biases (Supporting Information, Supplemental Analyses). We ran all analyses and visualized the data using the *phytools* and *ggplot2* packages on the R platform (Revell, 2012; Wickham, 2016; R Core Team, 2019).

4.2.3 Female Fecundity and Oviposition Site

Given that the number of eggs may correlate negatively with egg size (Gomez-Mestre *et al*., 2012), which may affect comparisons of fecundity among species, we conducted an exploratory analysis with a smaller database for which we had egg diameter and number (*N* = 54 species; Supporting information, Table S1). We log-transformed these variables and ran a simple regression analysis using phylogenetic independent contrasts performed in the *phytools* package in R (Felsenstein, 1985; Revell, 2012; R Core Team, 2019). Although significant (*F* = 4.83; *P* = 0.032), the low value of the adjusted R^2 (0.067) indicated a very weak relationship between those two variables. Thus, we did not account for egg size in the fecundity analyses, which enabled us to increase our sample size.

Because females of larger species usually produce a larger number of eggs (Prado & Haddad, 2005; Nali *et al*. 2014), we first ran a Phylogenetic Generalized Least Squares (PGLS) regression analysis between log number of eggs per clutch and log female SVL to extract the residuals. The residual values were then used as a proxy for fecundity measurement, eliminating the effect of female body size. Then, to test restrictions to fecundity due to arboreality, fecundity was compared among four oviposition site categories for Anura (aquatic, arboreal, terrestrial, and hidden) and three oviposition site categories for Hylidae (aquatic, arboreal, and hidden). We ran phylogenetic ANOVAs for Anura and for Hylidae using the same statistical procedures described above. We ran all analyses and visualized the data using the *phytools*, *nlme* and *ggplot2* packages in R (Revell, 2012; Wickham, 2016; Pinheiro et al., 2019; R Core Team, 2019).

4.3 RESULTS

4.3.1 Dataset

We compiled data for a total of 385 species in 32 anuran families: 271 aquatic, 48 arboreal, 35 hidden, and 31 terrestrial (Supporting information, Table S1, Figs. S1 and S3). For Hylidae, we analyzed a total of 221 species: 175 aquatic, 30 arboreal, and 16 hidden (Supporting information, Table S1, Figs. S2 and S4). From this large dataset, each analysis included a different subset of species according to the type of data available for each species.

4.3.2 Sexual Size Dimorphism and Oviposition Site

For anurans, we had representatives of aquatic, arboreal, terrestrial, and hidden oviposition sites; we found no differences in SDI when we compared among these sites (phylogenetic ANOVA, N = 385 species of 32 families; F = 7.27; P = 0.205). However, variation in SDI was much higher in species with aquatic oviposition (Fig. 1A; Table 1). For the Hylidae family, we had representatives of aquatic, arboreal, and hidden oviposition sites; similarly, the overall phylogenetic ANOVA indicated no differences in SDI among oviposition sites (N = 221 species; F

= 10.34; *P* = 0.282), but the post hoc simulations indicated a difference between species with aquatic and hidden oviposition sites (*P* = 0.048). We also found a tendency of species with hidden oviposition to show SDI closer to 1 (males and females with similar body sizes) compared to the other oviposition categories (Fig. 1; Table 1). We had very similar results in our additional analyses with random equal sample sizes (Supporting Information, Supplemental Analyses).

4.3.3 Female Fecundity and Oviposition Site

Fecundity, based on the residuals of number of eggs per clutch relative to female body size, differed significantly among oviposition sites for anurans (236 species of 32 families; *F* = 104.62; *P* = 0.001; Fig. 2A; Supporting information, Table S2). For the Hylidae family, we had representatives from aquatic, arboreal, and hidden oviposition sites, and we also found a significant difference in fecundity (103 species; *F* = 50.89; *P* = 0. 004; Fig. 2B; Supporting information, Table S2). For both Anura and Hylidae, our results showed that fecundity in aquatic breeders was higher compared to that of other oviposition sites. Moreover, for anurans, fecundity in arboreal breeders was similar to those of terrestrial and hidden (Fig. 2A); for hylids, arboreal fecundity was similar to that of hidden (Fig. 2B). However, hylids with arboreal clutches showed a tendency to have lower fecundity (Fig. 2B).

4.4 DISCUSSION

Most anurans show female-biased sexual size dimorphism (SSD), however there is a great variation in the degree of SSD across species (Shine, 1979; Nali *et al*., 2014). Our results indicate that oviposition site may impose some restrictions to female size and fecundity, which may contribute to the variation in SSD observed among frogs. In many animal groups, SSD has been classically explained based on selective pressures in which (1) larger males gain direct reproductive advantages because of male-male competition or as a consequence of female choice (leading to male-biased SSD) or (2) larger females are favored because of increased fecundity (leading to female-biased SSD; Reeve & Fairbairn, 1999; Dale *et al*., 2007; Kupfer, 2009; Nali *et al*., 2014). Thus, SSD may be the result of differences in the effects of natural and sexual selection on body sizes of males and females, making the study of SSD a challenge for evolutionary biologists (Oufiero & Garland, 2007; Littleford-

Colquhoun *et al*., 2019). In the case of anurans, many studies have focused on sexual selection, fecundity, and differences in growth rate, age, and breeding strategies to explain differences between male and female size (e.g. Monnet & Cherry, 2002; Han & Fu, 2013; Nali *et al*., 2014; de Sá *et al*., 2019). Our data show that the reproductive habitat may also play an important role in the evolution of SSD in frogs.

We did not find an association between SSD and type of oviposition site. Mean SDIs were statistically similar among species breeding in different microhabitat types, for both Anura and Hylidae. For most oviposition sites we compared, SDI ranged from 0.82 – 0.86, which means that males are 14 – 18% smaller than females independent of the phylogenetic lineage analyzed here (Anura and Hylidae). Studies on anuran mating strategies have shown that physical or mechanical constraints may influence pair formation, leading females to choose males that have similar sizes (‘size-assortative’ mating) (e.g. Bastos & Haddad, 1996; Lu *et al*., 2010); indeed, assortative mating has been shown to be a general tendency in animals (Jiang *et al*., 2013; Janicke *et al*., 2019). Specifically for frogs, where the majority of species exhibit axillary amplexus and external fertilization, juxtaposition of cloacae may be crucial for fertilization success. For some species, optimum fertilization rate was attained when males were approximately 20% smaller than females (Robertson, 1990; Bourne, 1993; Bastos & Haddad, 1996), which coincides with the SDI values we found for species that deposit eggs in the water, on the vegetation, or in exposed terrestrial habitats. The exception was the group of species that lay eggs in hidden/concealed sites, which showed SDI close to 1, i.e., males and females with similar body sizes (Fig. 1 and Table 1). Indeed, for hylids, the post hoc analysis showed significant differences in SDI between species that lay aquatic eggs vs. those with hidden clutches. In species that lay eggs in hidden sites, many selective pressures may contribute to decrease female size and, hence, attenuate SSD. In these species, the pair must fit in a restricted space during oviposition (e.g. rock crevices, tree holes, subterranean chamber) and this limitation might extend to the amount of eggs that can be laid in such space, which may diminish the selective pressures for increases in female body size. Furthermore, in many species, males construct chambers where eggs will be laid and females do not carry amplectant males, instead they follow males into these structures where amplexus occurs (e.g.

Haddad *et al*., 2005; Lucas *et al*., 2008; Faggioni *et al*., 2017), what may also reduce pressures for female body increase. In fact, studies with some anuran lineages have shown that when males construct subterranean chambers, males and females have similar body sizes (e.g. Heyer, 1978; Haddad *et al*., 2005; Berneck *et al*., 2017). Thus, our results suggest that the evolution of oviposition in hidden and limited spaces might have been accompanied by a reduction in female body size and decrease in SSD, in support of our hypothesis.

Another interesting result was that SDI was more variable among aquatic breeding frogs when compared to those that use other oviposition sites, ranging from 0.56 – 1.43 in Anura and 0.58 – 1.17 in Hylidae (Table 1). Intensity of sexual selection, in the forms of male-male competition (intrasexual selection) or female choice (intersexual selection) are quite different among anuran species exhibiting different reproductive strategies (e.g. temporal breeding pattern, reproductive mode), which may affect the intensity of selection on body size of males and females (Wells, 1977; Zamudio *et al*., 2016; de Sá *et al*., 2019). In explosive reproduction, which is more common among aquatic breeders (Wells, 1977; Prado *et al*., 2005), individuals form dense aggregations around and inside water bodies, where males attempt to amplect any individual, engage in scramble competition, and females have less opportunities for mate choice (Wells, 1977). This context may lead to a random mating relative to size (e.g. Wells, 1977; Howard & Kluge, 1985) and consequently to a greater variation in SSD. Alternatively, the explanation for the greater variation in SSD among aquatic breeders could be that juxtaposition of cloacae may be more critical for fertilization success in terrestrial habitats than in aquatic ones, because of fertilization facilitation provided by the water. The mechanics of fertilization in different environments deserves further investigation.

Advantages conferred by increases in female fecundity explain much of the female-biased SSD in frogs (Han & Fu, 2013), however selective forces vary according to species body size and reproductive pattern (Nali *et al*., 2014). Regarding other vertebrate groups, many studies in squamates have shown that females may be constrained in increasing fecundity because of the costs imposed by clutch mass burden, which may lead to trade-offs between fecundity and locomotor performance, affecting predator escape ability and survival (e.g. Seigel *et al*., 1987; Miles *et al*., 2000;Shine, 2003). Frog species exhibit a great diversity of habits, including aquatic, arboreal, terrestrial and fossorial, offering an opportunity to investigate the relationship between habitat use, performance and sexual dimorphism (Herrel *et al*., 2012). In many species, female frogs that deposit eggs on the vegetation above water, besides climbing the vegetation, carry amplectant males prior and during oviposition, and eventually need to scape from predators (Wells, 2007; Silva *et al*., 2019). Thus, we expected a lower fecundity in arboreal species due to the high costs of carrying both the male and the egg mass; this was partially corroborated for hylids, as we found a significant decrease in fecundity in these species when compared to aquatic ones. Furthermore, our data showed a tendency toward decreased fecundity for hylid species that lay eggs on vegetation (Fig. 2B) when compared to all other species in the family, suggesting that arboreality may influence fecundity in this lineage. The Hylidae family (*sensu* Faivovich et al., 2005) is one of the most diverse among anurans (Frost, 2020), composed mainly of arboreal species that exhibit the generalized aquatic reproductive mode (aquatic eggs and larvae), but also includes species with arboreal reproductive modes (Haddad & Prado, 2005; Touchon & Warkentin, 2008; Zamudio *et al*., 2016). Because we analyzed variation in fecundity for a limited number of species in the family, we suggest that this hypothesis deserves further investigation by adding more taxa to the comparative analysis, which will be possible with the accumulation of natural history studies and fecundity data.

The fact that fecundity of hylids that deposit eggs in hidden oviposition sites was similar to that of arboreal breeding species may be related to other limiting factors, such as the deposition of eggs in a restricted space, as discussed above. In the classical paper by Salthe and Duellman (1973), although analyzing a small diversity of species in different families, they described some interesting patterns. For instance, among species that lay eggs on vegetation, those that deposit eggs on leaves and tadpoles develop in lentic water have larger clutches and smaller eggs compared to species that deposit eggs on leaves and tadpoles develop in lotic habitats, and both arboreal modes exhibit larger clutches and smaller eggs compared to terrestrial breeders with direct development (Salthe & Duellman, 1973). Thus, what seems like a small environmental change, whether tadpoles develop in lentic or lotic environments, has the potential to influence fecundity. Terrestrial reproductive modes include a myriad of reproductive specializations so that eggs can be laid out of water (e.g. on humid floor, in rock crevices, on leaves above the water, in bromeliads, tree holes, subterranean chambers), including indirect and direct development (Haddad & Prado, 2005). Although we are aware that the reproductive modes in our analyses do not capture these detailed differences, and that some of our reproductive categories are limited in sample size, our results show that fecundity increase in females that breed arborealy and/or in limited space may be constrained, and therefore represents one more selective axis influencing the evolution of SSD.

When analyzing complex features, such as SSD and reproductive investment, at a broad phylogenetic scale, it is often difficult to disentangle the complex interactions between natural and sexual selection (e.g. John-Alder *et al*., 2007; Nali *et al*., 2014; Zamudio *et al*., 2016). By studying SSD in a broader (Anura) and a smaller lineage of frogs (Hylidae), we detected low variation in SSD across taxa reproducing in different microhabitats, albeit less pronounced in species laying eggs in concealed sites, and a tendency of reduced fecundity in hylids with arboreal reproductive mode. Thus, we conclude that the degree and direction of SSD in anurans result from a complex combination of evolutionary processes acting on both males and females at different evolutionary scales (Nali *et al*., 2014; de Sá *et al*., 2019; this study).

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TABLE

Table 1. Mean, standard deviation (SD) and range of sexual dimorphism index (SDI) for anurans and hylids in the four categories of oviposition sites. Species with SDI < 1 have female-biased dimorphism, and SDI >1 have male-biased dimorphism.

	SDI Anura			SDI Hylidae		
Oviposition site	Mean	SD	Range	Mean	SD	Range
Aquatic	0.86	0.11	0.56 – 1.43	0.86	0.10	0.58 – 1.17
Arboreal	0.83	0.08	0.66 – 1.04	0.82	0.08	0.66 – 1.04
Hidden	0.94	0.09	0.72 – 1.14	0.96	0.10	0.72 – 1.15
Terrestrial	0.84	0.10	0.65 – 1.02	NA	NA	NA

FIGURES

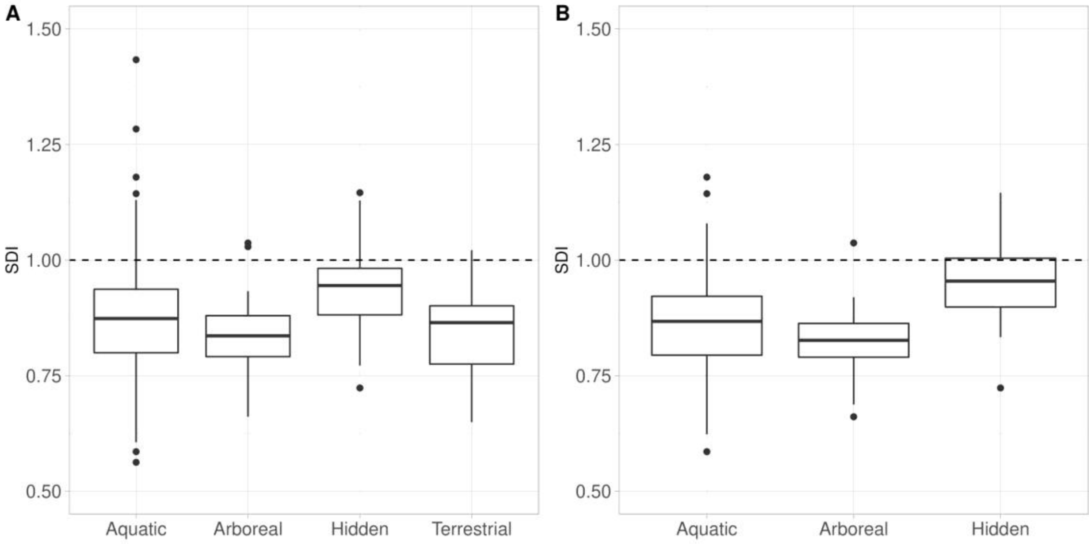


Figure 1. Boxplots showing the differences in sexual dimorphism index (SDI) among oviposition site categories for (A) 385 anuran species from 32 families, with aquatic, arboreal, hidden, and terrestrial clutches, and (B) 221 hylid species, with aquatic, arboreal, and hidden clutches. Species with SDI < 1 have female-biased dimorphism, those with SDI >1 have male-biased dimorphism, and the dashed lines indicate males and females with equal body sizes (SDI = 1). Overall Phylogenetic ANOVAs were not significant for either A or B, but the post hoc simulation showed differences between aquatic and hidden species in B (see text for details).

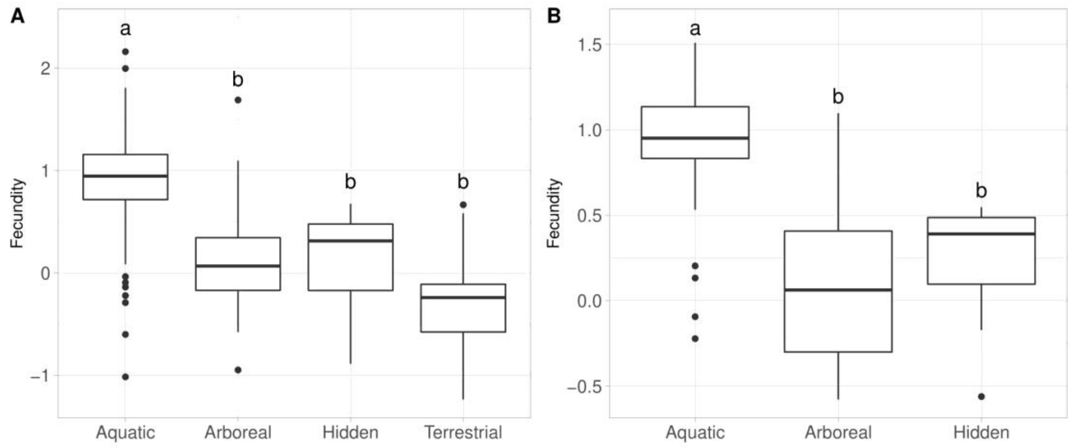


Figure 2. Boxplots showing the differences in the residuals of number of eggs per clutch relative to female body size (proxy for fecundity) among oviposition site categories for (A) 236 anuran species in 32 families, with aquatic, arboreal, hidden and terrestrial reproduction, and (B) 103 hylid species, with aquatic, arboreal and hidden reproduction. Letters above each boxplot indicate statistical significance under a phylogenetic ANOVA with post hoc simulations (see text for details).

SUPPORTING INFORMATION

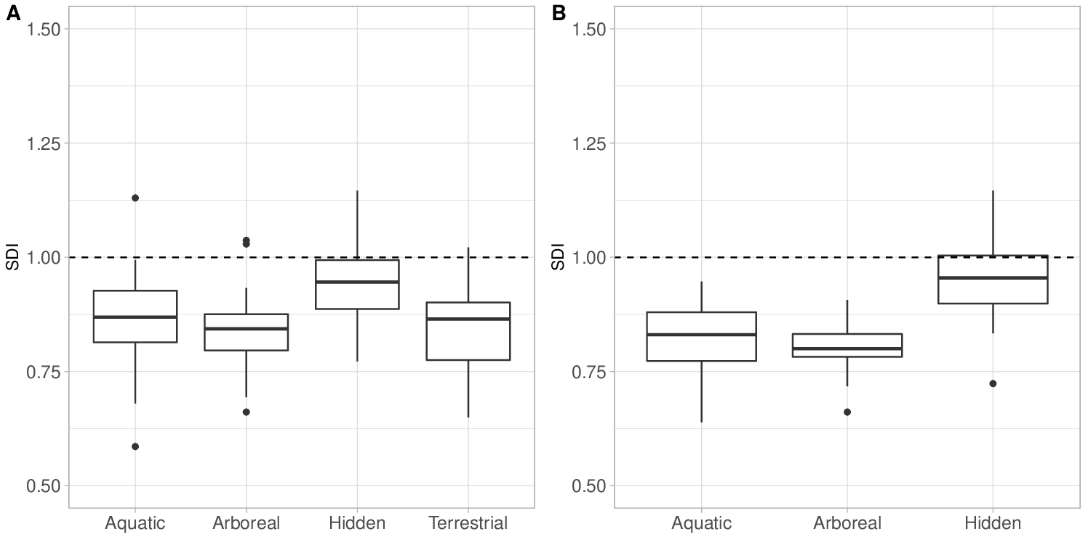
Supplemental Analyses

To account for possible biases in our analyses of SDI due to different sample sizes in oviposition site categories, we conducted additional phylogenetic ANOVAs. Please refer to the main article for details of the analyses and software references.

For Anura, the oviposition site category with fewer observations was terrestrial (N = 31), so we randomly sampled 31 species for each of the other three categories (aquatic, arboreal and hidden) by using the function *sample* in the R software. We then pruned the tree accordingly in the software Mesquite and ran the phylogenetic ANOVA with this reduced dataset. The phylogenetic ANOVA remained non-significant in this analysis, i.e., SDI was similar among all oviposition site categories (F = 9.12, P = 0.079). The post hoc tests indicated a difference between aquatic vs. hidden ($P < 0.05$), different from the main analysis. However, this tendency was already reported in the main article (species with hidden oviposition sites with higher SDI values). Thus, our interpretations did not change.

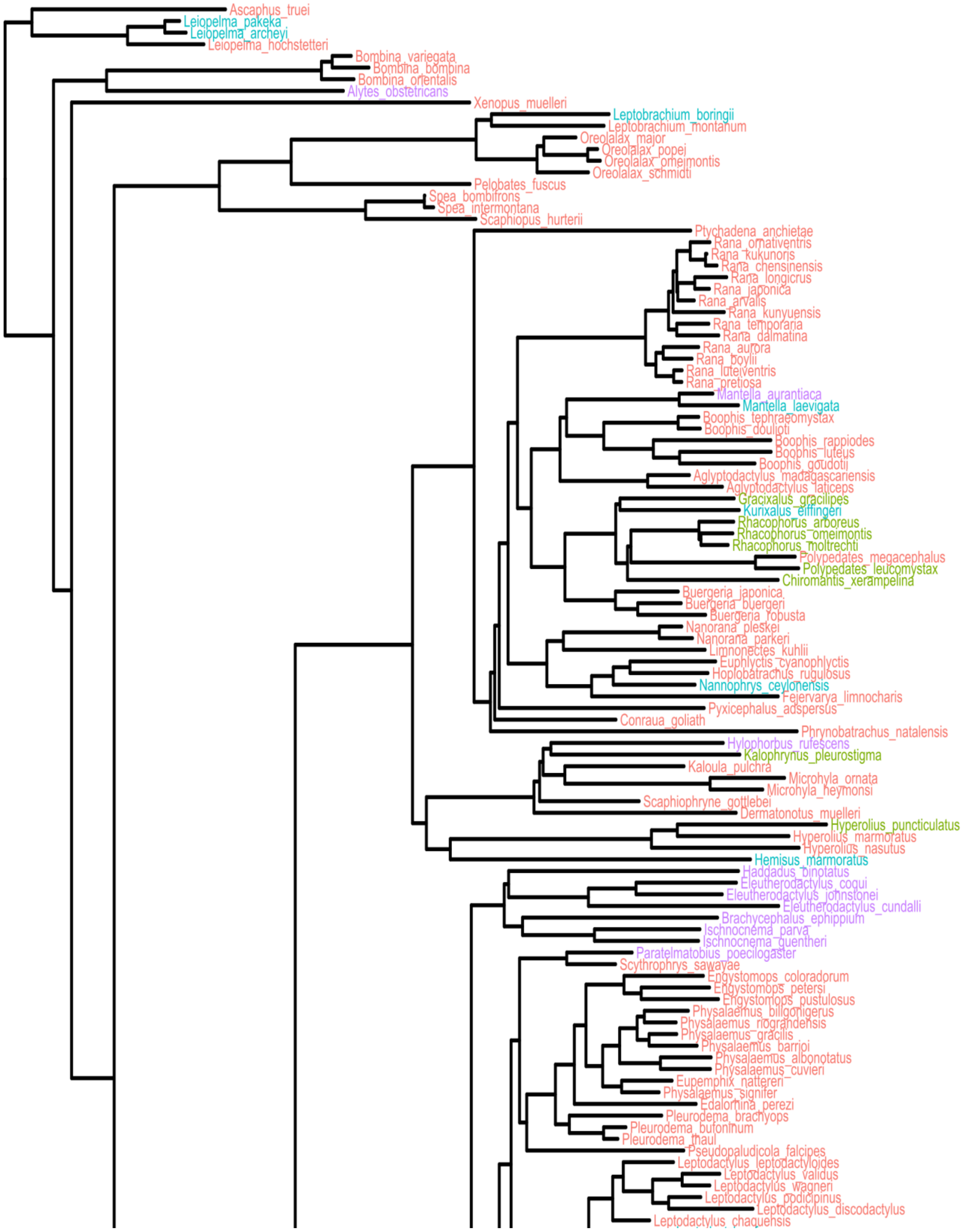
For Hylidae, the oviposition site category with fewer observations was hidden (N = 16), so we did the same procedure as described above for the other two categories (aquatic and arboreal). Post hoc tests indicated the same difference found in the main analysis (aquatic vs. hidden; $P < 0.05$). The overall phylogenetic ANOVA was significant (F = 16.29, $P < 0.05$), different from the main analysis in the article. However, since the post hoc differences were the same, our interpretations did not change.

The figure below shows the comparison of SDI among species with different oviposition sites in Anura (A) and Hylidae (B) and is comparable to our results shown in Figure 1 in the main article.



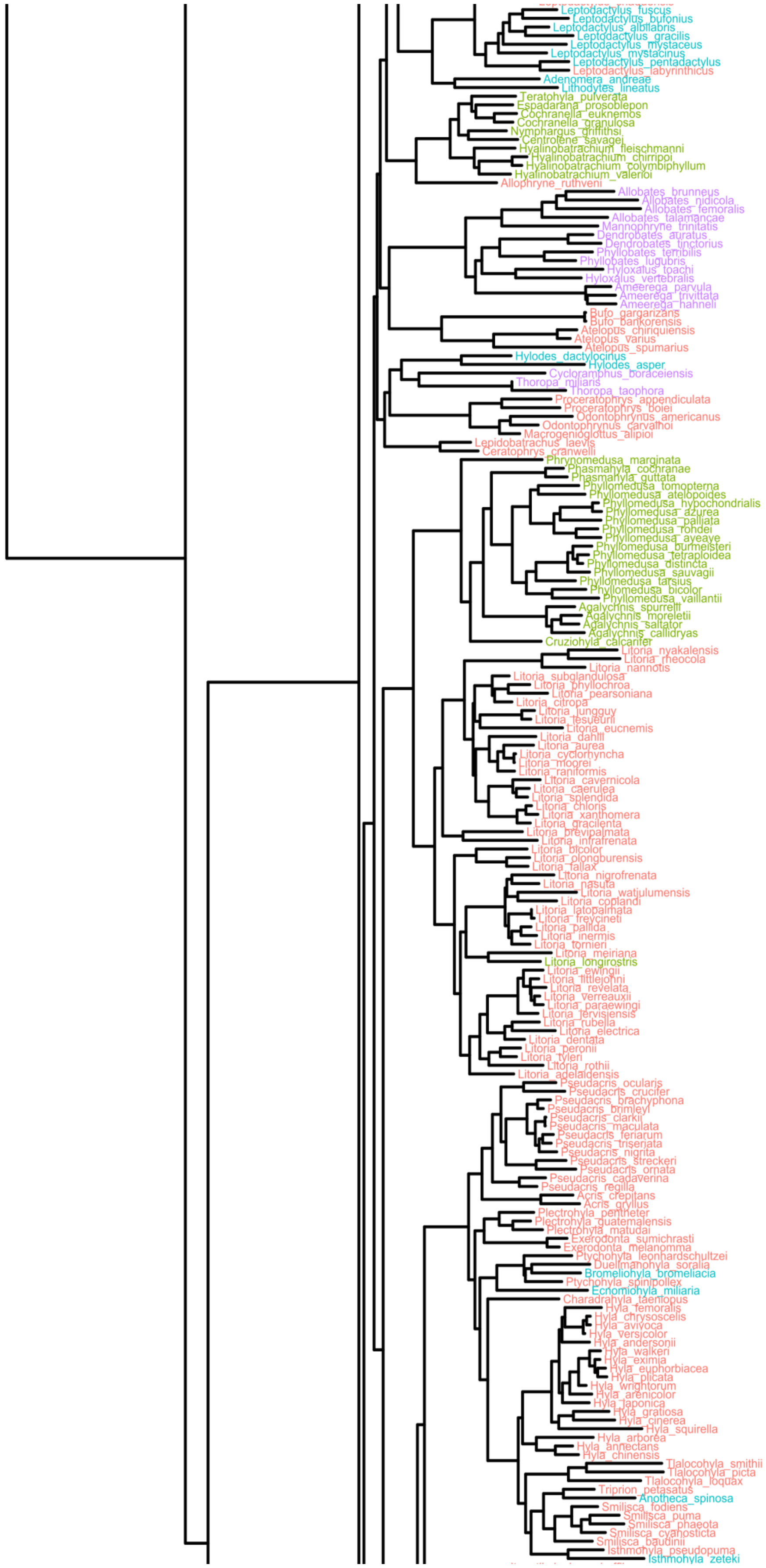
The 124 species selected in the Anura analysis in alphabetical order were: *Adenomera andreae, Agalychnis saltator, Agalychnis spurrelli, Allobates brunneus, Allobates femoralis, Allobates nidicola, Allobates talamancae, Alytes obstetricans, Ameerega hahneli, Ameerega parvula, Ameerega trivittata, Aplastodiscus arildae, Aplastodiscus cochranae, Aplastodiscus leucopygius, Aplastodiscus perviridis, Ascaphus truei, Boana crepitans, Boana heilprini, Boana lundii, Boana raniceps, Bokermannohyla martinsi, Bombina variegata, Brachycephalus ephippium, Bromeliohyla bromeliacia, Buergeria buergeri, Chiromantis xerampelina, Corythomantis greeningi, Cruziohyla calcarifer, Cycloramphus boraceiensis, Dendrobates auratus, Dendrobates tinctorius, Dendropsophus branneri, Dendropsophus brevifrons, Dendropsophus leucophyllatus, Dendropsophus robertmertensi, Dendropsophus sarayacuensis, Ecnomiohyla miliaria, Eleutherodactylus coqui, Eleutherodactylus cundalli, Eleutherodactylus johnstonei, Exerodonta melanomma, Exerodonta sumichrasti, Haddadus binotatus, Hemisus marmoratus, Hoplobatrachus rugulosus, Hyalinobatrachium chirripoi, Hyalinobatrachium colymbiphyllum, Hyalinobatrachium fleischmanni, Hyla arenicolor, Hylodes asper, Hylodes dactylocinus, Hylophorbus rufescens, Hyloxalus toachi, Hyloxalus vertebralis, Hyperolius puncticulatus, Ischnocnema guentheri, Ischnocnema parva, Isthmohyla zeteki, Kurixalus eiffingeri, Leiopelma archeyi, Leiopelma pakeka, Leptobrachium boringii, Leptodactylus bufonius, Leptodactylus discodactylus, Leptodactylus fuscus, Leptodactylus gracilis, Leptodactylus mystaceus, Leptodactylus mystacinus, Leptodactylus pentadactylus, Lithodytes lineatus, Litoria dentata, Litoria electrica, Litoria fallax, Litoria longirostris, Litoria* *nannotis, Litoria peronii, Litoria watjulumensis, Mannophryne trinitatis, Mantella aurantiaca, Mantella laevigata, Metacrinia nichollsi, Mixophyes fasciolatus, Myobatrachus gouldii, Nannophrys ceylonensis, Nyctimantis rugiceps, Nymphargus griffithsi, Osteopilus septentrionalis, Osteopilus wilderi, Paratelmatobius poecilogaster, Phasmahyla cochranae, Phasmahyla guttata, Phrynomedusa marginata, Phyllobates lugubris, Phyllobates terribilis, Phyllodytes luteolus, Phyllomedusa atelopoides, Phyllomedusa ayeaye, Phyllomedusa azurea, Phyllomedusa bicolor, Phyllomedusa distincta, Phyllomedusa hypochondrialis, Phyllomedusa rohdei, Phyllomedusa sauvagii, Phyllomedusa tetraploidea, Phyllomedusa tomopterna, Phyllomedusa vaillantii, Physalaemus albonotatus, Physalaemus riograndensis, Polypedates leucomystax, Pseudacris cadaverina, Pseudacris clarkii, Pseudacris crucifer, Rana japonica, Rana ornativentris, Rhacophorus moltrechti, Rhacophorus omeimontis, Scinax elaeochroa, Smilisca puma, Sphaenorhynchus lacteus, Stefania evansi, Thoropa miliaris, Thoropa taophora, Trachycephalus resinifictrix, Xenohyla truncata*.

The 48 species selected in the Hylidae analysis in alphabetical order were: *Agalychnis saltator, Anotheca spinosa, Aplastodiscus arildae, Aplastodiscus cochranae, Aplastodiscus leucopygius, Aplastodiscus perviridis, Boana heilprini, Boana pardalis, Boana rufitelus, Boana semilineata, Bokermannohyla martinsi, Bromeliohyla bromeliacia, Cruziohyla calcarifer, Dendropsophus branneri, Dendropsophus leucophyllatus, Dendropsophus marmoratus, Dendropsophus sarayacuensis, Dendropsophus triangulum, Ecnomiohyla miliaria, Hyla avivoca, Isthmohyla zeteki, Litoria adelaidensis, Litoria citropa, Litoria cyclorhyncha, Litoria dahlii, Litoria littlejohni, Litoria nasuta, Litoria nigrofrenata, Nyctimantis rugiceps, Osteopilus crucialis, Osteopilus marianae, Osteopilus vastus, Osteopilus wilderi, Phrynomedusa marginata, Phyllodytes luteolus, Phyllomedusa bicolor, Phyllomedusa burmeisteri, Phyllomedusa distincta, Phyllomedusa hypochondrialis, Phyllomedusa rohdei, Phyllomedusa sauvagii, Phyllomedusa tarsius, Phyllomedusa tomopterna, Phyllomedusa vaillantii, Pseudacris clarkii, Ptychohyla spinipollex, Scinax ruber, Trachycephalus resinifictrix.*



Supplemental Figure 1. Phylogeny of Anura extracted from Pyron & Wiens (2011) used in this study, with colored species according to spawning sites. Pink = aquatic; green = arboreal; blue = hidden; lilac = terrestrial.

Supplemental Figure 1. (continued).



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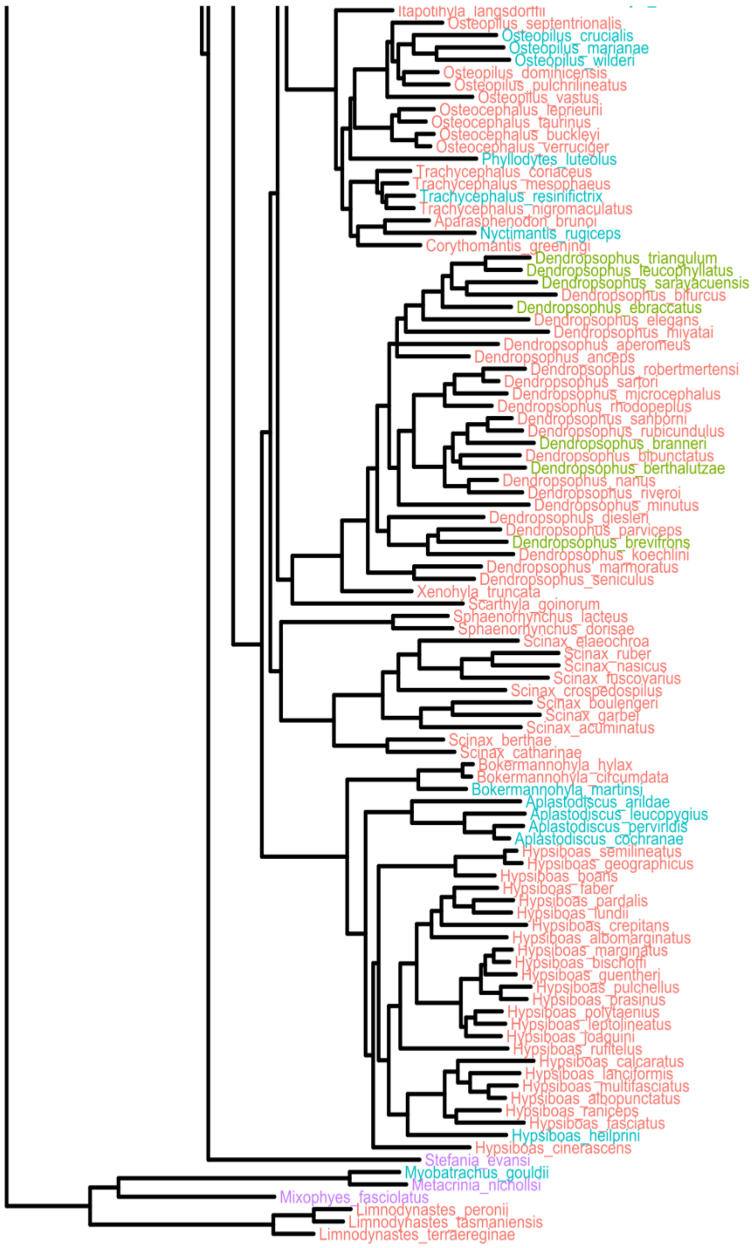
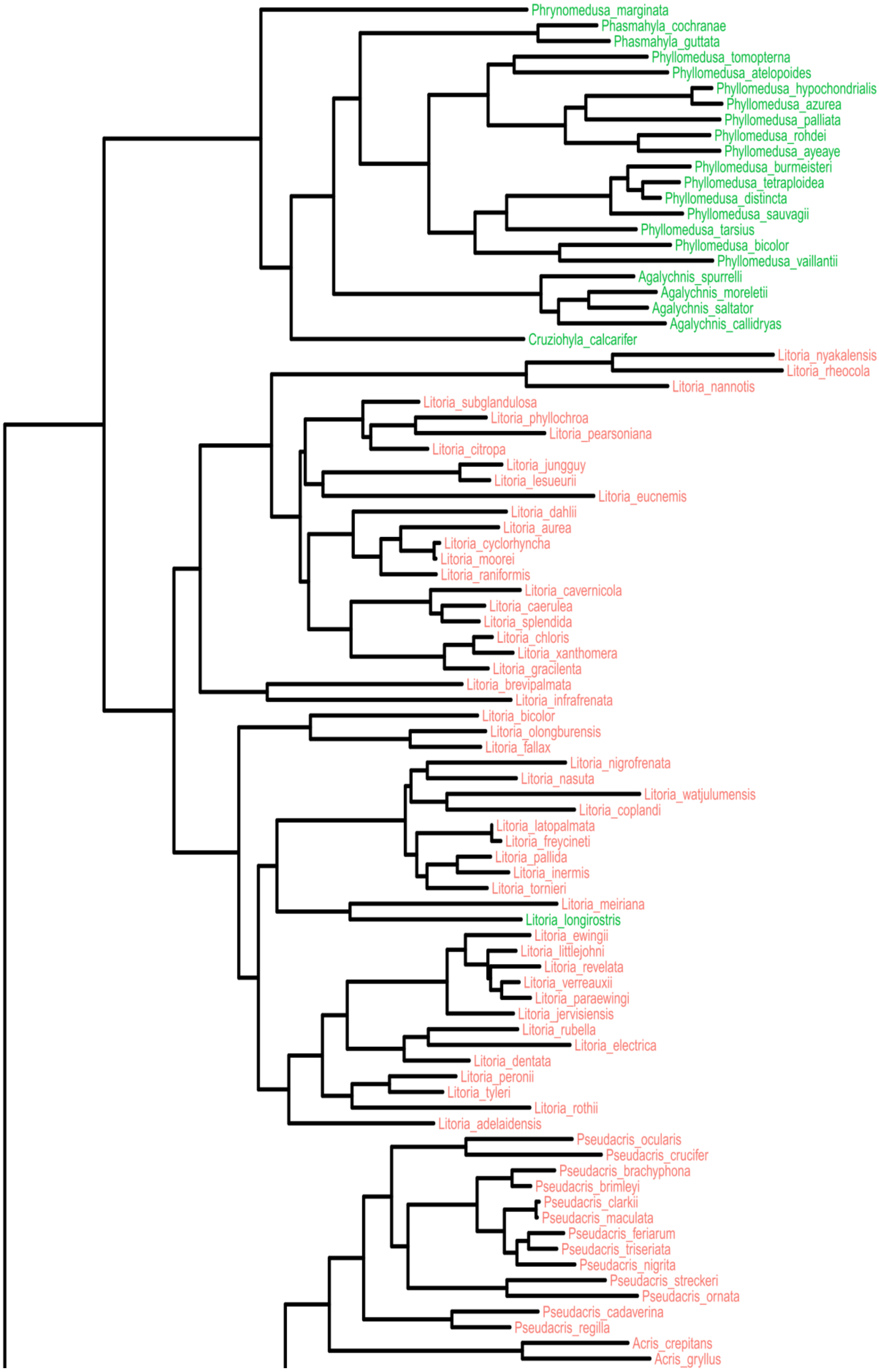
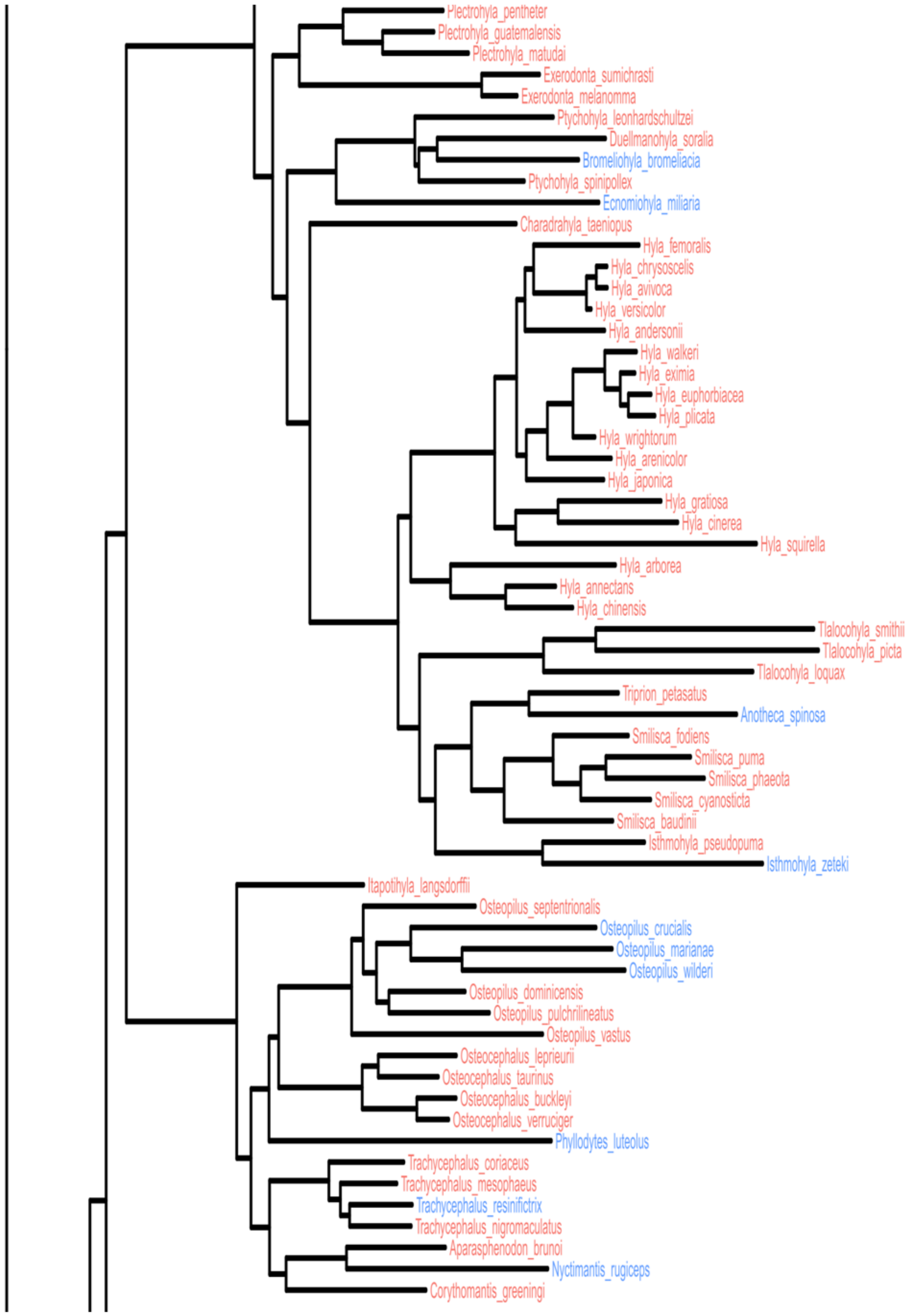




Supplemental Figure 2. Phylogeny of Hylidae extracted from Pyron & Wiens (2011) used in this study, with colored species according to spawning sites. Pink = aquatic; green = arboreal; blue = hidden

Supplemental Figure 2. (continued).



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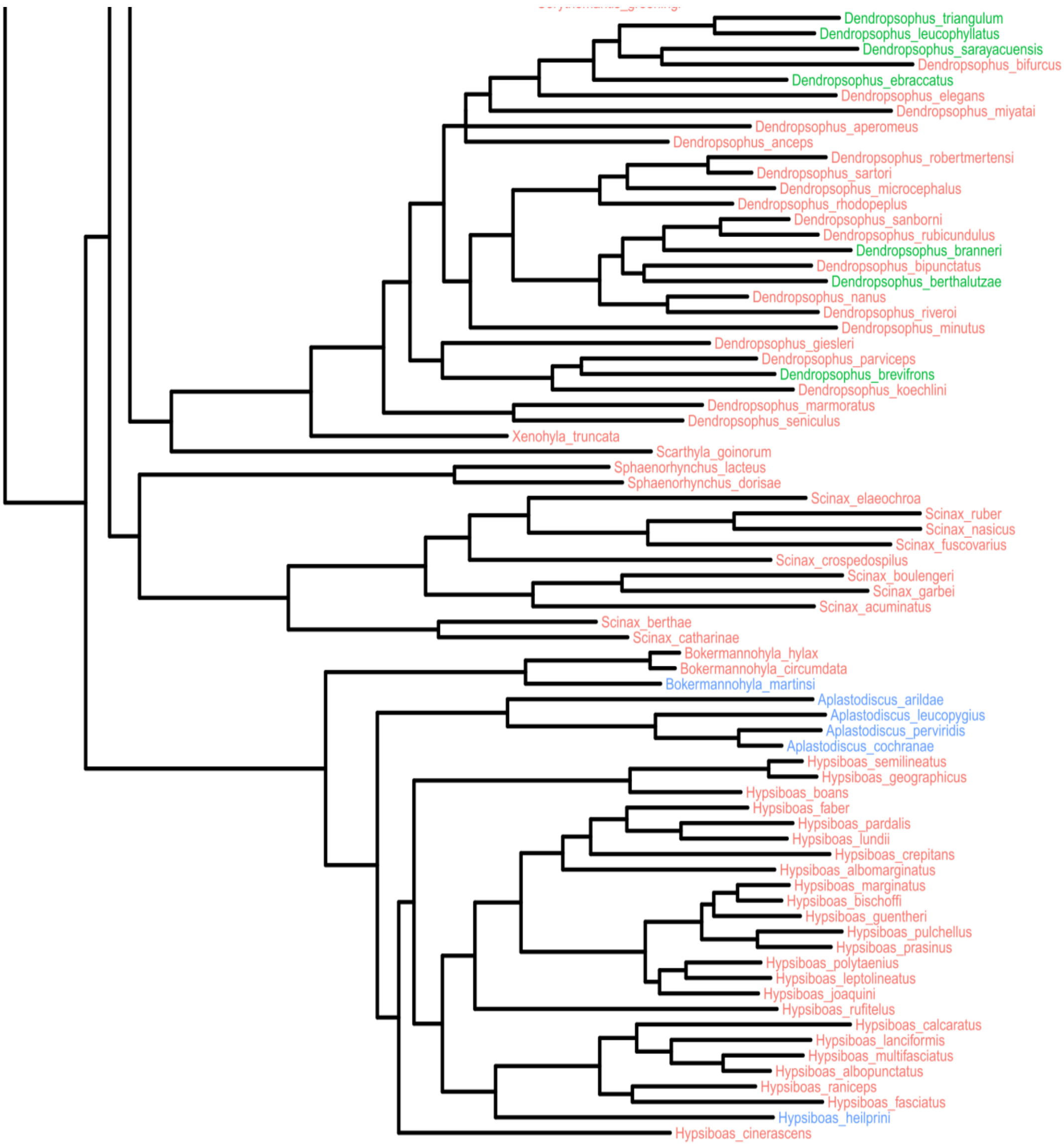
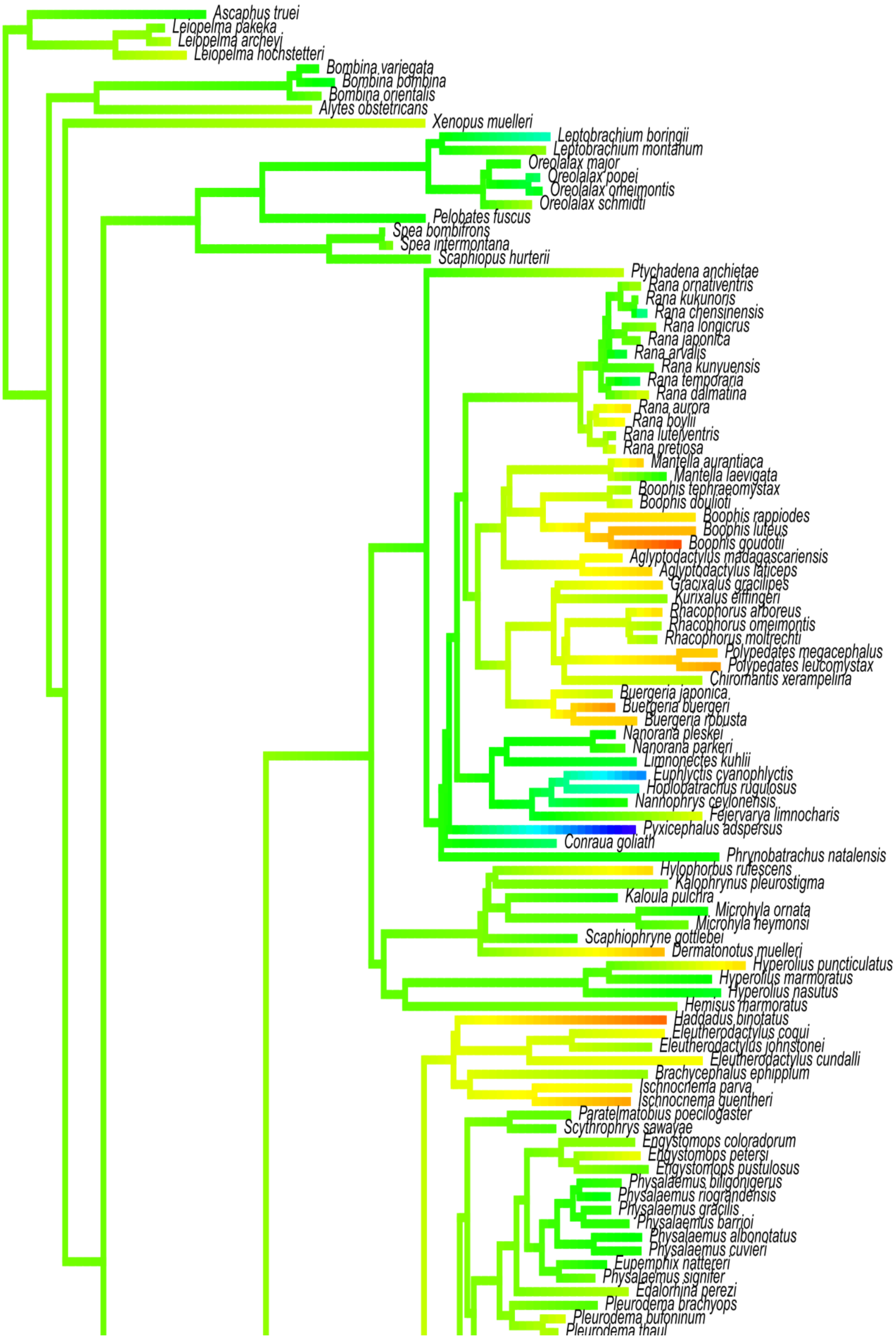
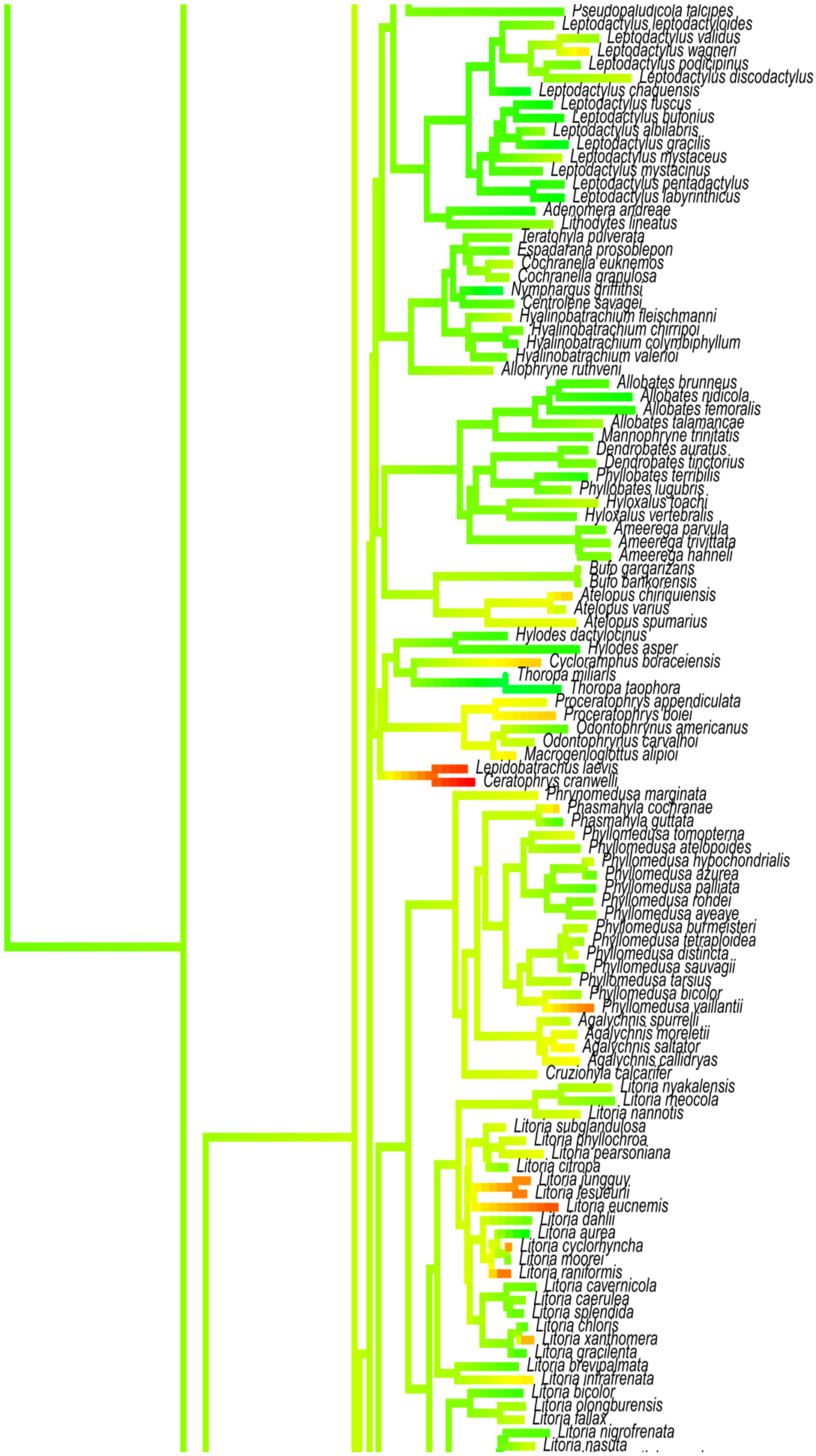




Supplemental Figure 3. Phylogeny of Anura extracted from Pyron & Wiens (2011) used in this study, with colored branches according to sexual dimorphism index (SDI; legend at the end of the figure).

Supplemental Figure 3. (continued).



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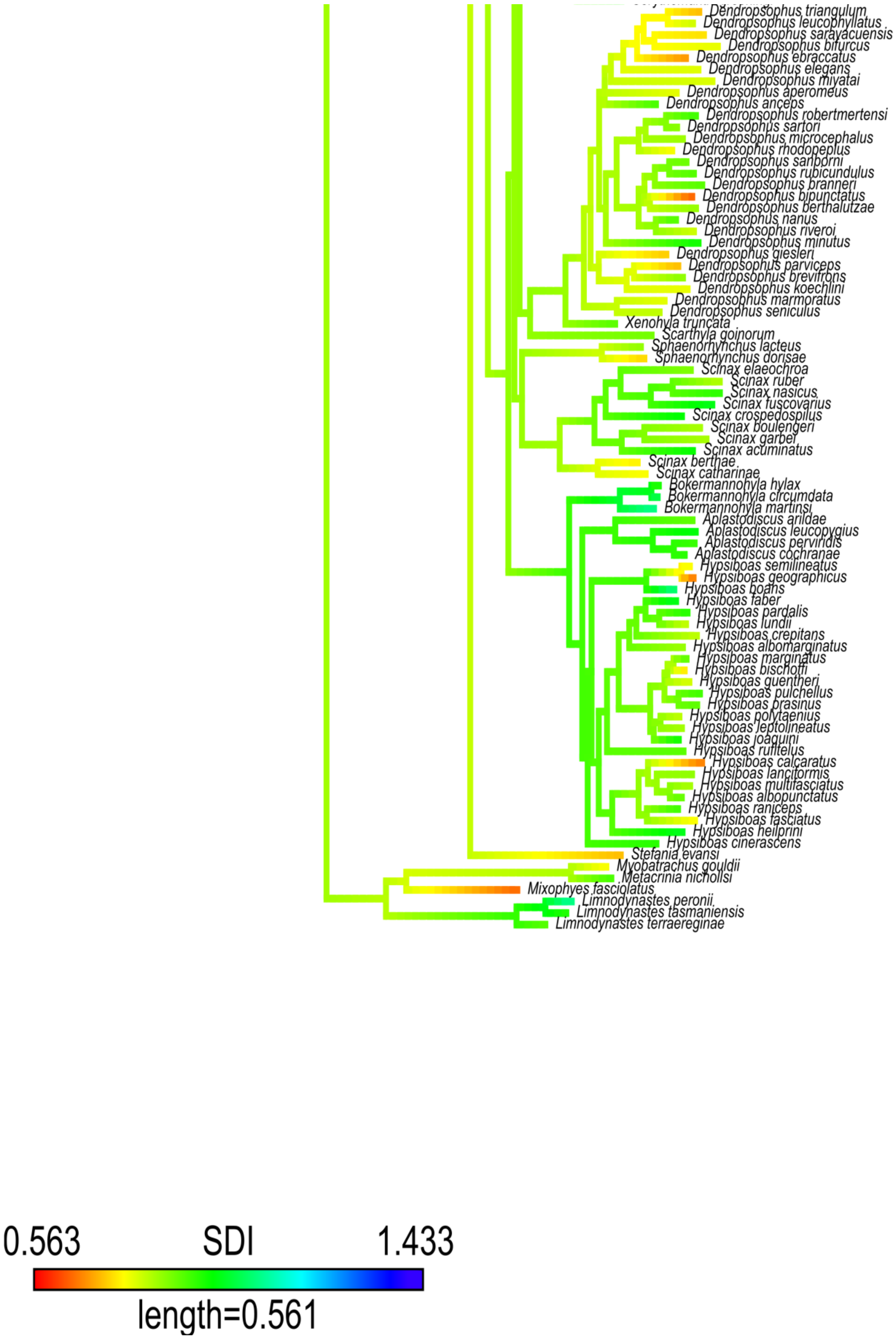

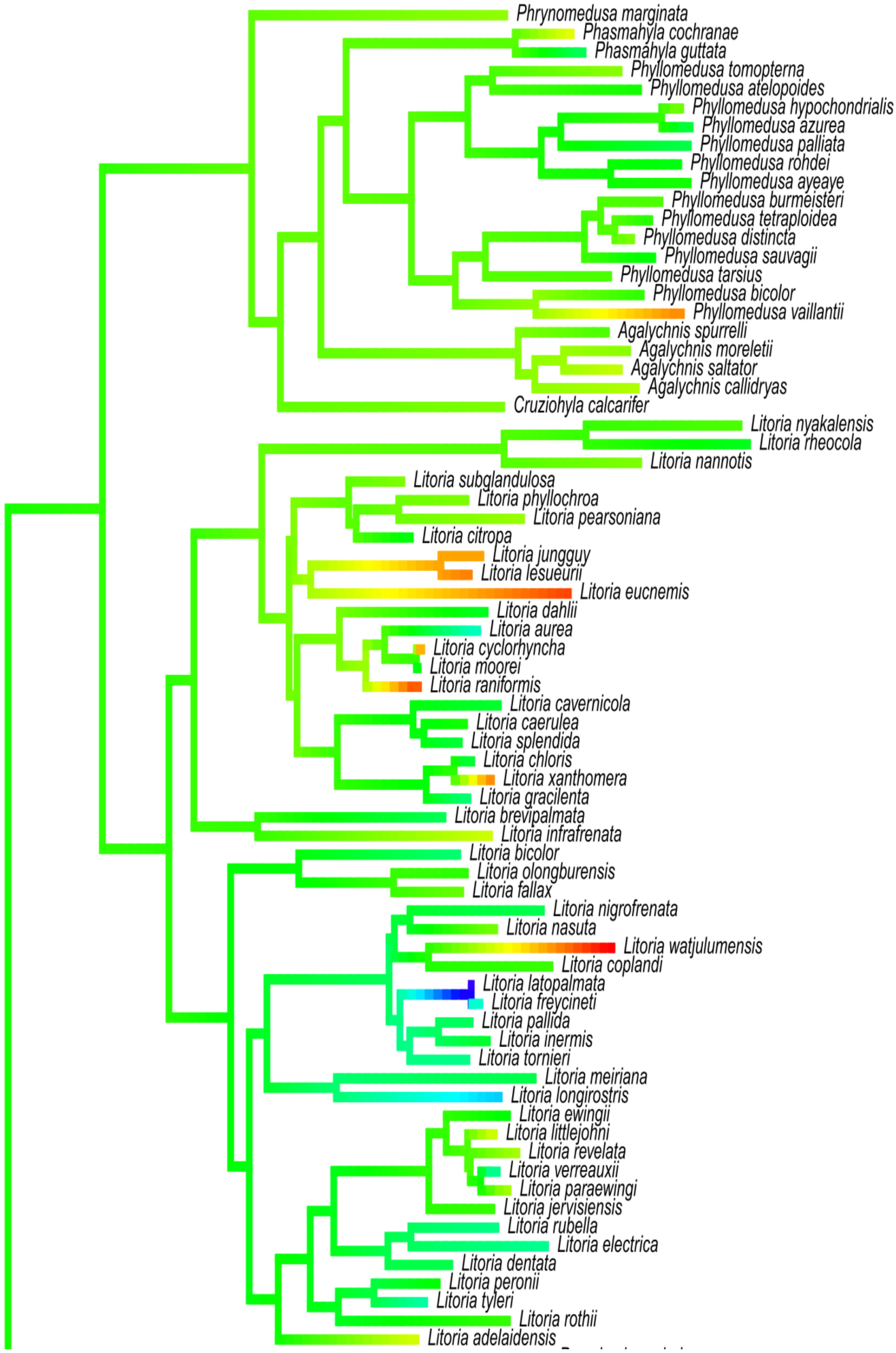

Supplemental Figure 4. Phylogeny of Hylidae extracted from Pyron & Wiens (2011) used in this study, with colored branches according to sexual dimorphism index (SDI; legend at the end of the figure).

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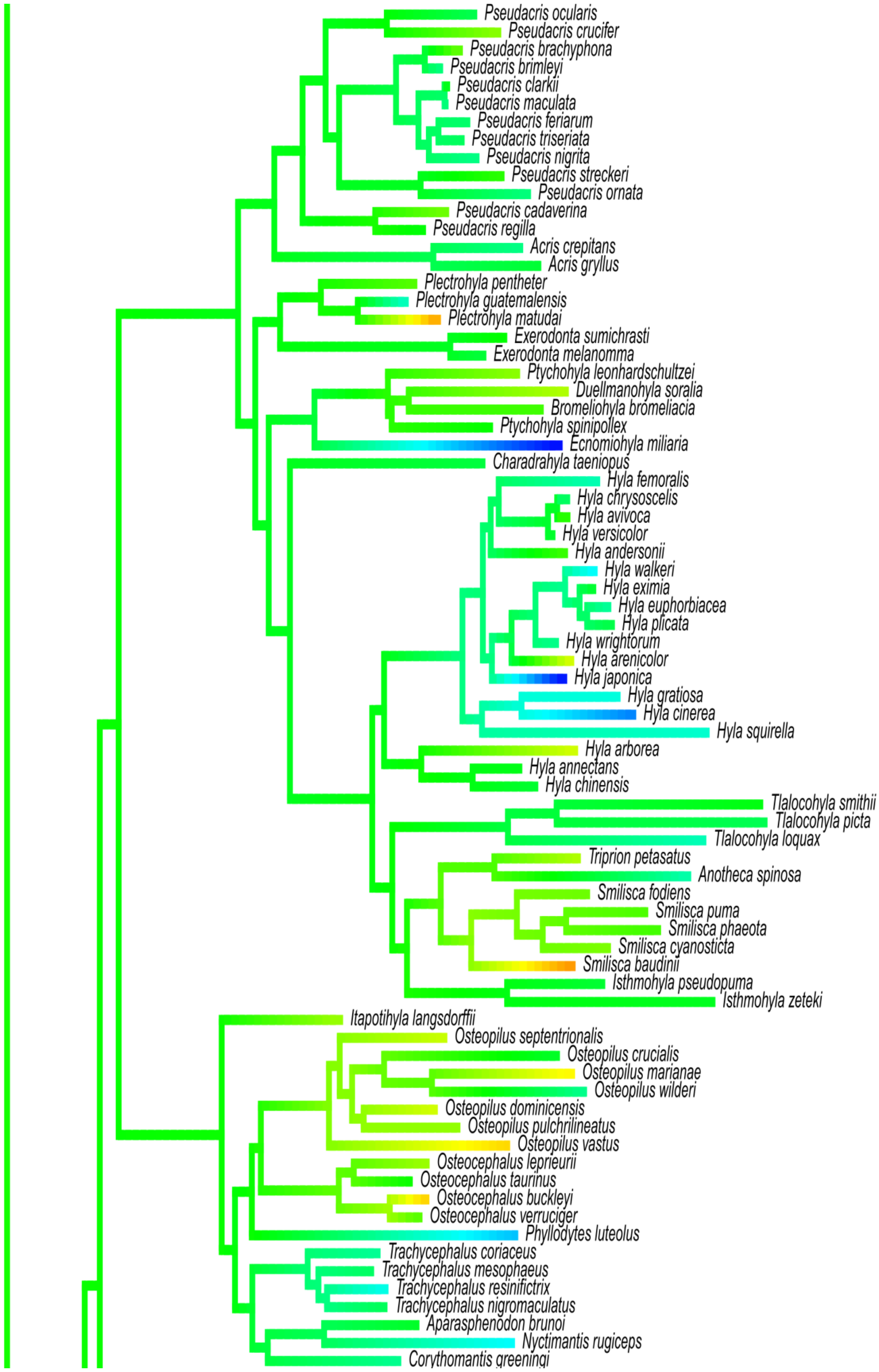

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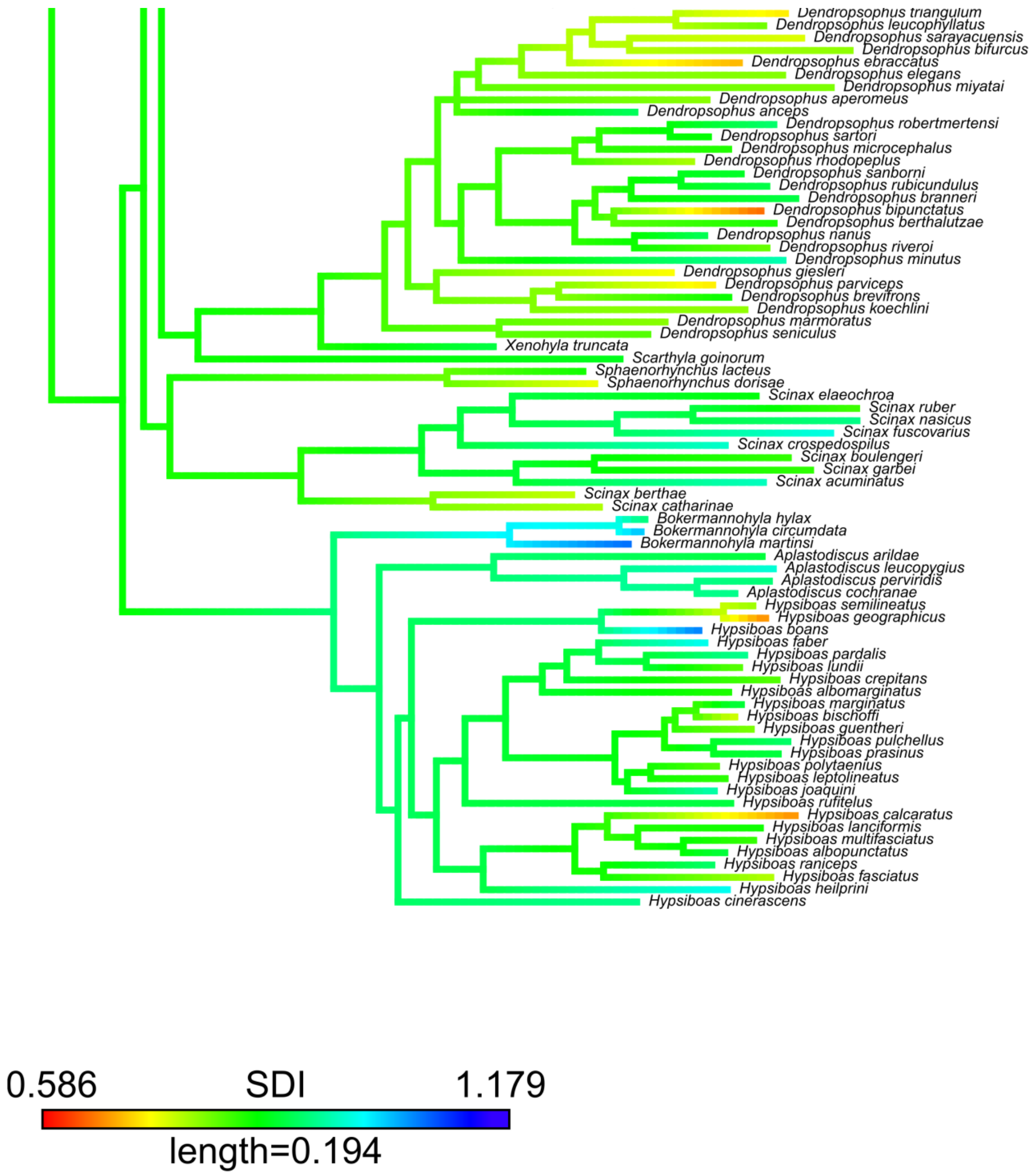

Supplemental Tables 1 and 2

Supplemental Table 1. Complete dataset used in this study, with abbreviated references on the table and complete references at the end. Male SVL, female SVL and egg size/oocyte diameter are expressed in mm; *species with direct development.

Family	Species	Male SVL (mm)	Female SVL (mm)	Egg size / oocyte diameter (mm)	N eggs per clutch / N oocytes per female	Oviposition site	References
Allophrynidae	*Allophryne ruthveni*	22.6	27		300	aquatic	Duellman, 1997; Gottsberger and Gruber, 2004; La Marca et al, 2004
Alytidae	*Alytes obstetrican*	41.74	49.69		63.67	terrestrial	Stewart, 1967
Bombinatoridae	*Bombina orientalis*	42.1	47	2.29	165	aquatic	Márquez et al., 1997; Márquez, 1992; Ribeiro and Rebelo, 2011; Bosch and Boyero, 2004
Bombinatoridae	*Bombina bombina*	34.7	34.9	1.49	190	aquatic	Okada, 1966; Kuzmin, 1999; Kaplan, 1989; Kaplan, 1992
Bombinatoridae	*Bombina variegata*	41.7	43.48	1.99	72	aquatic	Kuzmin, 1999; Wells, 1977; Bülbül et al., 2018b; Bülbül et al., 2018C; Rafin´ska, 1991
Brachycephalidae	*Ischnocnema guentheri*	25.53	36.64		35	terrestrial*	Giasson, 2008; Haddad, 1991; Giaretta and Facure, 2008; Lutz, 1947
Brachycephalidae	*Ischnocnema parva*	15.67	19.86	1.1	20	terrestrial*	Giasson, 2008; Giaretta and Facure, 2008; Martins et al., 2010
Brachycephalidae	*Brachycephalus ephippium*	14.33	16.66	5.1	5	terrestrial*	Pombal-Jr, 1992; Pombal Jr et al., 1994
Bufonidae	*Atelopus spumarius*	27.5	35			aquatic	Rodriguez and Duellman, 1994; Jorge, 2014
Bufonidae	*Atelopus varius*	33	40.5		950	aquatic	Savage, 2002; Crump, 1988; Pounds and Crump, 1987
Bufonidae	*Atelopus chiriquiensis*	31	42.5	2.5	364	aquatic	Savage, 2002; Lindquist and Swihart, 1997
Bufonidae	*Bufo bankorensis*	86	99		3725	aquatic	Schimidt, 1927; Pope, 1931; Huang et al., 1996
Bufonidae	*Bufo gargarizans*	61.7	72.2		4000	aquatic	Fei et al., 2009; Yu and Guo, 2013
Centrolenidae	*Hyalinobatrachium valerioi*	21.8	24.3		35	arboreal	Savage, 2002; Kubicki, 2007; Vockenhuber et al., 2009
Centrolenidae	*Hyalinobatrachium colymbiphyllum*	25	26.8		50	arboreal	Savage, 2002; Kubicki, 2007; Savage, 2002; Hughey et al., 2017
Centrolenidae	*Hyalinobatrachium chirripoi*	25.5	29		70	arboreal	Kubicki, 2007; Kubicki, 2004

Centrolenidae	*Hyalinobatrachium fleischmanni*	22.4	27.5		30	arboreal	Savage, 2002; Kubicki 2007; Jacobson, 1985
Centrolenidae	*Centrolene savagei*	21.1	23.6			arboreal	Vargas-Salinas et al., 2014; Diaz-Gutierrez et al., 2013
Centrolenidae	*Nymphargus griffithsi*	24.1	23.4			arboreal	Lynch and Duellman, 1973; Duellman and Trueb, 1994; Duellman and Savitzky, 1976
Centrolenidae	*Cochranella granulosa*	25.8	30.5		55	arboreal	Savage, 2002; Kubicki, 2007; Delia et al., 2017
Centrolenidae	*Cochranella euknemos*	25.5	31		55	arboreal	Savage, 2002; Kubicki, 2007; Kubicki, 2007; Savage and Starrett, 1967
Centrolenidae	*Espadarana prosoblepon*	24.1	26.4		35.4	arboreal	Lynch and Duellman, 1973; Savage, 2002; Kubicki, 2007; Basto-Riascos et al., 2017; Jacobson, 1985
Centrolenidae	*Teratohyla pulverata*	26	29.5		42	arboreal	Savage, 2002; Delia et al., 2017
Ceratophryidae	*Ceratophrys cranwelli*	88.9	158		3696	aquatic	Perotti, 1997; Natale et al., 2011; Marangoni et al., 2009
Ceratophryidae	*Lepidobatrachus laevis*	73	120.5	2.5	1378	aquatic	Perotti, 1997; Amin et al., 2015; Springer and Schalk, 2016
Conrauidae	*Conraua goliath*	270	254	3.47	100	aquatic	Sabater-Pi, 1985; Sabater-Pi, 1985
Craugastoridae	*Haddadus binotatus*	34.5	53.1			terrestrial*	Dias et al., 2012; Haddad and Sazima, 1992; Canedo and Rickli, 2006
Cycloramphidae	*Thoropa taophora*	72.75	72.43		765.66	terrestrial	Hartmann, 2004; Giaretta and Facure, 2004; Consolmagno et al., 2016
Cycloramphidae	*Thoropa miliaris*	57.26	56.03	2.3	400	terrestrial	Feio, 2002; Giaretta and Facure, 2004
Cycloramphidae	*Cycloramphus boraceiensis*	38.66	53.01		81.75	terrestrial	Hartmann, 2004; Giaretta and Facure, 2003; Kakazu, 2009
Dendrobatidae	*Ameerega hahneli*	18	20.5		22	terrestrial	Rodriguez and Duellman, 1994; Gottsberger and Gruber, 2004; Haddad and Martins, 1994
Dendrobatidae	*Ameerega trivittata*	37.9	43.6		50	terrestrial	Silverstone, 1976; Duellman, 1996; Myers and Daly, 1979; Rodriguez and Duellman, 1994; Roithmair, 1994
Dendrobatidae	*Ameerega parvula*	19	21.2		8	terrestrial	Silverstone, 1976; Crump, 1974; Wells, 2007; Poelman et al., 2010
Dendrobatidae	*Hyloxalus vertebralis*	16.1	17.9	2.6	13	terrestrial	Coloma, 1995; Edwards, 1971; Hervas et al., 2015
Dendrobatidae	*Hyloxalus toachi*	23.1	28.2	2.4	11	terrestrial	Coloma, 1995; Quiguango-Ubillús and Coloma, 2008
Dendrobatidae	*Phyllobates lugubris*	19.2	22.2		18	terrestrial	Silverstone, 1976; Lötters et al., 2007; Weygoldt, 1987; Donnelly et al., 1990
Dendrobatidae	*Phyllobates terribilis*	41.1	43.2		15	terrestrial	Myers et al., 1978; Wells, 2007; Weygoldt, 1987
Dendrobatidae	*Dendrobates tinctorius*	41	46.5	4.2	5	terrestrial	Silverstone, 1975; Summers et al., 1999; Rojas and Pasukonis, 2019
Dendrobatidae	*Dendrobates auratus*	30.3	33.7	3.5	8	terrestrial	Silverstone, 1975, Summers, 1989; Dunn, 1941; Savage, 2002; Eens and Pinxten, 2000; Wells, 1978; Hervas et al., 2015

Dendrobatidae	*Mannophryne trinitatis*	23.1	25.6		10	terrestrial	Sexton, 1960; Jowers and Downie, 2005
Dendrobatidae	*Allobates talamancae*	20.4	24		18	terrestrial	Savage, 2002; Pröhl, 2005; Lechelt et al., 2014
Dendrobatidae	*Allobates femoralis*	25.8	27.3		22.7	terrestrial	Silverstonee, 1976; Crump, 1974; Hödl et al., 2004; Spring et al., 2019
Dendrobatidae	*Allobates nidicola*	19.6	20.2	2.4	4	terrestrial	Caldwell and Lima, 2003
Dendrobatidae	*Allobates brunneus*	17.9	19.6		17	terrestrial	Caldwell and Lima, 2003; Lima et al., 2009
Dicroglossidae	*Fejervarya limnocharis*	39	48.8		1560	aquatic	Inger, 1966; Chen, 1991; Ye et al., 1993; Xu and Li, 2013
Dicroglossidae	*Nannophrys ceylonensis*	46.6	48.7		12	hidden	Wickramasinghe et al., 2004
Dicroglossidae	*Hoplobatrachus rugulosus*	82.4	71.7		2000	aquatic	Chen, 1991; Huang et al., 1990; Vassilieva et al., 2017
Dicroglossidae	*Euphlyctis cyanophlyctis*	67	48		1000	aquatic	Gramapurohit et al., 2005; Khan and Malik, 1987; Tabassum et al., 2011
Dicroglossidae	*Limnonectes kuhlii*	55.6	54.9		80	aquatic	Yang, 1991; Chen, 1991; Tsuji, 2004; Tsuji and Lue, 2000
Dicroglossidae	*Nanorana parkeri*	45.7	49.4	2.18	189	aquatic	Hu et al., 1987; Lu et al., 2016
Dicroglossidae	*Nanorana pleskei*	36.6	37.3		96	aquatic	Ye et al., 1993; Wang et al., 2017
Eleutherodactylidae	*Eleutherodactylus cundalli*	32.3	41.7	4.2	48	terrestrial*	Diesel et al., 1995; Schwartz and Henderson, 1991
Eleutherodactylidae	*Eleutherodactylus johnstonei*	23.1	26.9		20	terrestrial*	Ortega et al., 2005; Savage, 2002; Ovaska and Hunte, 1992; Pers. Obs. C. F. B. Haddad
Eleutherodactylidae	*Eleutherodactylus coqui*	35.6	45.9		28	terrestrial*	Woolbright, 1989; Towsend et al., 1994; Duellman and Trueb, 1994; Wells, 1977
Hemiphractidae	*Stefania evansi*	45.8	63.9		23	terrestrial*	Kok et al., 2006; Duellman and Hoogmoed, 1984; Kok and Benjamin, 2007
Hemisotidae	*Hemisus marmoratus*	27.9	31.8		200	hidden	Rödel, 2000; Wager, 1965; Grafe et al., 2005
Hylidae	*Boana cinerascens*	39	41.2		426	aquatic	Telles et al., 2013; Crump, 1974; Telles et al., 2013
Hylidae	*Boana heilprini*	49.4	49.3		332	hidden	Landestoy, 2013; Trueb, 1974; Nali et al., 2014; Landestoy, 2013
Hylidae	*Boana fasciata*	35.6	46.2		569	aquatic	Crump, 1974; Duellman, 1996; Crump, 1974
Hylidae	*Boana raniceps*	55.7	60.2		1991	aquatic	Kopp et al., 2010; Santoro and Brandão, 2014; Prado, 2004; Prado et al., 2005; Kopp et al., 2010; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana albopunctata*	46.1	51.19			aquatic	Cardana 1995; Uetanabaro et al. 2008; de Sá et al., 2014
Hylidae	*Boana multifasciata*	48.7	57.98			aquatic	Azevedo-Ramos et al., 2004a; Summers et al., 2007; Cardana, 1995; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana lanciformis*	74.9	87		1617	aquatic	Crump, 1974

Hylidae	*Boana calcarata*	35.9	53.9		1143	aquatic	Summers et al., 2007; Gottsberger and Gruber, 2004; Crump, 1974; Summers et al., 2007
Hylidae	*Boana rufitela*	46.2	51.1			aquatic	Duellman and Dennis, 2001
Hylidae	*Boana joaquini*	49	50.86			aquatic	C. P. A. Prado, Unpubl. Data; Garcia et al., 2003; Maneyro and Rosa, 2004; Saito, 2013
Hylidae	*Boana leptolineata*	28	33.12			aquatic	C. P. A. Prado, Unpubl. Data; Reinke and Deiques, 2010; Kwet and DiBernardo, 1999
Hylidae	*Boana polytaenia*	30.87	37.46		291.33	aquatic	Gridi-Papp, 1997
Hylidae	*Boana prasina*	47.6	52.73	1.56	916.2	aquatic	Haddad, 1991; C. P. A. Prado, Unpubl. Data; Pombal JR and Haddad, 2005
Hylidae	*Boana pulchella*	45.8	49.5			aquatic	Maneyro and Rosa, 2004; Moreira et al., 2007; Lutz, 1973; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana guentheri*	36.5	45.5			aquatic	Moreira et al., 2007; Lutz, 1973
Hylidae	*Boana bischoffi*	43.205	57.25	1.98	859	aquatic	Pombal-Jr and Haddad 2005; Haddad, 1991; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana marginata*	48.4	53.5			aquatic	C. P. A. Prado, Unpubl. Data; Kwet, 2001
Hylidae	*Boana albomarginata*	49.01	57.45		1318	aquatic	Hartmann et al., 2010; Giasson and Haddad, 2007
Hylidae	*Boana crepitans*	53.9	65.5		2053	aquatic	Duellman and Dennis, 2001; Stebbins and Hendrickson, 1959; Nascimento et al., 2015
Hylidae	*Boana lundii*	57.1	69.6			aquatic	C. P. A. Prado, Unpubl. Data; Kopp et al., 2010; Pers. Comm. C. M. Mazzarelli
Hylidae	*Boana pardalis*	61.75	65.21			aquatic	Giasson, 2008; Lutz, 1973; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana faber*	84	83.8	2.12	1986	aquatic	Martins and Haddad, 1988; Martins, 1993; C. P. A. Prado, Unpubl. Data
Hylidae	*Boana boans*	116	107		3154	aquatic	Emerson, 1997; Duellman, 1997; Magnusson et al., 1999; Crump, 1974
Hylidae	*Boana geographica*	44.2	66.6		2797	aquatic	Crump, 1974; Bittar et al., 2016; Bitar et al. 2012
Hylidae	*Boana semilineata*	40.6	52			aquatic	C. P. A. Prado, Unpubl. Data; Hartmann, 2004
Hylidae	*Aplastodiscus cochranae*	45.2	47.8			hidden	C. P. A. Prado, Unpubl. Data; Garcia et al., 2001; Garcia and Kwet, 2004
Hylidae	*Aplastodiscus perviridis*	39.66	42.47		227	hidden	Haddad et al., 2005; Pers Comm. B. V. M. Berneck
Hylidae	*Aplastodiscus leucopygius*	39.69	40.19		219	hidden	Haddad, 1991; Zina, 2006; C. P. A. Prado, Unpubl. Data; Haddad and Sawaya, 2000; Haddad and Prado, 2005; Haddad, 1991
Hylidae	*Aplastodiscus arildae*	36.14	40.1			hidden	Zina, 2006; Carvalho et al., 2006; C. P. A. Prado, Unpubl. Data
Hylidae	*Bokermannohyla martinsi*	61.5	56			hidden	Lutz, 1973; Haddad et al., 2013; P.C. Eterovick pers. comm.

Hylidae	*Bokermannohyla circumdata*	61.29	58.53			aquatic	Giasson 2008, Pers. Obs. C. F. B. Haddad, Haddad and Sawaya 2000, C. P. A. Prado, Unpubl. Data, Malagoli 2013
Hylidae	*Bokermannohyla hylax*	56.44	60.14			aquatic	Giasson, 2008; Pers. Obs. C. F. B. Haddad
Hylidae	*Ololygon catharinae*	33	42.7			aquatic	Lutz, 1973; Silvano et al., 2004
Hylidae	*Ololygon berthae*	19	25			aquatic	Moreira et al., 2007; Lutz, 1973; Moreira et al., 2007
Hylidae	*Scinax acuminatus*	42	43.1		879	aquatic	Prado and Haddad, 2003; Prado 2004; C. P. A. Prado, Unpubl. Data
Hylidae	*Scinax garbei*	35.4	42		550	aquatic	Crump, 1974
Hylidae	*Scinax boulengeri*	41.6	49.4		650	aquatic	Bevier, 1997; Solís et al., 2008a; Duellman and Dennis, 2001; Savage 2002
Hylidae	*Scinax crospedospilus*	30.54	31.14			aquatic	Pavan and Telles, 2004; Giasson, 2008; Pers. Obs. C. P. A. Prado
Hylidae	*Scinax fuscovarius*	47.6	47.8		1957	aquatic	Haddad, 1991; Uetanabaro et al., 2008; Rodrigues et al., 2005
Hylidae	*Scinax nasicus*	29.8	31.6		1584	aquatic	Perotti, 1997; Prado, 2004; Prado et al., 2005
Hylidae	*Scinax ruber*	32.6	39.1		591	aquatic	Bevier, 1997; Noronha et al., 2015; Crump, 1974; Duellman 1996; Duellman and Dennis, 2001
Hylidae	*Scinax elaeochroa*	30.6	35			aquatic	Solís et al., 2008b; Duellman and Dennis, 2001; Savage, 2002; Donnelly and Guyer, 1994; Solís et al., 2008b
Hylidae	*Sphaenorhynchus dorisae*	28	38			aquatic	Toledo et al., 2007; Azevedo-Ramos et al., 2004b
Hylidae	*Sphaenorhynchus lacteus*	36.5	42.5			aquatic	Rodriguez and Duellman, 1994; Benicio et al., 2011
Hylidae	*Scarthyla goinorum*	19	21.5			aquatic	Rodriguez and Duellman, 1994
Hylidae	*Xenohyla truncata*	38	42			aquatic	Silva et al., 2008; Lutz, 1973; Silva et al., 2008
Hylidae	*Dendropsophus seniculus*	32.5	39.5			aquatic	Lutz, 1973; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus marmoratus*	39.1	49.3	1.7	979	aquatic	Crump, 1974; Noronha et al., 2015; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus koechlini*	20.5	26	1.1	325	aquatic	Rodriguez and Duellman, 1994
Hylidae	*Dendropsophus brevifrons*	18.5	21.4	1.3	81	arboreal	Crump, 1974; Duellman and Crump, 1974
Hylidae	*Dendropsophus parviceps*	16.8	23.4	1.05	234	aquatic	Crump, 1974; Duellman and Crump, 1974; Rivadeneira et al., 2018
Hylidae	*Dendropsophus giesleri*	25.16	34.52		190	aquatic	Hartmann, 2004; Hartmann et al., 2010
Hylidae	*Dendropsophus minutus*	26.7	27.6	1	211	aquatic	Prado, 2004; Arzabe, 1998; Giasson, 2008; Crump, 1974; Prado, Unpubl. Data; Summers et al., 2007; Hartmann et al., 2010
Hylidae	*Dendropsophus riveroi*	18.5	22.8			aquatic	Duellman, 1996; Touchon and Warkentin, 2008

Hylidae	*Dendropsophus nanus*	19.5	21.3		242	aquatic	Prado, 2004; Del-Grande, 1995; Zina et al., 2007
Hylidae	*Dendropsophus berthalutzae*	18.91	22.1	1	57	arboreal	Hartmann et al., 2010; Hartmann, 2004
Hylidae	*Dendropsophus bipunctatus*	16.5	25.5			aquatic	Lutz, 1973; Wogel and Pombal-Jr, 2007
Hylidae	*Dendropsophus branneri*	17.07	18.83		288	arboreal	Verdade et al., 2010; Baracho, 2015
Hylidae	*Dendropsophus rubicundulus*	20	22			aquatic	Lutz, 1973; Toledo, 2007
Hylidae	*Dendropsophus sanborni*	18.79	21.1		130	aquatic	Del-Grande, 1995
Hylidae	*Dendropsophus rhodopeplus*	20.7	26.7	1.1	285	aquatic	Crump, 1974; Duellman, 1996; Rodriguez and Duellman, 1994; Crump, 1974
Hylidae	*Dendropsophus microcephalus*	22.8	26.8		180	aquatic	Stebbins and Hendrickson, 1959; Duellman and Dennis, 2001; Stebbins and Hendrickson, 1959
Hylidae	*Dendropsophus sartori*	24.8	28.6			aquatic	Duellman and Dennis, 2001
Hylidae	*Dendropsophus robertmertensi*	24.7	26.6			aquatic	Duellman and Dennis, 2001
Hylidae	*Dendropsophus anceps*	37	40.3			aquatic	Lutz, 1973; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus aperomeus*	19.8	25			aquatic	Duellman, 1982
Hylidae	*Dendropsophus miyatai*	20	25			aquatic	Bartlett and Bartlett, 2003; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus elegans*	25.74	32.34	1.3	300	aquatic	Bastos and Haddad, 1996; Hartmann, 2004
Hylidae	*Dendropsophus ebraccatus*	25.1	36.5	1.3	155	arboreal	Duellman and Dennis, 2001; Savage, 2002; Donnelly and Guyer, 1994; Gomez-Mestre et al., 2012
Hylidae	*Dendropsophus bifurcus*	25.1	31.8		186	aquatic	Crump, 1974
Hylidae	*Dendropsophus sarayacuensis*	25	33.5	2	113	arboreal	Crump, 1974; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus leucophyllatus*	33.9	42	1.5	587	arboreal	Crump, 1974; Savage, 2002; Touchon and Warkentin, 2008
Hylidae	*Dendropsophus triangulum*	25.4	35.4	1.6	501	arboreal	Crump, 1974; Duellman and Crump, 1974; Pers. Obs. C. F. B. Haddad
Hylidae	*Corythomantis greeningi*	73	77		700	aquatic	Silva et al., 2010; Loebmann, 2010; Jared et al., 1999; J. Zina pers. comm.
Hylidae	*Nyctimantis rugiceps*	61.9	61.3			hidden	Crump, 1974; Hödl, 1990; Duellman and Dennis, 2001; IUCN SSC Amphibian Specialist Group 2018. Nyctimantis rugiceps . The IUCN Red List of Threatened Species 2018: e.T55765A85904075. https://dx.doi.org/10.2305/IUCN.UK.2018-1.RLTS.T55765A85904075.en. Downloaded on 09 February 2020.
Hylidae	*Aparasphenodon brunoi*	58.1	65.2	1.36		aquatic	Haddad and Sawaya, 2000; Teixeira et al., 2002; Silva et al., 2008; Mesquita et al., 2004; Gomez-Mesa et al., 2017

Hylidae	*Trachycephalus nigromaculatus*	83.56	91.06		aquatic	Abrunhosa et al., 2006; Práger, 2010; Pers. Comm. A. C. L. M. Práger
Hylidae	*Trachycephalus resinifictrix*	76	76	436	hidden	Lima et al., 2005; Summers et al., 2007; Gottsberger and Gruber, 2004; Lutz, 1973; Schiesari et al., 2003; La Marca et al., 2010.
Hylidae	*Trachycephalus mesophaeus*	63.31	68.54	2367	aquatic	Hartmann et al., 2010; Hartmann 2004
Hylidae	*Trachycephalus coriaceus*	58.5	61.5	1430	aquatic	Rodriguez and Duellman, 1994; Crump, 1974; Gottsberger and Gruber, 2004; Schiesari & Moreira 1996
Hylidae	*Phyllodytes luteolus*	23	22		hidden	Schineider and Teixeira, 2001; Bokerman, 1966; Langone et al., 2008; Giaretta, 1996; C. P. A. Prado, Unpubl. Data
Hylidae	*Osteocephalus verruciger*	53	64.5		aquatic	Trueb and Duellman, 1971; Jungfer et al., 2013
Hylidae	*Osteocephalus buckleyi*	43.3	61.7	1600	aquatic	Trueb and Duellman, 1971; Jungfer and Weygoldt, 1999
Hylidae	*Osteocephalus taurinus*	69.9	81	2000	aquatic	Jungfer et al., 2013; Duellman, 1997; Trueb and Duellman, 1971; Lima et al., 2005
Hylidae	*Osteocephalus leprieurii*	44.7	57.1	848	aquatic	Jungfer and Hödl, 2002; Trueb and Duellman, 1971; Crump, 1974; Gottsberger and Gruber, 2004
Hylidae	*Osteopilus vastus*	96.7	136.9		aquatic	Wells, 2007; Galvis et al., 2014; Trueb, 1974; Wells, 2007
Hylidae	*Osteopilus pulchrilineatus*	31.6	40.1		aquatic	Trueb, 1974; Galvis et al., 2014
Hylidae	*Osteopilus dominicensis*	57.8	76.8		aquatic	Galvis et al., 2014; Trueb, 1974
Hylidae	*Osteopilus wilderi*	25.8	27.3		hidden	Lannoo et al., 1986; Dunn, 1926; Lehtinen and Nussbaum, 2003; Trueb 1974
Hylidae	*Osteopilus marianae*	28	38.7		hidden	Dunn, 1926; Lehtinen and Nussbaum, 2003; Trueb, 1974
Hylidae	*Osteopilus crucialis*	92.6	104		hidden	Rodriguez and Duellman, 1994; Lehtinen and Nussbaum, 2003; Trueb, 1974
Hylidae	*Osteopilus septentrionalis*	53.9	71.2	130	aquatic	Salinas, 2006; Trueb, 1974; Wright and Wright, 1949; Savage, 2002; Salinas, 2006
Hylidae	*Itapotihyla langsdorffii*	71.61	91.49	1741.5	aquatic	Hartmann, et al., 2010; Hartmann, 2004
Hylidae	*Isthmohyla zeteki*	22.5	25.4	24	hidden	Hertz et al., 2012; Lannoo et al., 1987; Duellman and Dennis, 2001; Savage, 2002; Lannoo et al., 1986
Hylidae	*Isthmohyla pseudopuma*	39.7	44.3	2150	aquatic	Duellman and Dennis, 2001; Savage, 2002; Crump and Towsend, 1990
Hylidae	*Smilisca baudinii*	60.2	90	2225	aquatic	Duellman and Dennis, 2001; Savage, 2002; Donnelly and Guyer, 1994
Hylidae	*Smilisca cyanosticta*	56	70	1147	aquatic	Duellman and Dennis, 2001
Hylidae	*Smilisca phaeota*	65	78	1829	aquatic	Savage, 2002
Hylidae	*Smilisca puma*	38	46		aquatic	Duellman, 1967; Savage, 2002; Duellman, 1967

Hylidae	*Smilisca fodiens*	49.4	61.1			aquatic	Wells, 1977; Duellman and Dennis, 2001; Pers. Obs. K. R. Zamudio; Wells, 1977
Hylidae	*Triprion spinosus*	61.1	63.4	1.8	316	hidden	Jungfer, 1996; Duellman and Dennis, 2001; Savage, 2002; Schiesari, et al., 2003
Hylidae	*Triprion petasatus*	54.6	70.7			aquatic	Duellman and Trueb, 1964; Duellman and Dennis, 2001
Hylidae	*Tlalocohyla loquax*	39.3	40.5		250	aquatic	Savage, 2002; Duellman and Dennis, 2001; Savage, 2002
Hylidae	*Tlalocohyla picta*	20.2	22.1			aquatic	Duellman and Dennis, 2001
Hylidae	*Tlalocohyla smithii*	24.3	27.7			aquatic	Duellman and Dennis, 2001
Hylidae	*Hyla chinensis*	30.6	34.2		459	aquatic	Pope, 1931; Ye et al., 1993; Huang et al., 1990; Chen, 1991
Hylidae	*Hyla annectans*	34.2	38.8		90	aquatic	Liao and Lu, 2010; Duellman and Trueb, 1986; Yang, 1991, Ye et al., 1993; Liao and Lu, 2010; Duellman and Trueb, 1986; Ao and Bordoloi, 2000
Hylidae	*Hyla arborea*	24.8	33		1282	aquatic	Toledo, 2007; Chen, 1991; Kuzmin, 1999; Wells, 1977
Hylidae	*Dryophytes squirellus*	29.5	30		950	aquatic	Mitchell and Pague, 2014; Wright and Wright, 1949; Fellers, 1979
Hylidae	*Dryophytes cinereus*	53.1	48.9		875	aquatic	Mitchell and Prague, 2014; Garton and Brandon, 1975; Saenz et al., 2006; Gunzburger, 2006
Hylidae	*Dryophytes gratiosus*	58.5	59	1.39	867	aquatic	Emerson, 1997; Prestwich et al., 1989; Travis, 1983; Mitchell and Prague, 2014; Wright and Wright, 1949; Gunzburger and Travis, 2007
Hylidae	*Dryophytes japonicus*	32.7	28		920	aquatic	Kusano et al., 1991; Okada, 1966; Kuzmin, 1999; Hirai and Matsui, 2000
Hylidae	*Dryophytes arenicolor*	35.3	47.2			aquatic	Summers et al., 2007; Barber, 1999; Wright and Wright, 1949; Wells, 1977; Summers et al., 2007; Barber, 1999
Hylidae	*Dryophytes wrightorum*	34	36			aquatic	Wright and Wright, 1949
Hylidae	*Dryophytes plicatus*	39.7	43.8			aquatic	Duellman and Dennis, 2001
Hylidae	*Dryophytes euphorbiaceus*	34.7	36.4		774	aquatic	Luría-Manzano and Gutiérrez-Mayén, 2014; Duellman and Dennis, 2001; Luría-Manzano and Gutiérrez-Mayén, 2014
Hylidae	*Dryophytes eximius*	29.9	33.5		851	aquatic	Duellman and Dennis, 2001; Hernández-Salinas, et al., 2018
Hylidae	*Dryophytes walkeri*	32	31.6			aquatic	Wilson et al., 2013; Duellman and Dennis, 2001; Wilson et al., 2013
Hylidae	*Dryophytes andersonii*	35.5	42.5		500	aquatic	Wright and Wright, 1949; Hulse et al., 2001; Wells, 1977
Hylidae	*Dryophytes versicolor*	41.5	46.5		1800	aquatic	Wright and Wright, 1949; Smith, 1950; Fellers, 1979; Gibbs and Breisch, 2001
Hylidae	*Dryophytes avivoca*	33.5	40.5		632	aquatic	Redmer et al., 1999; Wright and Wright, 1949; M. Redmer, unpublished data; Redmer et al., 1999

Hylidae	*Dryophytes chrysoscelis*	39.5	42	2000	aquatic	Toledo, 2007; Mitchell and Prague, 2014; Wright and Wright, 1949; Hulse et al., 2001; Fellers, 1979; Ritke and Semlitsch, 1991
Hylidae	*Dryophytes femoralis*	30.5	31.5		aquatic	Wright and Wright, 1949
Hylidae	*Charadrahyla taeniopus*	58	64.2		aquatic	Duellman and Dennis, 2001; Summers et al., 2007; Serrano, 2018
Hylidae	*Ecnomiohyla miliaria*	81.6	69.7		hidden	McCranie et al., 2003; Duellman and Dennis, 2001; Savage, 2002; McCranie et al., 2003
Hylidae	*Ptychohyla spinipollex*	37.1	42.8		aquatic	Duellman and Dennis, 2001
Hylidae	*Bromeliohyla bromeliacia*	27	32.4	14	hidden	Lee, 2000; Duellman and Dennis, 2001; Langone et al., 2008
Hylidae	*Duellmanohyla soralia*	29.3	38		aquatic	Pers. Comm. C. Vásquez-Almazán
Hylidae	*Ptychohyla leonhardschultzei*	31.6	39.9		aquatic	Duellman and Dennis, 2001
Hylidae	*Exerodonta melanomma*	27.1	30.1		aquatic	Duellman and Dennis, 2001
Hylidae	*Exerodonta sumichrasti*	26.2	30.2		aquatic	Summers et al., 2007; Duellman, 1970; Duellman and Dennis, 2001
Hylidae	*Plectrohyla matudai*	33.1	49		aquatic	Duellman and Campbell, 1992; Duellman and Dennis, 2001
Hylidae	*Plectrohyla guatemalensis*	47.5	48.6		aquatic	Summers et al., 2007; McCranie et al., 1987; Duellman and Campbell 1992
Hylidae	*Sarcohyla pentheter*	46.2	56.2		aquatic	Duellman and Dennis, 2001
Hylidae	*Acris gryllus*	22	24.5	232	aquatic	Wright and Wright, 1949; Stebbins, 1951
Hylidae	*Acris crepitans*	22.8	24.2	500	aquatic	Wright and Wright, 1949; Duellman and Dennis, 2001; Degenhardt et al., 1996; Smith, 1950; Wagner, 1989; Saenz et al., 2006; McCallum and Trauth, 2007
Hylidae	*Pseudacris regilla*	32.5	37.2	807	aquatic	Duellman and Dennis, 2001; Wright and Wright, 1949; Wells, 1977
Hylidae	*Pseudacris cadaverina*	33	40.9		aquatic	Duellman and Dennis, 2001; Wells, 1977
Hylidae	*Pseudacris ornata*	30	32	30	aquatic	Wright and Wright, 1949; Seyle and Trauth, 1982
Hylidae	*Pseudacris streckeri*	33	39	450	aquatic	Wright and Wright, 1949; Wells, 1977
Hylidae	*Pseudacris nigrita*	24.5	26	59	aquatic	Caldwell, 1987; Wright and Wright, 1949; Stebbins, 1951
Hylidae	*Pseudacris triseriata*	26.5	28.8	449	aquatic	Summers et al., 2007; Emerson and Hess, 2001; Duffitt and Finkler, 2011; Wright and Wright, 1949; Morrison and Hero, 2003
Hylidae	*Pseudacris feriarum*	25.5	27.5		aquatic	Mitchell and Prague, 2014; Wright and Wright, 1949
Hylidae	*Pseudacris maculata*	25.5	27		aquatic	Wright and Wright, 1949
Hylidae	*Pseudacris clarkii*	24.5	28	1000	aquatic	Wright and Wright, 1949; Smith, 1950

Hylidae	*Pseudacris brimleyi*	27.92	29.8	300	aquatic	Wright and Wright, 1949; Gosner and Black, 1958; Mitchell, 1986; Brandt and Walker, 1933
Hylidae	*Pseudacris brachyphona*	24.6	30.3	950	aquatic	Hulse et al., 2001
Hylidae	*Pseudacris crucifer*	25.2	31.8	750	aquatic	Gibbs and Breisch, 2001; Emerson, 1997; Zimmitti, 1999; Mitchell and Prague, 2014; Wright and Wright, 1949; Hulse et al., 2001
Hylidae	*Pseudacris ocularis*	13.5	14.8		aquatic	Wright and Wright, 1949; Harper, 1939
Hylidae	*Litoria adelaidensis*	45	60		aquatic	Byrne et al., 2002
Hylidae	*Litoria rothii*	48	57		aquatic	Byrne et al., 2002
Hylidae	*Litoria tyleri*	48	50		aquatic	Byrne et al., 2002
Hylidae	*Litoria peronii*	48.4	55.7	1078.8	aquatic	Tyler, 1978; Wells, 1977; Byrne et al., 2002
Hylidae	*Litoria dentata*	40	44		aquatic	Byrne et al., 2002
Hylidae	*Litoria electrica*	38	40		aquatic	Byrne et al., 2002
Hylidae	*Litoria rubella*	32.9	34.9	507.5	aquatic	Tyler, 1978; Tyler, 1998; Byrne et al., 2002
Hylidae	*Litoria jervisiensis*	37	44		aquatic	Byrne et al., 2002
Hylidae	*Litoria paraewingi*	28	36		aquatic	Byrne et al., 2002
Hylidae	*Litoria verreauxii*	33	34		aquatic	Byrne et al., 2002
Hylidae	*Litoria revelata*	28	36		aquatic	Byrne et al., 2002
Hylidae	*Litoria littlejohni*	51	68		aquatic	Byrne et al., 2002
Hylidae	*Litoria ewingii*	40	46		aquatic	Byrne et al., 2002
Hylidae	*Litoria longirostris*	27	26		arboreal	Tyler, 1978; Tyler, 1998, Tyler, 1985; Anstis, 2013; Anderson et al., 2010; McDonald and Storch, 1993
Hylidae	*Litoria meiriana*	20	22		aquatic	Byrne et al., 2002
Hylidae	*Litoria tornieri*	34	36		aquatic	Byrne et al., 2002
Hylidae	*Litoria inermis*	33	37		aquatic	Byrne et al., 2002
Hylidae	*Litoria pallida*	34	37		aquatic	Byrne et al., 2002
Hylidae	*Litoria freycineti*	40	49		aquatic	Summers et al., 2007; Byrne et al., 2002; Moore, 1961
Hylidae	*Litoria latopalmata*	39	32		aquatic	Byrne et al., 2002
Hylidae	*Litoria coplandi*	36	43		aquatic	Byrne et al., 2002
Hylidae	*Litoria watjulumensis*	41	70		aquatic	Byrne et al., 2002

Hylidae	*Litoria nasuta*	45	56		aquatic	Byrne et al., 2002
Hylidae	*Litoria nigrofrenata*	42	46		aquatic	Byrne et al., 2002
Hylidae	*Litoria fallax*	26	32		aquatic	Byrne et al., 2002
Hylidae	*Litoria olongburensis*	28.7	34		aquatic	Byrne et al., 2002
Hylidae	*Litoria bicolor*	27	29		aquatic	Byrne et al., 2002
Hylidae	*Nyctimystes infrafrenatus*	102	135		aquatic	Byrne et al., 2002
Hylidae	*Nyctimystes brevipalmatus*	43	47		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea gracilenta*	42	45		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea xanthomera*	56	85		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea chloris*	62	68		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea splendida*	106	118		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea caerulea*	72.1	84	1800	aquatic	Moore, 1961; Tyler, 1983; Byrne et al., 2002
Hylidae	*Ranoidea cavernicola*	51	57		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea raniformis*	65	104		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea moorei*	71	78		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea cyclorhynchus*	69	108		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea aurea*	91.8	93.9	6500	aquatic	Moore, 1961; Byrne et al., 2002
Hylidae	*Ranoidea dahlii*	63	71		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea eucnemis*	48	77		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea lesueurii*	40	61		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea jungguy*	48	71		aquatic	Richards and Alford, 1992; Donnellan and Mahony, 2004
Hylidae	*Ranoidea citropa*	57	65		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea pearsoniana*	29	37		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea phyllochroa*	32	40		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea subglandulosa*	40	50		aquatic	Byrne et al., 2002; Gomez-Mestre et al., 2012
Hylidae	*Ranoidea nannotis*	52	65		aquatic	Byrne et al., 2002
Hylidae	*Ranoidea rheocola*	38	43		aquatic	Byrne et al., 2002

Hylidae	*Ranoidea nyakalensis*	48	58			aquatic	Byrne et al., 2002
Hylidae	*Cruziohyla calcarifer*	52	65		80	arboreal	Duellman and Dennis, 2001; Savage, 2002; Summers et al., 2007
Hylidae	*Agalychnis callidryas*	48.2	62.5		265	arboreal	Duellman and Dennis, 2001; Savage, 2002; Wells, 1977; Donnelly and Guyer, 1994; Briggs, 2008; Emerson, 1997; Gomez-Mestre et al., 2008
Hylidae	*Agalychnis saltator*	43.3	57		46	arboreal	Duellman and Dennis, 2001; Savage, 2002; Roberts, 1994; Faivovich et al., 2010
Hylidae	*Agalychnis moreletii*	59	74.45		75	arboreal	Briggs, 2008; Faivovich et al., 2010; Emerson, 1997; Gomez-Mestre et al., 2008; Lee, 1996
Hylidae	*Agalychnis spurrelli*	62	75		67	arboreal	Duellman and Dennis, 2001; Gomez-Mestre et al., 2008; Faivovich et al., 2010; Scott and Starrett, 1974
Hylidae	*Phyllomedusa vaillantii*	52.1	78.8		1114	arboreal	Crump, 1974; Gottsberger and Gruber, 2004
Hylidae	*Phyllomedusa bicolor*	97	115		859.5	arboreal	Neckel-Oliveira and Wachlevski, 2004; Pers. Obs. C. F. B. Haddad; Rodriguez and Duellman, 1994
Hylidae	*Phyllomedusa tarsius*	86.9	104.9		548	arboreal	Crump, 1974
Hylidae	*Phyllomedusa sauvagii*	77.3	88.4		103	arboreal	Rodrigues et al., 2007
Hylidae	*Phyllomedusa distincta*	56	70	2.59	214	arboreal	Pombal-Jr and Haddad, 2005; Castanho, 1994; Pers. Obs. C. F. B. Haddad; C. P. A. Prado, Unpubl. Data
Hylidae	*Phyllomedusa tetraploidea*	59.2	69.73	2.95	171	arboreal	C. P. A. Prado, Unpubl. Data; Pombal-Jr and Haddad, 2005
Hylidae	*Phyllomedusa burmeisteri*	63.4	76.7		195	arboreal	Abrunhosa and Wogel, 2004; Haddad, 1991; C. P. A. Prado, Unpubl. Data
Hylidae	*Phyllomedusa ayeaye*	31.77	37.02		31	arboreal	Pers. Obs. R. C. Nali; Pers. Obs. C. F. B. Haddad; Pers. Comm. M. M. Borges
Hylidae	*Pithecophus rohdei*	38.9	44.4			arboreal	Wogel et al., 2005; Wogel et al., 2006
Hylidae	*Pithecopus palliatus*	42.1	46.3		60	arboreal	Crump, 1974
Hylidae	*Pithecopus azureus*	39	43		89	arboreal	Dias et al., 2012; Prado and Haddad, 2003; Prado, 2004; C. P. A. Prado, Unpubl. Data; Dias et al., 2012
Hylidae	*Pithecopus hypochondrialis*	35.2	44			arboreal	Lima et al., 2015; Duellman, 1997; Abrunhosa and Wogel, 2004; Lima et al., 2015
Hylidae	*Callimedusa atelopoides*	36.5	42.5		20	arboreal	Rodriguez and Duellman, 1994; Duellman et al., 1988
Hylidae	*Callimedusa tomopterna*	45.3	57.2		71	arboreal	Gottsberger and Gruber, 2004; Crump, 1974
Hylidae	*Phasmahyla guttata*	35.5	38.6			arboreal	Costa and Carvalho-e-Silva, 2008; Hartmann et al., 2010
Hylidae	*Phasmahyla cochranae*	33.5	45.15		32	arboreal	Haddad, 1991
Hylidae	*Phrynomedusa marginata*	30.56	38.71			arboreal	Giasson, 2008

Hylodidae	*Hylodes asper*	38.4	40.4			hidden	de Sá et al., 2018; de Sá et al., 2015; Nogueira-Costa and Wachlevski, 2015; Hartmann et al., 2010
Hylodidae	*Hylodes dactylocinus*	25.2	27			hidden	Narvaes and Rodrigues, 2005
Hyperoliidae	*Hyperolius nasutus*	22.3	22.2		200	aquatic	Stewart, 1967; Wager, 1965; Schiøtz, 2006; Rödel et al., 2006
Hyperoliidae	*Hyperolius marmoratus*	28.9	29.6		400	aquatic	Stewart, 1967; Channing, 2001; Dyson et al., 1998
Hyperoliidae	*Hyperolius puncticulatus*	25	33.5	1.8		arboreal	Channing, 2001; Chipman, 1999
Leiopelmatidae	*Leiopelma hochstetteri*	38	47	5.5	22	aquatic	Inger, 1954; Najera-Hillman, 2009
Leiopelmatidae	*Leiopelma archeyi*	31	37	4.5		*hidden	Bell, 1978; Bell et al., 2004; Summers et al., 2005; Bell, 2010
Leiopelmatidae	*Leiopelma pakeka*	38.26	43.1	6	1 a 19	*hidden	Bell, 1978; Bell et al., 2004; Summers et al., 2005; Bell, 2010
Leiopelmatidae	*Ascaphus truei*	47	49	6.1	47.8	aquatic	Bell, 2010
Leprodactylidae	*Lithodytes lineatus*	38.5	44.7			hidden	Noronha et al., 2015; Bernarde and Kokobum, 2009; Lima et al., 2005; Schlüter et al., 2009
Leprodactylidae	*Adenomera andreae*	23.3	24.1		9	hidden	Heyer, 1973; Crump, 1974; Lima et al., 2006
Leprodactylidae	*Leptodactylus labyrinthicus*	152.3	155		4099	aquatic	Salles, 2014; Silva et al., 2005; Zina and Haddad, 2005
Leprodactylidae	*Leptodactylus pentadactylus*	141.5	151.5		1000	hidden	Noronha et al., 2015; Hero and Galatti, 1990; Savage, 2002; Rivero, 1961, Rodriguez and Duellman, 1994; Duellman, 1997; Wells, 1977, Duellman and Trueb, 1994
Leprodactylidae	*Leptodactylus mystacinus*	52.9	57.9		401	hidden	Summers et al., 2007; Oliveira-Filho and Giaretta, 2008; Uetanabaro et al., 2008; Summers et al., 2007
Leprodactylidae	*Leptodactylus mystaceus*	45.1	54.8		281	hidden	Salles, 2014; Heyer, 1978; Crump, 1974; Salles, 2014
Leprodactylidae	*Leptodactylus gracilis*	43	43			hidden	Heyer, 1978
Leprodactylidae	*Leptodactylus albilabris*	35.2	40.7		138	hidden	Dent, 1956; Heyer, 1978; Schwartz and Henderson, 1991
Leprodactylidae	*Leptodactylus bufonius*	46	47.7		425	hidden	Salles, 2014; Faggioni, 2011; Salles, 2014
Leprodactylidae	*Leptodactylus fuscus*	42.6	43.6		214	hidden	Salles, 2014; Prado, 2004; Salles, 2014
Leprodactylidae	*Leptodactylus chaquensis*	71.3	71.3		4936	aquatic	Prado et al., 2002; Salles, 2014; Prado, 2004; Prado and Haddad, 2003; Prado et al., 2002; Salles 2014
Leprodactylidae	*Leptodactylus discodactylus*	27.4	33.6		234	aquatic	Heyer and Bellin, 1973; Duellman, 1978; Crump, 1974
Leprodactylidae	*Leptodactylus podicipinus*	35.2	39.5		2102	aquatic	Summers et al., 2007; Prado, 2004; Martins, 1996; Summers et al., 2007
Leprodactylidae	*Leptodactylus wagneri*	50	66.9		1740	aquatic	Heyer, 1994; Crump, 1974; Crump, 1974
Leprodactylidae	*Leptodactylus validus*	37.8	44.3			aquatic	Downie, et al., 1996; Heyer, 1994; Downie et al., 1996

Leprodactylidae	*Leptodactylus leptodactyloides*	40.9	47.5			aquatic	Rodrigues et al., 2011; Heyer, 1994; Duellman, 1996; Rodrigues et al., 2011
Leprodactylidae	*Pseudopaludicola falcipes*	14.8	16.3			aquatic	Laufer and Barreneche, 2008; Haddad and Cardoso, 1987
Leprodactylidae	*Pleurodema thaul*	41.7	49.7			aquatic	Duellman and Veloso, 1977; Faivovich et al., 2012
Leprodactylidae	*Pleurodema bufoninum*	45	56			aquatic	Duellman and Veloso, 1977; Faivovich et al., 2012
Leprodactylidae	*Pleurodema brachyops*	31.5	34.5			aquatic	Rodriguez, 2004; Faivovich et al., 2012; Rivero, 1961
Leprodactylidae	*Edalorhina perezi*	26.9	32.2		93	aquatic	Schlüter, 1990; Murphy, 2003; Duellman, 1996; Crump, 1974
Leprodactylidae	*Physalaemus signifer*	23.77	26.72		273	aquatic	Nascimento, 2003; Pupin et al., 2010
Leprodactylidae	*Eupemphix nattereri*	41.16	42.68	1.6	2516	aquatic	Nascimento, 2003; Uetanabaro et al., 2008; Giaretta and Facure, 2006
Leprodactylidae	*Physalaemus cuvieri*	27.97	29.18	1.37	558.5	aquatic	Prado, 2004; Pombal-Jr and Haddad, 2005; Nascimento, 2003; Haddad, 1991
Leprodactylidae	*Physalaemus albonotatus*	29.6	30.2		719	aquatic	Rodrigues et al., 2004; Prado, 2004
Leprodactylidae	*Physalaemus barrioi*	27.01	28.55			aquatic	Nascimento, 2003; Pers. Obs. C. F. B. Haddad
Leprodactylidae	*Physalaemus gracilis*	26.28	27.93		311	aquatic	Nascimento, 2003; Camargo et al., 2005; Pupin et al., 2010
Leprodactylidae	*Physalaemus riograndensis*	16.81	16.91			aquatic	Nascimento, 2003
Leprodactylidae	*Physalaemus biligonigerus*	36.2	38.7		9574	aquatic	Nascimento, 2003; Perotti, 1997; Pers. Obs. C. P. A. Prado; Pers. Comm. G. P. Faggioni
Leprodactylidae	*Engystomops pustulosus*	25.68	28.44		234.2	aquatic	Toledo, 2007; Nascimento, 2003; Ryan, 1983
Leprodactylidae	*Engystomops petersi*	24.27	31.01			aquatic	Cannatella and Duellman, 1984; Nascimento, 2003
Leprodactylidae	*Engystomops coloradorum*	18.77	21.62			aquatic	Cannatella and Duellman, 1984; Nascimento, 2003
Leprodactylidae	*Scythrophrys sawayae*	15.31	16.71		33	aquatic	Garcia, 1996
Leprodactylidae	*Paratelmatobius poecilogaster*	18.82	20.91			terrestrial	Domenico et al., 2014; Haddad and Prado, 2005; Giasson, 2008
Mantellidae	*Aglyptodactylus laticeps*	43.5	59	1.76	3636	aquatic	Inger, 1966; Dring, 1979; Alcala, 1986
Mantellidae	*Aglyptodactylus madagascariensis*	41	53		1600	aquatic	Glos, 2003; Glos and Linsenmair, 2004
Mantellidae	*Boophis goudotii*	50	80	2	1000	aquatic	Glaw and Vences, 2007; Glos and Linsenmair, 2004
Mantellidae	*Boophis luteus*	38.5	54	2	200	aquatic	Blommers-Schlosser, 1979;Glaw and Vences, 2007;Nussbaum et al., 2008
Mantellidae	*Boophis rappiodes*	24	32	2	260	aquatic	Blommers-Schlosser, 1979;Glaw and Vences, 2007;Nussbaum et al., 2008
Mantellidae	*Boophis doulioti*	38.5	48.3	1.22	3445	aquatic	Glos, 2003

Mantellidae	*Boophis tephraeomystax*	38.5	45.5			aquatic	Glos, 2003; Linsenmair and Glos, 2005
Mantellidae	*Mantella laevigata*	26.8	28.1	3.5		hidden	Blommers-Schlosser, 1979; Nussbaum et al., 2008
Mantellidae	*Mantella aurantiaca*	22	30		74	terrestrial	Vences et al., 1998; Heying, 2001
Megophryidae	*Oreolalax schmidti*	43.1	51		120	aquatic	Fei et al., 2009
Megophryidae	*Oreolalax omeimontis*	53.7	54.1		183	aquatic	Ye et al., 1993; Fei et al., 1999
Megophryidae	*Oreolalax popei*	65.2	61.9		350	aquatic	Fei et al., 2009; Shaffer et al., 1994
Megophryidae	*Oreolalax major*	64.6	67.5			aquatic	Ye et al. 1993; Fei et al., 1999
Megophryidae	*Leptobrachium montanum*	52.1	60.2			aquatic	Fei et al., 2009
Megophryidae	*Leptobrachium boringii*	76.7	66.8		298	hidden	Ye et al., 1993; Zheng et al., 2010
Microhylidae	*Dermatonotus muelleri*	52.84	74.15		10991	aquatic	Perotti, 1997; Marangoni et al., 2009; Fabrezi et al., 2012
Microhylidae	*Scaphiophryne gottlebei*	28.91	30.85		182	aquatic	Rosa et al., 2011; Mercurio and Andreone, 2006; Rosa et al., 2011
Microhylidae	*Microhyla heymonsi*	19.8	22.2		157	aquatic	Yang, 1991; Chen, 1991; Huang et al., 1990; Sheridan, 2009
Microhylidae	*Microhyla ornata*	23.2	23.9	0.97	225	aquatic	Yang, 1991; Ye et al., 1993; Pope, 1931; Chen, 1991; Huang et al., 1990; Shimizu and Ota, 2003
Microhylidae	*Kaloula pulchra*	60.9	63.6		4126	aquatic	Fei et al., 2009
Microhylidae	*Kalophrynus pleurostigma*	40.4	44.8		4000	arboreal	Inger, 1966; Pope, 1931; Malkmus and Dehling, 2008; Lim and Ng, 1991
Microhylidae	*Hylophorbus rufescens*	30	40.5		13	terrestrial*	Zweifel, 1956; Bickford, 2004
Myobatrachidae	*Limnodynastes terraereginae*	69	76			aquatic	Parker, 1940; Roberts and Seymour, 1989
Myobatrachidae	*Limnodynastes tasmaniensis*	33.2	34.9	1.5	400	aquatic	Horton, 1982; Edwards et al., 2004; Parker, 1940; Schaube, 2004; Wilson et al., 2013; Horton, 1982; Roberts and Seymour, 1989; Littlejohn et al., 1993
Myobatrachidae	*Limnodynastes peronii*	51.7	46.6		850	aquatic	Hengl and Burgin, 2002; Schauble, 2004; Barker et al., 1995; Wells, 1977; Seebacher and Grigaltchik, 2014
Myobatrachidae	*Mixophyes fasciolatus*	63	97		970	terrestrial*	Stratford et al., 2010; Parker, 1940; Morrison and Hero, 2003; Stratford et al., 2010
Myobatrachidae	*Metacrinia nichollsi*	23	25	4.8	27	terrestrial*	Parker, 1940; Anstis, 2008
Myobatrachidae	*Myobatrachus gouldii*	44	57	5.1	40	hidden	Vertucci et al., 2017; Parker, 1940; Barker et al., 1995; Nokhbatolfoghahai et al., 2010; Roberts, 1981
Odontophrynidae	*Macrogenioglottus alipioi*	82.05	108.48			aquatic	Hartmann, 2004; Hartmann et al., 2010
Odontophrynidae	*Odontophrynus carvalhoi*	54.2	66			aquatic	Costa et al., 2017

Odontophrynidae	*Odontophrynus americanus*	46.01	51		4000	aquatic	Giaretta, 1994; Uetanabaro et al., 2008; Grenat et al., 2012
Odontophrynidae	*Proceratophrys boiei*	48.18	65.81	1.85	1296	aquatic	Giasson, 2008; Canelas and Bertoluci, 2007; Giaretta and Facure, 2008; Pombal-Jr and Haddad, 2005
Odontophrynidae	*Proceratophrys appendiculata*	49.49	63.18	3.4	841.7	aquatic	Giasson, 2008; Boquimpani-Freitas et al., 2002; Dias et al., 2013
Pelobatidae	*Pelobates fuscus*	41.1	42.6		1740	aquatic	Wright and Wright, 1949; Stebbins, 1951; Wells, 1977
Phrynobatrachidae	*Phrynobatrachus natalensis*	27.5	28.5		650	aquatic	Stewart, 1967; Wager, 1965; Wager,1930
Pipidae	*Xenopus muelleri*	58	72			aquatic	Rabb and Rabb, 1963; Rabb and Rabb, 1962
Ptychadenidae	*Ptychadena anchietae*	51	62			aquatic	Channing, 2001; Barbault, 1984; Mertens, 1938; Akef and Schneider, 1995
Pyxicephalidae	*Pyxicephalus adspersus*	203	115		4000	aquatic	Cook et al., 2001; Wager, 1965; Wells, 1977; Yetman et al., 2012; Yetman and Ferguson, 2011; Balinsky and Balinsky, 1954
Ranidae	*Rana pretiosa*	56	69.8	2.31	997	aquatic	Yang, 1991
Ranidae	*Rana luteiventris*	63.3	72.1		2400	aquatic	Fei et al., 2009; Licht, 1971
Ranidae	*Rana boylii*	56	73		980	aquatic	Greene and Funk, 2009; Maxell et al., 2003; Bull and Hayes, 2001; Reaser, 2000
Ranidae	*Rana aurora*	54.85	73.58		800	aquatic	Nussbaum et al., 1983; Stebbins, 1951; Wright and Wright, 1949; Wheeler et al., 2018
Ranidae	*Rana dalmatina*	45.2	56.7		1068	aquatic	Pope,1931; Kuzmin, 1999
Ranidae	*Rana temporaria*	64.2	61.2		2247	aquatic	Okada, 1966; Maeda and Matsui, 1990
Ranidae	*Rana kunyuensis*	40.9	44.8		918	aquatic	Pope, 1931; Kuzmin, 1999
Ranidae	*Rana arvalis*	60	58		1599	aquatic	Fei et al., 2009; Chen et al., 2012
Ranidae	*Rana japonica*	48.1	53.7		1500	aquatic	Inger and Bacon, 1968; Kuzmin,, 1999; Wells, 1977; Loman and Andersson, 2007; Sas et al., 2007
Ranidae	*Rana longicrus*	41.5	47.9		400	aquatic	Ye et al., 1993
Ranidae	*Rana chensinensis*	48	41.9		1400	aquatic	Fei et al., 2009
Ranidae	*Rana kukunoris*	56.3	61.9	2.24	1350	aquatic	Okada, 1966; Inger and Bacon, 1968; Ye et al., 1993; Lu et al., 2009; Chen et al., 2012
Ranidae	*Rana ornativentris*	49.3	58.5		12000	aquatic	Fei et al., 2009; Chen and Lu, 2011; Lu et al., 2008
Rhacophoridae	*Buergeria robusta*	49.1	67.1			aquatic	Huang et al., 2001
Rhacophoridae	*Buergeria buergeri*	40.05	58.9		386.5	aquatic	Ueda et al., 1998; Fukuyama and Kusano, 1992
Rhacophoridae	*Buergeria japonica*	25.5	31.1		600	aquatic	Huang et al., 2001; Okada, 1966; Haramura, 2008
Rhacophoridae	*Chiromantis xerampelina*	63	76		192	arboreal	Jennions and Passmore 1993

Rhacophoridae	*Polypedates leucomystax*	43.5	62.7		337	arboreal	Inger, 1966; Yang, 1991; McKay, 2006; Yorke, 1983; Feng and Narins, 1991; Rognes, 2015
Rhacophoridae	*Polypedates megacephalus*	49	67.1	2.19	362	aquatic	Fei et al., 2009; Li et al., 2017; Rognes, 2015
Rhacophoridae	*Zhangixalus moltrechti*	42.1	49.8		180	arboreal	Fei et al., 2009; Chang et al., 2014
Rhacophoridae	*Zhangixalus omeimontis*	64.7	76.7		650	arboreal	Liao and Lu, 2011; Liao and Lu, 2010; Luo et al., 2016
Rhacophoridae	*Zhangixalus arboreus*	60.3	81.4		288	arboreal	Okada, 1966; Pope, 1931; Kasuya et al., 1996; Kusano and Hatanaka, 2006
Rhacophoridae	*Kurixalus eiffingeri*	32.8	38		79	hidden	Fei et al., 2009; Chuang et al., 2019
Rhacophoridae	*Gracixalus gracilipes*	22	29.5	2.1	5	arboreal	Yang, 1991; Rowley et al., 2015
Scaphiopodidae	*Scaphiopus hurterii*	58	63	2.3		aquatic	Saenz et al., 2006; Wells, 1977; Richmond, 1947; Bragg, 1944
Scaphiopodidae	*Spea intermontana*	50.5	57.2		325	aquatic	Wright and Wright, 1949; Wells, 1977
Scaphiopodidae	*Spea bombifrons*	45	48.5		462	aquatic	Wright and Wright, 1949; Nussbaum et al., 1983; Stebbins, 1951; Wells 1977

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Supplemental Table 2. Mean, standard deviation (SD) and range of number of eggs per clutch for anuran species (all families) and Hylidae species in the three categories of oviposition sites.

	N eggs Anura			N eggs Hylidae		
Oviposition site	Mean	SD	Range	Mean	SD	Range
Aquatic	1324.34	1802.02	22– 12000	1048.23	980.81	30 – 6500
Arboreal	296.17	649.16	5 – 4000	232.90	279.92	20–1114
Hidden	233.75	232.82	9 – 1000	224	157.69	14 – 436
Terrestrial	96.41	227.22	4 –970	NA	NA	NA

5 CONCLUSÕES

No primeiro capítulo, onde descrevemos a biologia reprodutiva da perereca *Dendropsophus haddadi*, encontramos que a espécie apresenta atividade noturna. O macho vocaliza para atrair a fêmea e exibe sinais visuais, um comportamento não comum em espécies noturnas. Além disso, cuidado parental foi observado em uma fêmea de *D. haddadi* que juntou os ovos da desova com suas patas traseiras, e depois ficou em cima dos ovos de outra desova por cerca de 20 minutos. Esta foi a primeira observação deste comportamento para o gênero.

No segundo capítulo, investigamos a relação entre variação no dimorfismo sexual em tamanho (SSD), fecundidade e locais de oviposição em anuros. Não houve diferenças no SSD entre as espécies de anuros e nem entre os hilídeos que ovipositam em diferentes locais (desova aquática, arborícola, terrestre e escondida). Porém, em espécies que desovam em locais escondidos, o dimorfismo sexual em tamanho foi menor, com machos e fêmeas apresentando tamanhos similares. Isto poderia ser explicado pelo fato de haver uma limitação para casais em amplexo e desovas nesses espaços restritos. Além disso, em muitas espécies com desovas escondidas, as fêmeas não carregam os machos em amplexo. Desta forma, sugerimos que em espécies com desovas escondidas deve haver uma menor pressão para o aumento da fecundidade e das fêmeas, atenuando o SSD.

Como esperado, a fecundidade nas espécies arborícolas, tanto para Anura quanto para Hylidae, foi menor que a das espécies aquáticas. Para os anuros, a fecundidade nas espécies arborícolas foi semelhante à das espécies com desovas terrestres e escondidas. Para os hilídeos, a fecundidade das espécies arborícolas foi semelhante à das espécies com desovas escondidas. No entanto, os hilídeos com desovas arborícolas mostraram uma tendência a ter uma menor fecundidade. Nossos resultados sugerem que a arborealidade pode restringir a fecundidade, devido aos custos relacionados ao transporte dos machos pelas fêmeas durante o amplexo e a oviposição.

Neste trabalho, concluímos que os locais de oviposição podem influenciar a fecundidade e o tamanho das fêmeas, consequentemente, afetar o dimorfimo sexual em tamanho em anuros em diferentes esacalas evolutivas. No entanto, a ausência de dados básicos de história natural, tais como locais de oviposição e tamanho e número de ovos, para um grande número de espécies de anuros, dificulta a realização de estudos que buscam investigar e testar hipóteses sobre a evolução dos modos reprodutivos e dimorfismo sexual em anuros. Desta forma, estudos descritivos de aspectos da história natural das espécies ainda são necessários, pois eles são a base para entendermos os processos e mecanismos envolvidos na evolução de muitos aspectos da biologia de anuros.