

PREDAÇÃO E DEFESA EM ANUROS: REVISÃO, DESCRIÇÃO E EVOLUÇÃO

LUÍS FELIPE TOLEDO

**Tese apresentada ao Instituto de Biociências
da Universidade Estadual Paulista “Julio de
Mesquita Filho”, Campus de Rio Claro, para
a obtenção do título de Doutor em Ciências
Biológicas (Área de Concentração: Zoologia)**

**Rio Claro
Estado de São Paulo – Brasil
Agosto de 2007**

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Orientador: Prof. Dr. CÉLIO FERNANDO BAPTISTA HADDAD

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FEAR OF THE DARK

Tammy Akeo

Adapted by

Sombra

IN THE NIGHT, THE “CURURU FROG” RUNS
LOOKING BACK, JUMP AFTER JUMP,
HOPING NOT TO SEE ANYTHING.
ITS EYES TREMBLE IN FEAR AS IT SLOWS
SEARCHING THE DARK FOR ITS PREDATORS.
THE FROG WATCHES THE DARK JUST AS THE PREDATOR WATCHES THE
FROG.
THE EYES OF THE PREDATOR DANCE AS THE FROG MOVES,
CAREFULLY WATCHING EACH AND EVERY MOTION.
THE FROG SCANS THE BLACK AROUND HIM,
QUICKLY ANALYZING ALL THAT IT SEES.
THE FROG IS SAFE AS LONG AS ITS EYES DON’T SEE THE PREDATOR’S.
NOTHING CATCHES THE FROG EYES, AND IT LETS OUT A SIGH OF RELIEF.
THEN THE FROG HEARS IT, THE SOUND OF BREATHING,
SLOW AND STEADY IT TURNS AROUND
WIDE-EYED WITH FEAR
AND LOOKS INTO THE EYES THAT HAVE WATCHED IT.
A SMILE SPREADS ACROSS HIS FACE REALIZING THE GAME IS OVER.
THE FROG EYES, WIDE WITH TERROR, STARE BACK AT HIS FINALLY.
HIS EYES GAZED DEEP INTO THE FROG
TO A PLACE NO ONE IS ALLOWED.
NOW CORNERED, THE FROG TURNS TO THE PREDATOR WITH BEGGING EYES,
LONGING TO BE SOMEWHERE ELSE, ANYWHERE BUT HERE.
AND NOW, IF YOU WERE THE CURURU,
WHAT SHOULD YOU DO?

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RESUMO GERAL

Até a presente tese, a informação sobre predação e estratégias defensivas em anuros estava fragmentada e desconexa na literatura científica. Na ausência de uma revisão sobre o tema, algumas especulações foram geradas baseadas nas impressões pessoais de diversos pesquisadores. Por exemplo, existem muitos ou poucos relatos de anuros sendo apresados? Um determinado comportamento defensivo já foi descrito em algum lugar, ou é inédito? Qual a relação entre os predadores e os mecanismos de defesa dos anuros? Essas e outras perguntas estavam em aberto. Mesmo em livros texto, os quais geralmente revisam os assuntos abordados de forma abrangente, nota-se o parco conhecimento sobre o tema, sendo estes sempre os menores capítulos dos livros e de conteúdo razoavelmente superficial. Todavia, muita informação já foi gerada e muita ainda está por vir. É nesse sentido que idealizamos e realizamos o presente estudo, visando reunir grande parte do conhecimento atual e gerar novas previsões e hipóteses testáveis. Assim, relacionamos os predadores atuais e naturais dos anfíbios anuros (incluindo as desovas e pós-metamórficos) e revisamos as principais estratégias defensivas dos adultos (pós-metamórficos). Muitos dados apresentados são inéditos e outros compilados da literatura, mas ambos analisados de maneira integrada e sempre dando enfoque evolutivo nas discussões apresentadas. Consideramos este estudo um ponto inicial para compreendermos mais profundamente as estratégias defensivas dos anuros e sua relação com os predadores naturais.

ABSTRACT

Until the present moment, the information about defensive strategies and predation upon anurans was fragmented and disconnected in the scientific literature. In the absence of an overview of the subject, some speculations have been raised based on personal points of view of several scientists. For example, are there many or few reports of predation upon anurans? A specific defensive behavior has already been described or not? How is the relationship between the defensive strategies and predator mechanisms? These and odder questions were hard to answer. Even in text books, where the subjects are treated in a broad way we can notice the poor knowledge of the subject and these are always the shorter and superficial chapters. However, many information is already available and many is about to come. Therefore, we idealized and did the present thesis, aiming to joint a large part of the current knowledge and promoting some previsions and testable hypotheses. So, we related the actual and natural predators of anurans (including eggs and post-metamorphics) and reviewed the main defensive strategies of the adults (post-metamorphics). A great amount of the data presented is novel and other set of data were found in the available literature, but both were analyzed simultaneously with an evolutive approach. We consider this thesis a starting point of a deeper comprehension of the anurans' defensive strategies and their relationship with natural predators.

INTRODUÇÃO

Anfíbios anuros são apesados por uma série de animais, desde pequenos invertebrados (e.g., Toledo, 2003) a vertebrados de grande porte (e.g., Martins et al., 1993; Canale & Lingnau, 2003), provavelmente em decorrência de sua grande abundância na natureza, tamanho relativamente pequeno e pele macia (Duellman & Trueb, 1994). Sendo assim, ao longo de sua história evolutiva, a intensa pressão seletiva causada pela predação, deve estar intimamente relacionada ao surgimento de uma grande diversidade de estratégias defensivas, observadas nas espécies atuais (e.g., Edmunds, 1974; Ryan, 1985; Hödl & Amézquita, 2001). Tais adaptações podem ser categorizadas como ecológicas, morfológicas, morfofisiológicas e/ou comportamentais.

Como estratégias defensivas ecológicas, destacam-se a utilização de abrigos durante o repouso (e.g., Stewart & Rand, 1991; Michael, 1997) ou durante a atividade (e.g., vocalização: Hartmann, 2004) e o fato de que muitas espécies investem em uma prole numerosa e possuem modos reprodutivos que podem conferir proteção contra predação (e.g., Heyer, 1969; Haddad & Sawaya, 2000).

Quanto à morfologia, considera-se que o padrão de coloração dos indivíduos atua como elemento defensivo primário ou secundário e ocorre de diferentes maneiras. A mais difundida entre os anuros é a camuflagem (Hödl & Amézquita, 2001), a qual pode imitar o padrão de cores e formas do hábitat em que a espécie ocorre, ou atribui aos indivíduos um padrão disruptivo (Duellman & Trueb, 1994). Existem também padrões de coloração que podem confundir os predadores ao dar-lhes a impressão de que a presa é maior do que seu tamanho real (referências em Duellman & Trueb, 1994). Ademais, o polimorfismo (e.g., Hoffman & Blouin, 2000; Bourne, 2001), o mimetismo e/ou o aposematismo (e.g., Symula et al., 2001; Vences et al., 2003) também atuam como estratégias defensivas contra predadores visualmente orientados (Duellman & Trueb, 1994). Além do padrão de coloração, algumas características morfológicas também podem atuar como causadoras de padrões disruptivos ou de camuflagem. Diversas espécies possuem estruturas dérmicas (e.g., chifres, pregas tarsais e apêndices calcâneos) que modificam o contorno do corpo dificultando sua localização por predadores (Sazima, 1978; Duellman & Trueb, 1994).

Dentre os recursos defensivos morfofisiológicos, o mais difundido é a presença de glândulas epidérmicas (revisão em Toledo & Jared, 1995), as quais podem secretar, por exemplo, substâncias adesivas (Manzanilla et al., 1998; Kwet & Solé, 2002), odoríferas (Sazima, 1974; Waye & Shewchuk, 1995; Grant, 2001; Kizirian et al., 2003) e/ou tóxicas, de irritantes (Jazen, 1962; Powell & Lieb, 2002) a letais (Rabor, 1952; Daly & Meyers, 1967; Tokuyama & Daly, 1983). Em alguns casos, essas secreções revelaram-se eficazes contra diversos predadores, tais como anfíbios (Formanowicz Jr. & Brodie Jr., 1979), répteis (Brodie Jr., 1978; Manzanilla et al., 1998), aves (Brodie Jr. & Nussbaum, 1987) e mamíferos (Brodie Jr. & Formanowicz Jr., 1981; Pearl & Hayes, 2002). Contudo, em muitas outras situações, as toxinas secretadas parecem não conferir proteção aos anuros, sendo estes apresados por insetos, peixes, anfíbios, répteis e aves (ver Cardoso & Sazima, 1976; Haddad & Bastos, 1997; Cochran & Cochran, 2003). Ademais, alguns predadores apresentam estratégias comportamentais e fisiológicas especializadas para a dieta de anuros potencialmente venenosos (ver Frazer, 1973).

Todos os mecanismos defensivos mencionados acima podem ou devem ser executados através de comportamentos simples ou elaborados. Alguns comportamentos estão associados à morfologia, como direcionar as glândulas e/ou regiões com coloração aposemática em direção ao possível predador (Hanson & Vial, 1956; Sazima & Caramaschi, 1986; Torr, 1991; Williams et al., 2000), ou realizar posturas em que padrões disruptivos se acentuem (Sazima, 1978; Rocha et al., 1998; Garcia, 1999). Caracteres morfológicos como espinhos e dentes, além de suas funções normais (e.g., estímulo sexual e alimentação, respectivamente), também podem ser utilizados contra predadores em potencial (Vaz-Ferreira & Gehrau, 1975; Hartmann et al., 2003).

Algumas das estratégias defensivas são comuns a muitas espécies, como tanatose (Zamprogno et al., 1998; Abbadié-Bisogno et al., 2001; Gramapurohit et al., 2001), inflar o corpo (Hödl & Amézquita, 2001) e emitir gritos de agonia (Sazima, 1975; Hödl & Gollmann, 1986; Azevedo-Ramos, 1995; Williams et al., 2000). Outras estratégias talvez sejam comuns a todas as espécies de anuros, como, por exemplo, o comportamento de fuga (Duellman & Trueb, 1994; Williams et al., 2000). Por outro lado, existem estratégias que são conhecidas apenas para algumas espécies (ver Channing & Howell, 2003; Hartmann et al., 2003).

Além de variar de maneira interespecífica, alguns comportamentos defensivos podem variar de maneira intraespecífica. Neste último caso podem variar ao longo da distribuição geográfica da espécie (Bjager, 1980; Williams et al., 2000) ou conforme a lateralidade dos indivíduos (Robins et al., 1998). Alguns comportamentos estão relacionados ao posicionamento das glândulas secretoras de veneno (Sazima & Caramaschi, 1986; Williams et al., 2000), outros estão relacionados à filogenia dos taxa envolvidos (Summers & Colugh, 2001; Hödl & Amézquita, 2001) e outros consistem de convergências etológicas entre espécies ecologicamente semelhantes (Sazima, 1975; Garcia, 1999). A execução de comportamentos defensivos pode estar ainda relacionada a condições momentâneas, como condições fisiológicas (Gomes et al., 2002), durante o cuidado parental (Vaz-Ferreira & Gehrau, 1975; Giaretta & Cardoso, 1995; Toledo et al., 2004) ou durante as agregações reprodutivas (Tuttle et al., 1982).

Algumas das estratégias defensivas possuem nomes específicos, como tanatose (Hartmann et al., 2003; McCallum et al., 2003), comportamento de fuga (McCallum et al., 2003) ou mordidas (Giaretta & Cardoso, 1995; Hartmann et al., 2003). Todavia, muitos dos comportamentos defensivos registrados ainda não possuem nomes específicos, havendo necessidade de realizar uma descrição sucinta toda vez que nos referimos a estes. Este é, por exemplo, o caso do comportamento de esticar as pernas traseiras para trás e manter o corpo achatado rente ao solo (e.g., Sazima, 1975; Garcia, 1999), o comportamento de entrelaçar as pernas e erguê-las, mantendo as costas em contato com o solo (Channing & Howell, 2003), ou o comportamento manter a porção anterior do corpo em contato com o solo e erguer a porção posterior do corpo (Sazima & Caramaschi, 1988; Kizirian, 2003). Ademais, poucos são os estudos que avaliaram a eficácia das estratégias defensivas utilizadas pelos anuros (Sazima, 1974; Formanowicz & Brodie, 1979; Manzanilla et al., 1998; Rödel & Braun, 1999; Pearl & Hayes, 2002) e quase nada se conhece sobre a evolução dos diferentes comportamentos defensivos (e.g., Williams et al., 2000).

Neste contexto, o presente estudo realiza uma revisão dos comportamentos defensivos conhecidos para diferentes famílias de anuros; descreve comportamentos inéditos; sugere nomes categóricos (em Inglês a princípio) apropriados a cada um dos comportamentos abordados; realiza um mapeamento dos comportamentos sobre árvores filogenéticas atuais (e.g., Faivovich et al., 2005; Frost et al., 2006; Grant et al., 2006)

para inferir sobre a origem dos comportamentos defensivos (e.g., origem filogenética vs. convergência ecológica); e levanta hipóteses sobre a real eficiência dos comportamentos na presença de predadores em potencial.

MATERIAL & MÉTODOS

Área de Estudo

Para a realização do presente estudo, além de informações extraídas da literatura, de relatos de inúmeros pesquisadores (mencionados nos respectivos capítulos) e de animais vivos encaminhados ao laboratório de herpetologia, foram realizadas diversas coletas em campo, de acordo com a disponibilidade de recursos financeiros e tempo. Os 56 municípios visitados (em 14 Estados) estão listados a seguir. Entre parênteses estão algumas localidades específicas.

ALAGOAS: Passo de Camarajibe; AMAZONAS: Manaus e Presidente Figueiredo; BAHIA: Caraíva, Feira de Santana, Ilhéus, Una, Uruçuca, Salvador (capital e praia do forte) e Sooretama; ESPÍRITO SANTO: Anchieta, Aracruz, Conceição da Barra e Jaquaré; GOIÁS: Alto Paraíso (Vale da Lua e Chapada dos Veadeiros) e São João D'Aliança; MINAS GERAIS: Camanducaia (Monte Verde), Grão Mogol, Pirapora, São Roque de Minas (Serra da Canastra), Santana do Riacho (Serra do Cipó) e São Tomé das Letras; MATO GROSSO DO SUL: Três Lagoas; PARÁ: Belém; PARANÁ: São José dos Pinhais e Tijucas do Sul; PERNAMBUCO: Fernando de Noronha e Tamandaré; RIO GRANDE DO SUL: São Francisco de Paula; SANTA CATARINA: Angelina, Itapema, Lages, Mafra, Rancho Queimado e Treviso; SERGIPE: Itabaiana; SÃO PAULO: Apiaí e Iporanga (PETAR), Barra do Turvo (PEJ), Bertiooga, Botucatu, Campinas (Barão Geraldo), Campos do Jordão, Cananéia (PEIC), Cotia, Iguape (PEJ), Itirapina (EEI), Pilar do Sul, Piracicaba, Ribeirão Branco, Rio Claro (FEENA, MSJ e Itapé), Santa Rita do Passa Quatro, São Luiz do Paraitinga (PESM-NSV), São Sebastião (Maresias), Sorocaba, Ubatuba (PEIA e PESM-NP).

Coleta de dados

A cada encontro com anfíbios anuros na natureza foram registrados dados gerais, como: I) a localidade e data; II) bioma e microambiente ocupado; III) período da observação (diurno ou noturno); IV) temperatura do ar; V) espécie; VI) comprimento rostro-cloacal (CRC: medido com paquímetro de 0,05 mm de precisão); VII) sexo e classe de idade do indivíduo (juvenil ou adulto) (ver ficha de campo).

Com relação ao comportamento foram registrados: I) a atividade do anuro no momento do encontro; II) a reação do anuro à aproximação do pesquisador; III) a reação durante a tentativa ou captura efetiva do indivíduo; e IV) a reação do indivíduo capturado a estímulos provocados pelo pesquisador. Estes estímulos variaram de caso a caso sendo os mais comuns a: sacudida, pressão nas pernas, toques na cabeça no corpo ou próximos à boca, virar o anuro de barriga para cima, realizar movimentos bruscos com as mãos ou objetos em direção aos indivíduos, embora sem tocá-los. Essas formas de estímulo já foram utilizadas anteriormente e costumam gerar bons resultados (e.g., Hödl & Gollmann, 1986; Toledo et al., 2005). Nenhum desses estímulos causou injúrias aos anuros, os quais foram libertados (na maioria dos casos) em ambiente natural após a estimulação. Em seguida foram observados por mais cerca de três minutos, período em que ainda podem desempenhar comportamentos defensivos (Bajger, 1980).

Foram também provocados encontros em laboratório entre os anuros e serpentes não peçonhentas, predadores em potencial. Para tanto, serpentes encontradas nos ambientes estudados foram apresentadas aos anuros dentro de viveiros, sendo registrados os comportamentos realizados pelos anuros frente ao encontro, ataque (quando houver) e subjugação (quando houver). Foram também registradas as reações das serpentes frente ao repertório defensivo apresentado pelos anuros. Os experimentos foram realizados no laboratório de Herpetologia e Jacarezário, vinculados ao Departamento de Zoologia da UNESP em Rio Claro, nos quais já são mantidas diversas espécies de serpentes que se alimentam de anuros em ambiente natural (e.g., *Chironius* spp. e *Liophis* spp.).

Somente foram coletados, transportados, anestesiados, fixados e depositados na coleção de anuros CFBH do Departamento de Zoologia da UNESP de Rio Claro, os indivíduos que necessitaram de confirmação de identificação. Autorizações de captura e

transporte de anfíbios e répteis foram concedidas pelo Centro de Conservação e Manejo de Répteis e Anfíbios do IBAMA (processo número: 02010.001495/04-32).

Durante a aproximação ou manipulação dos anuros, tanto por parte do pesquisador como por parte de predadores, podem ser emitidas vocalizações, tais como cantos de soltura (que aparentemente não possuem caráter defensivo), gritos de agonia e gritos de alarme. Nestes casos as vocalizações serão gravadas com gravador cassete Marantz PMD222 e microfone externo direcional Audiotecnica AT835b. As análises de som foram realizadas através do programa Raven 1.2.1 configurado a 16 bits de resolução, 44,1 kHz de frequência de amostragem e “FFT” e “frame length” a 256. As vocalizações serão descritas e as terminologias utilizadas seguirão as adotadas por Duellman & Trueb (1994).

Coletores: L. F. T. & _____; Data: ____/____/____
Localidade: _____ Temp. ar: _____ °C
Espécie: _____ Sexo/ Idade: _____
CRC: _____ mm; Peso: _____ g; Microambiente: _____
Atividade: _____ Coloração: Aposmtc Camuflid outro: _____
Reação à aproximação: Imóvel Fuga outro: _____

Reação ao manuseio: _____

 Teste para Tanatose: não sim – Tipo: I (qq jeito) II (fechadinho)
Olho: Fechado aberto – OBS: _____
 Teste para Grito Agonia: não sim – Boca aberta fechada.
 Teste para _____: não sim: _____
 Toques em _____ (parte do corpo): Reação: _____
Tipo de Secreção: Odor Grudenta Tóxica Mucosa outra: _____
OBS: _____

Coletores: L. F. T. & _____; Data: ____/____/____
Localidade: _____ Temp. ar: _____ °C
Espécie: _____ Sexo/ Idade: _____
CRC: _____ mm; Peso: _____ g; Microambiente: _____
Atividade: _____ Coloração: Aposmtc Camuflid outro: _____
Reação à aproximação: Imóvel Fuga outro: _____

Reação ao manuseio: _____

 Teste para Tanatose: não sim – Tipo: I (qq jeito) II (fechadinho)
Olho: Fechado aberto – OBS: _____
 Teste para Grito Agonia: não sim – Boca aberta fechada.
 Teste para _____: não sim: _____
 Toques em _____ (parte do corpo): Reação: _____
Tipo de Secreção: Odor Grudenta Tóxica Mucosa outra: _____
OBS: _____

RESULTADOS

Os resultados da presente tese estão organizados em capítulos que já foram ou estão sendo preparados para publicação em revistas especializadas. Cada capítulo dará origem a um artigo. Assim, esta tese resultou nos seguintes capítulos/artigos:

1. Toledo, L. F. Araújo, O. G. S., Vonesh, J. & Haddad, C. F. B. Anuran egg predators and the evolution of reproductive modes. *South American Journal of Herpetology*, submitted.
2. Toledo, L. F. 2005. Predation of juvenile and adult anurans by invertebrates: current knowledge and perspectives. *Herpetological Review*, 36(4): 395-400.
3. Toledo, L. F., Silva, R. R. & Haddad, C. F. B. 2007. Anurans as prey: an exploratory analysis and size relationships between predators and their prey. *Journal of Zoology*, 271: 170-177.
4. Toledo, L. F. & Haddad, C. F. B. When frogs scream! A review of anuran defensive vocalizations. *Herpetological Journal*, submitted.
5. Toledo, L. F., Sazima, I. & Haddad, C. F. B. Behavioral defenses of anurans: an overview. In preparation.
6. Toledo, L. F. & Haddad, C. F. B. Colors and mimicry as defensive strategies of anurans. *Journal of Zoology*, submitted.

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CAPÍTULO 1

PREDADORES DOS OVOS DE ANUROS E A EVOLUÇÃO DOS MODOS REPRODUTIVOS

Luís Felipe Toledo, Olívia Gabriela S. Araújo, James R. Vonesh & Célio F. B. Haddad



Harry Greene, 1997

CAPÍTULO 1

ANURAN EGG PREDATORS AND THE EVOLUTION OF REPRODUCTIVE MODES

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ABSTRACT

While anurans face stage-specific predators throughout ontogeny, embryonic stages may be particularly vulnerable due to their more limited suite of anti-predator responses. Some authors have suggested that the evolution of more terrestrial reproductive strategies in anurans (e.g., arboreal or terrestrial eggs, direct development) is an adaptive response to selection by aquatic egg predators. Thus, if current predation is indicative of the selective pressures that shaped these life history strategies, we would predict that the eggs of species with aquatic reproductive strategies would experience greater predation than those of species with more derived reproductive strategies. Here we review published studies of egg predation in anurans to evaluate whether there is evidence that aquatic eggs are more vulnerable to predation. Furthermore, we listed the actual anuran egg predators, found the main predators, and evaluated the effectiveness of some egg laying sites. Eggs deposited in the water and not in foam nests were the most preyed. The family Brachycephalidae was much less preyed than expected, and it could reflect ineffective field observations and/or positive effectiveness of their reproductive strategy: laying eggs with a patchy distribution on the forest floor, in cryptic places, and out of the water. Therefore, we present a review that supports the hypothesis of selective pressures in favour of the egg-laying out of the water.

RESUMO

Anuros enfrentam diferentes predadores ao longo de suas fases ontogenéticas, das quais a fase de ovos deve ser particularmente vulnerável devido à sua limitação de respostas defensivas. Alguns autores sugerem que a evolução de desovas fora de corpos d'água (e.g., no solo, em árvores ou por desenvolvimento direto) é uma resposta adaptativa à seleção exercida pelos predadores aquáticos. Assim, se a predação observada atualmente é um indicativo de pressão seletiva que moldou essas estratégias reprodutivas, nós poderíamos prever que ovos depositados em água sejam mais apresados do que aqueles com estratégias reprodutivas alternativas. Assim, nós revisamos os estudos sobre predação de desovas para avaliar se existe evidência que suporte que os ovos depositados na água sejam mais apresados que os ovos depositados fora da água. Além disso, nós listamos os predadores conhecidos de ovos de anuros, identificamos os principais predadores e inferimos sobre o sucesso de determinadas estratégias reprodutivas. Os ovos depositados na água e não em ninho de espuma foram os mais apresados dentre todas as combinações de estratégias. Os ovos de indivíduos da família Brachycephalidae foram menos apresados do que o esperado; isto poderia estar relacionado com um viés de observação em campo, ou realmente condizer com um maior sucesso adquirido pelas estratégias reprodutivas adotadas por este grupo: depositar ovos de maneira distribuída pelo chão das florestas, em locais crípticos e fora da água. Assim, apoiamos a sugestão de uma pressão para a deposição de ovos fora da água.

INTRODUCTION

The embryonic stage of anuran development may be the life history stage most vulnerable to predation (Hödl, 1986; Chivers *et al.*, 2001). Eggs are externally fertilized, lack shells, and are often deposited in the environment without the benefit of parental care (e.g., only 10% of frogs species have been reported to exhibit parental care; Duellman and Trueb, 1986; Haddad and Prado, 2005). Furthermore, relative to later stages, embryos have a more limited suite of anti-predator defences. It has been suggested that several reproductive modes (currently there are 39 recognized reproductive modes in anurans, the greatest diversity among tetrapods: Haddad and Prado, 2005) have evolved in response to selective pressures exerted by aquatic egg predation (Downie, 1990; Magnusson and Hero, 1991; Martins, 1993; Haddad and Sawaya, 2000; Prado *et al.*, 2002).

In leptodactylids there is a trend to lay eggs in foam nests or in terrestrial environments, with the most ancestral strategy, eggs laid directly in the water, restricted to a few groups (e.g., Prado *et al.*, 2002). Similarly, in some hylid and hyperoliid frogs, eggs are laid arboreally, frequently on leaves or wrapped within them (e.g., Duellman and Trueb, 1994; De la Riva, 1999; Prado *et al.*, 2006). This shift toward non-aquatic reproductive modes is primarily found in tropical taxa and has been hypothesized to be driven by the combination of reduced desiccation risk in the humid tropics, a way to escape disturbance by water turbulence, and high levels of aquatic egg predation (e.g., Heyer, 1969; Magnusson and Hero, 1991; Haddad and Prado, 2005). Selection by predators is also thought to have driven the evolution of parental care as well as other defensive traits in several species (e.g., in mantellids: Lehtinen, 1993; leptodactylids: Martins, 2001; and aromobatids: Bourne *et al.*, 2001; Toledo *et al.*, 2004); toxic eggs (review in Gunzburger and Travis, 2005); plasticity in the timing of anuran eggs hatching (Warkentin, 1995; 2000; Chivers *et al.*, 2001); and plasticity in breeding behaviors, e.g., selecting a safer oviposition site (Holomuzki, 1995; Spieler and Linsenmair, 1997; Summers, 1999; Lips, 2001).

While the selective pressures of embryonic predators may be a good explanation for the evolution of some specialized reproductive modes and plastic responses to egg predators, the relationship remains equivocal. While the strength of past egg predation

is unknown, it is worth noting that egg predation in species with derived reproductive strategies can also be very high (Duellman and Trueb, 1994; Vonesh 2000; 2005). Magnusson and Hero (1991) attempted to demonstrate that aquatic predators have exerted and continue to exert selective pressure on the evolution of terrestrial oviposition strategies in anurans, however a recent reanalysis of these data revealed no significant relationship (Haddad and Prado, 2005).

Besides reducing egg predation, non-aquatic oviposition strategies may have other fitness benefits, e.g., secure egg masses to a homogeneous and immobile substrate, which could also improve hatching success (Richards, 1993). Furthermore, laying eggs in foam nests, instead of in gelatinous masses, may have several other functions. For example, foam nests may provide a source of food, sheltering, an adequate temperature, water balance, and oxygen supply (Gorzula, 1977; Downie, 1990; Haddad and Prado, 2005 and references therein). Consequently, it is likely that different selective pressures (including predation) act in the evolution of reproductive modes (Heyer, 1969; Magnusson and Hero, 1991; Prado *et al.*, 2002; Haddad and Prado, 2005).

Here we review the scientific literature regarding embryonic predation in anurans to help elucidate general patterns across anurans. We were interested in exploring the following questions; 1) which predator taxa are responsible for most anuran egg predation and 2) how does that vary with anuran reproductive strategy. By reviewing these studies we hope to generate insights on the relation between predation and reproductive modes in anurans and improve discussion about the role of predator pressure on the evolution of the reproductive modes (e.g., Heyer, 1969; Magnusson and Hero, 1991; Prado *et al.*, 2002).

MATERIAL AND METHODS

We compiled studies that report egg predation by searching in web-based-databases and by performing an exhaustive reading of the most accessible herpetological journals (e.g., *Amphibia-Reptilia*, *Copeia*, *Herpetologica*, *Herpetological Journal*, *Herpetological Review*, and *Journal of Herpetology*). For each study, we recorded the name and taxonomic group of the prey and predator species, the anuran

egg laying site, (i.e., aquatic, arboreal, terrestrial, or subterranean); and the spawn type, (i.e., eggs in a gelatinous mass or in foam nests). Specific names of the amphibians (both preys and predators) and number of species in each family follow Frost (2006). The specific names of the non-amphibian predators are the same as presented in the original publications. We did not include studies that failed to report prey and/or predator identities (e.g., Kaiser and Gibson, 2004). Experimental studies were not considered in most of the analysis; in some experimental studies the predator and its prey do not co-exist in nature, so this may produce unrealistic data (see discussion in Gunzburger and Travis, 2005).

RESULTS

We found 363 reports of anuran egg predation (APPENDIX I), including experimental studies (N = 225) and natural observations in the field (N = 138; Fig. 1). From these data we recognized 23 taxonomic groups of predators (Table1). In observational field studies of naturally occurring egg predation, dipterans larvae were the most common invertebrate (46.8 %) and anuran larvae the most common vertebrate predators (42.1 %) with anuran larvae being the most common predators over all (23.2 %; Fig. 2). About 67 % of the predators are typically terrestrial (e.g., primates, canids, snakes, anurans, spiders, and dipterans) and the remaining 33 % are aquatic (e.g., fishes, tadpoles, salamander larvae, and crustaceans).

Approximately 72 % of the preyed eggs were involved with a gelatinous mass (Fig. 3A) and about 59 % were laid in the water (Fig. 3B). About 38 % of the natural observations involved species that lay eggs in aquatic and gelatinous egg masses (AGEM). Almost 20 % of the reports on egg predation were on hylid eggs followed by leptodactylid (ca. 14 %), ranid (ca. 13 %), and hyperoliid (ca. 12 %). The remaining nine anuran families corresponded to about 41 % of the reports (Fig. 4). The number of species in each anuran family was positively correlated with the number of reports of egg predation within the family (linear regression analysis: $r^2 = 0.33$; $df = 14$; $P = 0.026$; Fig. 5). The point related to the family Brachycephalidae was an outlier very distant from the 95 % confidence interval (Fig. 5).

Table 1. Anuran egg predator groups, number of predation reports (N = 363), number of predator species (N = 157), and predator habitat (based on the species listed in appendix I). This table includes experimental studies and field observations.

Predator Group	Number of reports (number of predator species)	Predator most typical habitat
<u>Invertebrates</u>		
Hirudinea	6 (5)	Aquatic
Platyhelminthes	2 (1)	Terrestrial
Arachnida	3 (2)	Terrestrial
Gastropoda	1 (1)	Terrestrial
Crustacea	5 (5)	Aquatic
<u>Insecta</u>		
Coleoptera	16 (9)	Terrestrial
Diptera	33 (10)	Terrestrial
Hymenoptera	15 (10)	Terrestrial
Hemiptera	13 (9)	Aquatic
Odonata	8 (5)	Aquatic
Orthoptera	1 (1)	Terrestrial
Tricoptera	2 (2)	Terrestrial
<u>Vertebrates</u>		
Pisces	65 (19)	Aquatic
<u>Urodela</u>		
Adults	30 (14)	Terrestrial
Larvae	4 (1)	Aquatic
<u>Anura</u>		
Adults	15 (10)	Terrestrial
Tadpoles	109 (45)	Aquatic
<u>Reptile</u>		
Serpentes	9 (7)	Terrestrial
Testudines	16 (2)	Aquatic
Aves	1 (1)	
<u>Mammals</u>		
Canidae	1 (1)	Terrestrial
Primates	7 (2)	Terrestrial
Rodentia	1 (1)	Terrestrial

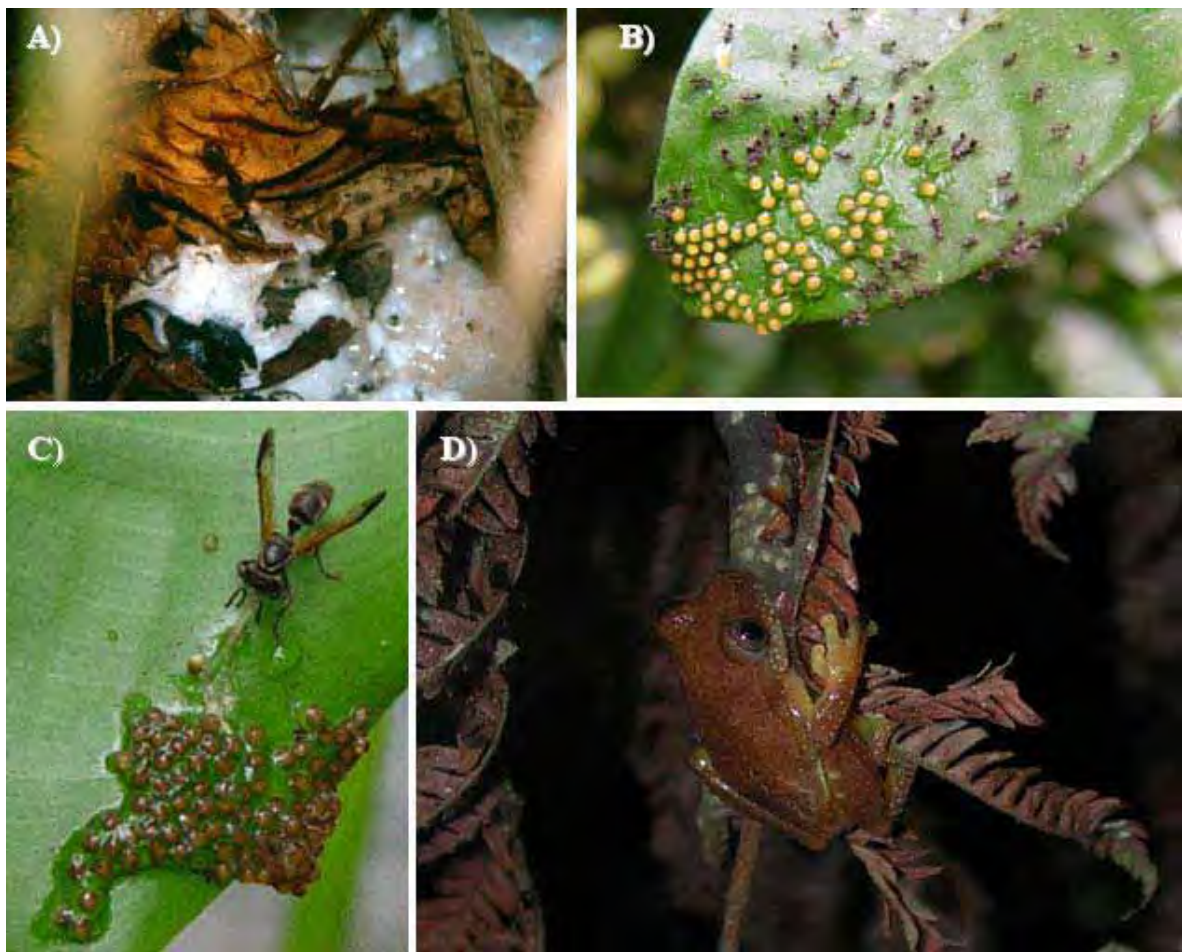


Figure 1. Predation on anuran eggs by invertebrates and vertebrates. A) Foam nest of *Leptodactylus labyrinthicus* being preyed by an ant (*Camponotus rufipes*); arboreal nests of *Dendropsophus ebraccatus* being preyed by B) social ants (*Azteca* sp.) and C) a wasp (*Polybia rejecta*); and D) an arboreal nest of *Hyperolius spinigularis* being preyed by another tree frog (*Afrixalus fornasini*). Pictures of L. F. Toledo (A), J. Touchon (B and C), and J. R. Vonesh (D).

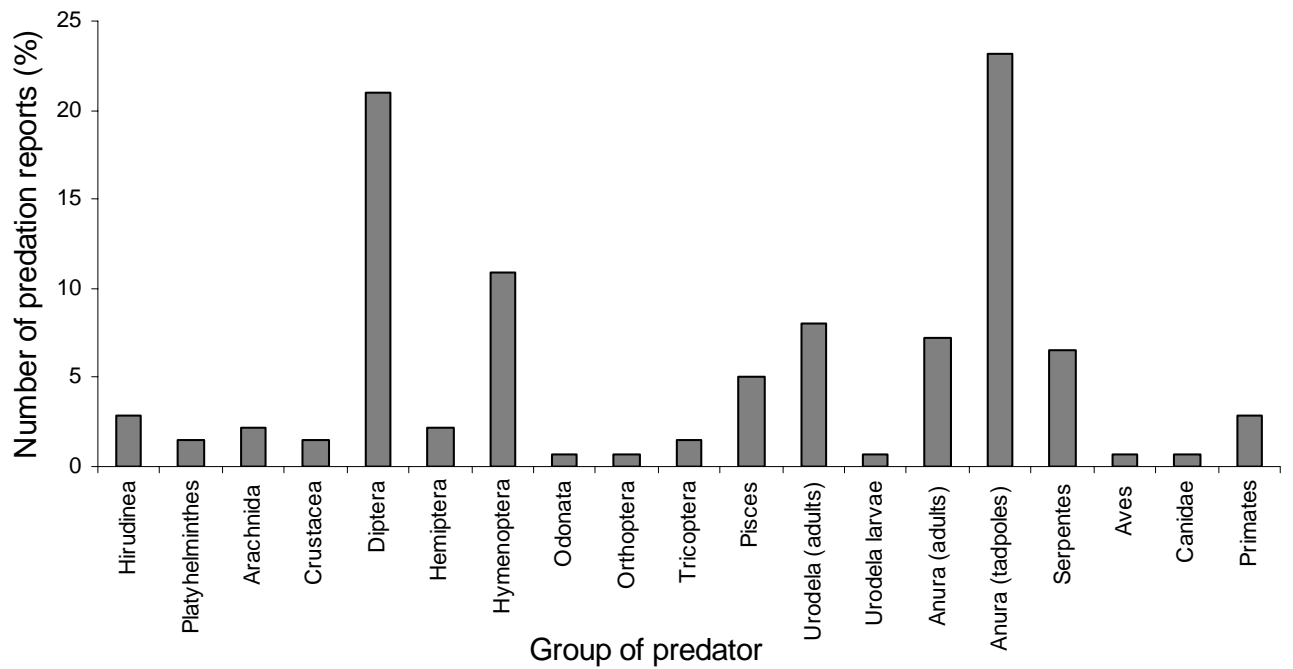


Figure 2. Percentage of preyed clutches (in natural conditions) by different groups of predators (N = 138).

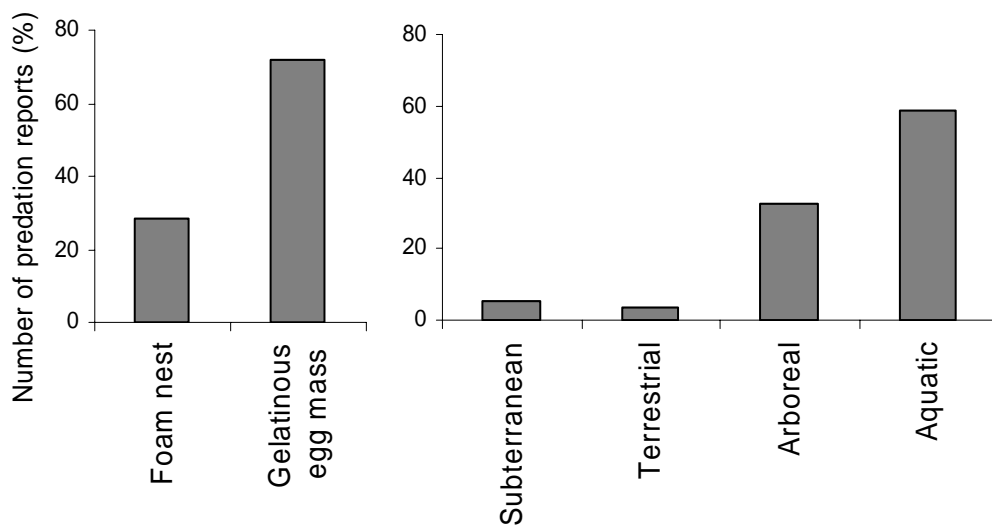


Figure 3. Percentage of preyed clutches (in natural conditions) in relation to A) the clutch characteristics and B) the egg laying sites (N = 138).

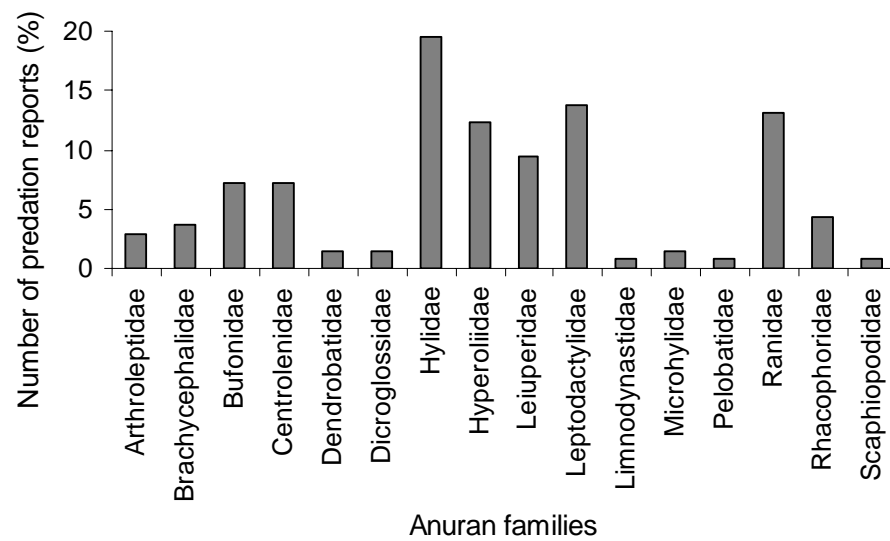


Figure 4. Percentage of preyed clutches over the 16 anuran families based on the 138 natural observations presented in the Appendix I.

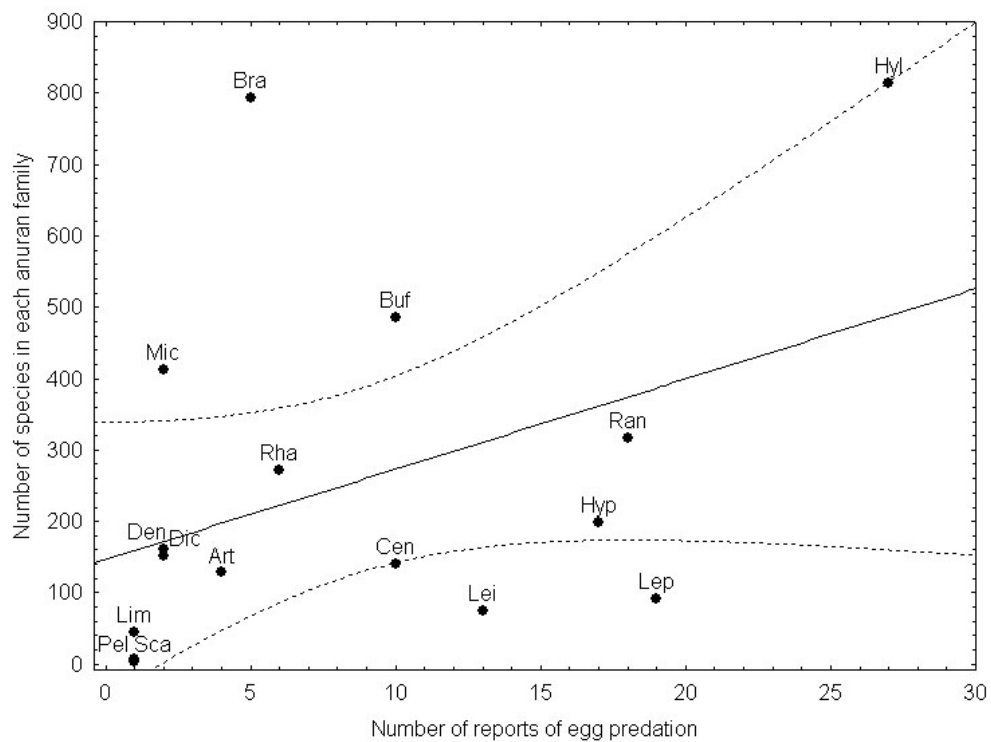


Figure 5. Linear regression (solid line) between number of species within an anuran family (accordingly to current systematics: Frost, 2006) and number of predation reports for each family. Dotted line shows the 95 % of confidence interval. Art: Arthroleptidae, Bra: Brachycephalidae, Buf: Bufonidae, Cen: Centrolenidae, Den: Dendrobatidae, Dic: Dicroglossidae, Hyl: Hylidae, Hyp: Hyperoliidae, Lei: Leiuperidae, Lep: Leptodactylidae, Lim: Limnodynastidae, Mic: Microhylidae, Pel: Pelobatidae, Ran: Ranidae, Rha: Rhacophoridae, Sca: Scaphiopodidae.

DISCUSSION

Our review covered a wide range of anuran taxa and the positive relationship found between species in the anuran families and reports in the families indicates that we collected a good sample of what we may find in nature. Although the majority of the predators listed are typically terrestrial, the aquatic ones probably exert the greatest predation pressure, based on the highest number of predation events observed in natural conditions. Looking across predator taxa and embryonic habitats, the main predators of anuran eggs appear to be anuran larvae. In some cases, reports of egg predation may represent feeding on trophic ovules deposited in the nests to feed tadpoles (e.g., Kam *et al.*, 1996; Prado *et al.*, 2005 and references therein). However, in most of the cases, tadpoles are carnivores that prey upon other species clutches (e.g., Downie, 1990; Shepard and Caldwell, 2005) or even conspecific eggs (e.g., Polis and Meyers, 1985; Hearnden, 1991; Prado *et al.*, 2005).

By revising the anuran reproductive modes, different authors considered that the mode represented by aquatic and gelatinous egg masses is the generalized and ancestral, called as reproductive mode 1 (reviews in Duellman and Trueb, 1994; Haddad and Prado, 2005). Hence, the other modes (e.g., in foam nests or out of the aquatic environment) have been differentiated from mode 1. Furthermore, it has been suggested that the differentiation of modes was caused by different selective pressures, including an attempt to reduce the predation risk (Downie, 1990; Magnusson and Hero, 1991; Martins, 1993; Haddad and Sawaya, 2000; Prado *et al.*, 2002; Haddad and Prado, 2005). The same scenario may be suggested from our results: the reproductive mode 1 (*sensu* Haddad and Prado, 2005) accumulated the greater number of reports of predation. It could be a sign of the greater predation pressure on eggs of this mode, resulting in a greater number of observations and, consequently, publications. Therefore, laying eggs out of natural water bodies, i.e., in arboreal, subterranean, terrestrial, or even in constructed nests in the margins of water bodies, may notably prevent egg predation.

On the other hand, one could state that our findings are circumstantial because aquatic and gelatinous egg masses (AGEM) are easier to be observed in nature. Although, it could be true when comparing with the probability of finding subterranean eggs, but it could not be when comparing with arboreal eggs and aquatic foam nests. In the first case, most of the clutches are laid on the vegetation associated to the margins of the water bodies. The difficulty in finding them is similar to the difficulty in finding

aquatic eggs (person. obs.). In the second case, the foam nests are even easier to find than AGEM (person. obs.). However, a stronger criticism that may arise is that the reproductive mode 1 is the most widespread among the anurans, probably because it is the ancestral mode (Haddad and Prado, 2005), and hence it is the most observed in nature. This fact could produce a larger number of reports of predation of eggs placed in AGEM.

The outlier point of the family Brachycephalidae in Fig. 5 may rely on an adaptive hypothesis. Most, if not all of brachycephalid species, lay their eggs on the ground, generally under fallen leaves in the forest floor (Duellman and Trueb, 1994). This strategy makes difficult for researches to observe predation events. However, it could also effectively prevent eggs from predation as the eggs are laid in cryptic places in an unpredicted random patchy distribution on the forest floor. Actually, the lack of predation reports in this family could be a combination of all these factors. The same short number of predation reports in relation to the number of species in the family was observed to adult individuals (Toledo *et al.*, 2007). Hence, if there is an effective defence involved in terrestrial nesting and in a random patchy distribution pattern of clutches and adults brachycephalids, it would, in part, explain the evolutionary success of the family, expressed in the huge number of species (see also Toledo *et al.*, 2007).

Tadpoles and post-metamorphic anurans also face several different predators (reviews in Gunzburger and Travis, 2005; Toledo, 2005; Toledo *et al.*, 2007). However, they can avoid predators by many behavioural and physiological adaptations (Duellman and Trueb, 1994). On the other hand, the defensive mechanisms of eggs are limited. By reviewing the egg predation literature we were able to recognize basically four defensive strategies for anuran eggs: 1) eggs can be unpalatable (review in Gunzburger and Travis, 2005) or difficult to be preyed upon (Grubb, 1972; Orians and Janzen, 1974); 2) eggs may be laid in cryptic sites (including egg crypsis) (e.g., Heyer, 1969); 3) eggs can be placed out of the water or in foam nests (e.g., Heyer, 1969); and 4) embryos may immaturesly hatch in the presence of the predator (e.g., Warkentin, 1995; 2000). All these strategies may occur lonely or jointly.

From this point we lack some other beta-analysis involving the reports of egg predation and experiments to address further questions, such as: in which scale are the specialized reproductive modes effective against predation? Are there specializations

among predators to prey eggs of species with specialized reproductive modes? Although we can not answer entirely these questions, our review improved the knowledge on the subject and provides substantial material to continue studying the relation of reproductive modes and predation.

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Appendix I. Reports (N = 363) of anurans that had their eggs preyed (N = 107 spp), egg laying site (aquatic: Q; arboreal: R; terrestrial: T; or subterranean: S), clutch type (gelatinous mass: G; foam nests: F), and the respective predators (N = 157 spp). An asterisk ‘*’ after anuran species names indicates experimental studies.

Anuran species (prey)	Spawn type	Predator species	Predator group	Source
ARTHROLEPTIDAE (1 sp.)				
<i>Arthroleptis sylvatica</i>	Q / G	<i>Ambystoma opacum</i>	Urodela	Walters, 1975
<i>Arthroleptis sylvatica</i>	Q / G	<i>Gerris buenoi</i>	Hemiptera	Eaton and Paszkowski, 1999
<i>Arthroleptis sylvatica</i>	Q / G	<i>Gerris pingreensis</i>	Hemiptera	Eaton and Paszkowski, 1999
<i>Arthroleptis sylvatica</i>	Q / G	<i>Limnephilus</i> sp.	Tricoptera	Stein, 1985
BOMBINATORIDAE (1 sp.)				
<i>Bombina variegata</i> *	Q / G	<i>Rana temporaria</i>	Tadpole	Heusser, 1970
BRACHYCEPHALIDAE (3 spp.)				
<i>Eleutherodactylus coqui</i>	T / G	<i>Megaseia scalaris</i>	Diptera	Villa and Townsend, 1983
<i>Eleutherodactylus guentheri</i>	T / G	<i>Echinanthera cephalostriata</i>	Serpentes	Moura-Leite <i>et al.</i> , 2003
<i>Eleutherodactylus</i> sp.	T / G	<i>Rhadinaea lachrymans</i>	Serpentes	Quijano and Rojas, 1995
<i>Eleutherodactylus</i> sp.	T / G	<i>Rhadinaea bilineata</i>	Serpentes	Sazima <i>et al.</i> , 1992
<i>Eleutherodactylus</i> sp.	T / G	<i>Leptotila cassinii</i>	Aves	Poulin <i>et al.</i> , 2001
BUFONIDAE (8 spp.)				
<i>Anaxyrus americanus</i> *	Q / G	<i>Ambystoma opacum</i>	Urodela	Walters, 1975
<i>Anaxyrus americanus</i> *	Q / G	<i>Notophthalmus viridescens</i>	Urodela	Walters, 1975
<i>Anaxyrus americanus</i> *	Q / G	<i>Arthroleptis sylvatica</i>	Tadpole	Petranka <i>et al.</i> , 1994
<i>Anaxyrus boreas</i> *	Q / G	<i>Ambystoma gracile</i>	Urodela	Licht, 1969
<i>Anaxyrus boreas</i> *	Q / G	<i>Gasterosteus aculeatus</i>	Pisces	Licht, 1969
<i>Anaxyrus boreas</i> *	Q / G	<i>Haemopsis</i> sp.	Hirudinea	Licht, 1969
<i>Anaxyrus boreas</i> *	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969
<i>Bufo bufo</i> *	Q / G	<i>Aeshna</i> sp.	Odonata	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Corixa dentipes</i>	Hemiptera	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Cymatia bonsdorffi</i>	Hemiptera	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Dysticus lapponicus</i>	Coleoptera	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Glaenocorista propinqua</i>	Hemiptera	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Leucorrhinia dubia</i>	Odonata	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Notonecta glauca</i>	Hemiptera	Henrickson, 1990

<i>Bufo bufo</i> *	Q / G	<i>Rhantus exoletus</i>	Coleoptera	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Lissotriton helveticus</i>	Urodela	Denton and Beebe, 1991
<i>Bufo bufo</i> *	Q / G	<i>Lissotriton vulgaris</i>	Urodela	Denton and Beebe, 1991
<i>Bufo bufo</i> *	Q / G	<i>Lissotriton vulgaris</i>	Urodela	Henrickson, 1990
<i>Bufo bufo</i> *	Q / G	<i>Rana temporaria</i>	Tadpole	Heusser, 1970
<i>Bufo terrestris</i>	Q / G (inside ovarium)	<i>Bufo terrestris</i>	Tadpole	Babbitt, 1995
<i>Chaunus marinus</i> *	Q / G	<i>Laccotrepes</i> sp.	Hemiptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Cybister</i> sp.	Coleoptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Cybister godeffroyi</i>	Coleoptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Hydaticus vittatus</i>	Coleoptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Sandracottus bakewelli</i>	Coleoptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Lethocerus insulanus</i>	Hemiptera	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Macrobrachium</i> sp.	Crustacea	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Holthuisana</i> sp.	Crustacea	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Cherax quadricarinatus</i>	Crustacea	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Austropelea lessoni</i>	Gastropoda	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Craterocephalus stercusmuscarum</i>	Pisces	Crossland and Alford, 1998
<i>Chaunus marinus</i>	Q / G	<i>Chaunus marinus</i>	Tadpole	Hearnden, 1991
<i>Chaunus marinus</i> *	Q / G	<i>Litoria bicolor</i>	Anura	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Litoria rubella</i>	Anura	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Litoria infrarenata</i>	Anura	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Litoria alboguttata</i>	Tadpole	Crossland, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Litoria alboguttata</i>	Anura	Crossland and Alford, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Limnodynastes ornatus</i>	Tadpole	Crossland, 1998
<i>Chaunus marinus</i> *	Q / G	<i>Limnodynastes ornatus</i>	Anura	Crossland and Alford, 1998
<i>Cranopsis vallyceps</i> *	Q / G	<i>Gambusia affinis</i>	Pisces	Grubb, 1972
<i>Cranopsis vallyceps</i> *	Q / G	<i>Ictalurus melas</i>	Pisces	Licht, 1968
<i>Cranopsis vallyceps</i> *	Q / G	<i>Lepomis cynellus</i>	Pisces	Licht, 1968
<i>Cranopsis vallyceps</i> *	Q / G	<i>Lepomis megalotis</i>	Pisces	Licht, 1968
<i>Cranopsis vallyceps</i> *	Q / G	Not identified mouse	Rodentia	Licht, 1968

<i>Epidalea calamita</i>	Q / G	<i>Lissotritron boscai</i>	Urodela	Tejedo, 1991
<i>Epidalea calamita</i>	Q / G	<i>Triturus pygmaeus</i>	Urodela	Tejedo, 1991
<i>Epidalea calamita</i>	Q / G	<i>Bufo bufo</i>	Tadpole	Banks and Beebee, 1987
<i>Epidalea calamita</i>	Q / G	<i>Epidalea calamita</i>	Tadpole	Banks and Beebee, 1987
<i>Epidalea calamita</i> *	Q / G	<i>Pelobates cultripes</i>	Tadpole	Tejedo, 1991
<i>Epidalea calamita</i>	Q / G	<i>Pelobates cultripes</i>	Tadpole	Tejedo, 1991
<i>Epidalea calamita</i> *	Q / G	<i>Pelodytes punctatus</i>	Tadpole	Tejedo, 1991
<i>Epidalea calamita</i> *	Q / G	<i>Pelodytes punctatus</i>	Tadpole	Tejedo, 1991
<i>Epidalea calamita</i> *	Q / G	<i>Rana dalmatina</i>	Tadpole	Heusser, 2001
<i>Epidalea calamita</i> *	Q / G	<i>Rana temporaria</i>	Tadpole	Heusser, 1970
<i>Epidalea calamita</i>	Q / G	<i>Rana temporaria</i>	Tadpole	Banks and Beebee, 1987
<i>Epidalea calamita</i> *	Q / G	<i>Lissotritron helveticus</i>	Urodela	Denton and Beebee, 1991
<i>Epidalea calamita</i> *	Q / G	<i>Lissotritron vulgaris</i>	Urodela	Denton and Beebee, 1991
<i>Rhinella margaritifera</i>	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Wells, 1979
<u>CENTROLENIDAE</u> (5 spp.)				
<i>Centrolene prosoblepon</i>	R / G	<i>Sibon argus</i>	Serpentes	Ryan and Lips, 2004
<i>Centrolene prosoblepon</i>	R / G	<i>Cupiennus</i> sp.	Arachnid	Hayes, 1983
<i>Cochranella granulosa</i>	R / G	<i>Sesarma roberti</i>	Crustacea	Hayes, 1983
<i>Hyalinobatrachium colymbiphyllyllum</i>	R / G	Not identified	Hymenoptera	McDiarmid, 1978; Villa <i>et al.</i> , 1982
<i>Hyalinobatrachium colymbiphyllyllum</i>	R / G	<i>Polybia</i> sp.	Hymenoptera	Drake and Ranvestel, 2005
<i>Hyalinobatrachium fleischmanni</i>	R / G	<i>Cupiennus</i> sp.	Arachnid	Hayes, 1983
<i>Hyalinobatrachium fleischmanni</i>	R / G	<i>Paroecanthus tibialis</i>	Orthoptera	Hayes, 1983
<i>Hyalinobatrachium fleischmanni</i>	R / G	<i>Drosophila</i> sp.	Diptera	Villa, 1977
<i>Hyalinobatrachium fleischmanni</i>	R / G	<i>Zygothricha</i> sp.	Diptera	Villa, 1978; 1980; Villa and Townsend, 1983
<i>Hyalinobatrachium puberatum</i>	R / G	<i>Drosophila</i> sp.	Diptera	Villa, 1977
<u>DENDROBATIDAE</u> (2 spp.)				
<i>Oophaga pumilio</i>	Q / G	<i>Oophaga pumilio</i>	Tadpole	Weygoldt, 1980; Brust, 1993
<i>Ranitomeya ventrimaculata</i>	Q / G	<i>Ranitomeya ventrimaculata</i>	Tadpole	Summers, 1999
<u>DICROGLOSSIDAE</u> (2 sp.)				
<i>Hoplobatrachus occipitalis</i>	Q / G	<i>Hoplobatrachus occipitalis</i>	Tadpole	Spieler and Linsenmair, 1997
<i>Hoplobatrachus tigrinus</i>	Q / G	<i>Hiruda birmanica</i>	Hirudinea	McCann, 1932
<u>HYLIDAE</u> (32 spp.)				

<i>Acris crepitans</i> *	Q / G	<i>Gambusia affinis</i>	Pisces	Grubb, 1972
<i>Agalychnis annae</i> *	R / G	<i>Megascelia scalaris</i>	Diptera	Villa and Townsend, 1983
<i>Agalychnis callidryas</i>	R / G	<i>Drosophila</i> sp.	Diptera	Villa, 1977
<i>Agalychnis callidryas</i>	R / G	Not identified	Hymenoptera	Villa <i>et al.</i> , 1982
<i>Agalychnis callidryas</i>	R / G	<i>Agelaia</i> sp.	Hymenoptera	Warkentin, 2000
<i>Agalychnis callidryas</i>	R / G	<i>Polybia rejecta</i>	Hymenoptera	Warkentin, 2000
<i>Agalychnis callidryas</i>	R / G	<i>Leptodeira septentrionalis</i>	Serpentes	Warkentin, 1995; 2000
<i>Agalychnis callidryas</i>	R / G	<i>Sibon argus</i>	Serpentes	Ryan and Lips, 2004
<i>Agalychnis callidryas</i> *	R / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>A. fasciatus</i>	Pisces	Roberts, 1994
<i>Agalychnis callidryas</i> *	R / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Agalychnis saltator</i>	R / G	<i>Polybia cf. rejecta</i>	Hymenoptera	Warkentin, 2000
<i>Agalychnis saltator</i> *	R / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Asyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Agalychnis saltator</i> *	R / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Dendropsophus ebraccatus</i>	R / G	<i>Drosophila</i> sp.	Diptera	Villa, 1977
<i>Dendropsophus ebraccatus</i>	R / G	<i>Agelaia</i> sp.	Hymenoptera	Warkentin, 2000
<i>Dendropsophus ebraccatus</i>	R / G	<i>Azteca</i> sp.	Hymenoptera	J. Touchon, unpubl. data

<i>Dendropsophus ebraccatus</i>	R / G	<i>Polybia rejecta</i>	Hymenoptera	J. Touchon, unpubl. data
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Asyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Dendropsophus ebraccatus*</i>	R / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Dendropsophus minutus</i>	Q / G	<i>Leptodactylus labyrinthicus</i>	Tadpole	Shepard and Caldwell, 2005
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>A. fasciatus</i>	Pisces	Roberts, 1994
<i>Dendropsophus phlebodes*</i>	Q / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Dendropsophus rubicundulus</i>	Q / G	<i>Leptodactylus labyrinthicus</i>	Tadpole	Shepard and Caldwell, 2005
<i>Hyla arborea</i>	Q / G	<i>Rana temporaria</i>	Tadpole	Heusser, 1970
<i>Hyla chrysoscelis*</i>	Q / G	<i>Gambusia affinis</i>	Pisces	Grubb, 1972
<i>Hyla chrysoscelis*</i>	Q / G	<i>Ilybius</i> sp.	Coleoptera	Resetarits, 1998
<i>Hyla chrysoscelis*</i>	Q / G	<i>Pachidiplax longipinnis</i>	Odonate	Resetarits, 1998
<i>Hyla vesicolor*</i>	Q / G	<i>Ambystoma maculatum</i>	Urodela	Walters, 1975
<i>Hyla vesicolor*</i>	Q / G	<i>Notophthalmus viridescens</i>	Urodela	Walters, 1975
<i>Hypsiboas boans*</i>	Q / G	Not identified	Coleoptera	Magnusson and Hero, 1991
<i>Hypsiboas boans*</i>	Q / G	<i>Allobates marchesianus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans*</i>	Q / G	<i>Hypsiboas boans</i>	Tadpole	Magnusson and Hero, 1991

<i>Hypsiboas boans</i> *	Q / G	<i>Hypsiboas geograficus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Leptodactylus knudseni</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Osteocephalus taurinus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Phyllomedusa vaillanti</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Odonate naiads</i>	Odonata	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Aequidens tetramerus</i>	Pisces	Magnusson and Hero, 1991
<i>Hypsiboas boans</i> *	Q / G	<i>Pyrrhulina</i> sp.	Pisces	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	Not identified	Coleoptera	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	Not identified	Coleoptera	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Allobates femoralis</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Allobates marchesianus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Hypsiboas boans</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Hypsiboas geograficus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Hypsiboas granosus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Leptodactylus knudseni</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Leptodactylus rhodomystax</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Osteocephalus taurinus</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Phyllomedusa bicolor</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Phyllomedusa tarsius</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Phyllomedusa tomopterna</i>	Tadpole	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Odonate naiads</i>	Odonata	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Aequidens tetramerus</i>	Pisces	Magnusson and Hero, 1991
<i>Hypsiboas geograficus</i> *	Q / G	<i>Pyrrhulina</i> sp.	Pisces	Magnusson and Hero, 1991
<i>Hypsiboas rosenbergi</i>	Q / G	Not identified	Platyhelminthes	Kluge, 1981
<i>Hypsiboas rosenbergi</i>	Q / G	<i>Belostoma porteri</i>	Hemiptera	Kluge, 1981
<i>Hypsiboas rosenbergi</i>	Q / G	<i>Engystomops pustulosus</i>	Tadpole	Kluge, 1981
<i>Hypsiboas rosenbergi</i>	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Kluge, 1981
<i>Hypsiboas rosenbergi</i>	Q / G	<i>Hypsiboas rosenbergi</i>	Tadpole	Kluge, 1981
<i>Isthmohyla pseudopuma</i>	Q / G	<i>Isthmohyla pseudopuma</i>	Tadpole	Crump, 1983
<i>Isthmohyla pseudopuma</i> *	Q / G	<i>Isthmohyla pseudopuma</i>	Tadpole	Crump, 1983

<i>Isthmohyla zeteki</i>	Q / G	<i>Isthmohyla zeteki</i>	Tadpole	Dunn, 1937
<i>Osteocephalus buckleyi</i> *	Q / G	<i>Hypsiboas boans</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus buckleyi</i> *	Q / G	<i>Hypsiboas geograficus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus buckleyi</i> *	Q / G	<i>Leptodactylus knudseni</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus buckleyi</i> *	Q / G	<i>Osteocephalus taurinus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	Not identified	Coleoptera	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Dendrophryniscus minutus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Hypsiboas geograficus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Leptodactylus knudseni</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Osteocephalus taurinus</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Phyllomedusa vaillanti</i>	Tadpole	Magnusson and Hero, 1991
<i>Osteocephalus taurinus</i> *	Q / G	<i>Pyrrhulina</i> sp.	Pisces	Magnusson and Hero, 1991
<i>Osteopilus brunneus</i>	Q / G	<i>Osteopilus brunneus</i>	Tadpole	Polis and Myers, 1985
<i>Phyllomedusa bicolor</i> *	R / G	Not identified	Coleoptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa bicolor</i> *	R / G	Not identified	Diptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa bicolor</i> *	R / G	Not identified	Primates	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa distincta</i>	R / G	<i>Liophis miliaris</i>	Serpentes	Castanho, 1996
<i>Phyllomedusa tarsius</i> *	R / G	Not identified	Coleoptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa tarsius</i> *	R / G	Not identified	Diptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa tarsius</i> *	R / G	Not identified	Primates	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa tomopterna</i> *	R / G	Not identified	Coleoptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa tomopterna</i> *	R / G	Not identified	Diptera	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa tomopterna</i> *	R / G	Not identified	Primates	Neckel-Oliveira and Machado, 2004
<i>Phyllomedusa vaillanti</i> *	R / G	<i>Hypsiboas geograficus</i>	Tadpole	Magnusson and Hero, 1991
<i>Phyllomedusa vaillanti</i> *	R / G	<i>Leptodactylus knudseni</i>	Tadpole	Magnusson and Hero, 1991
<i>Phyllomedusa vaillanti</i> *	R / G	<i>Osteocephalus taurinus</i>	Tadpole	Magnusson and Hero, 1991
<i>Phyllomedusa vaillanti</i> *	R / G	<i>Phyllomedusa vaillanti</i>	Tadpole	Magnusson and Hero, 1991
<i>Phyllomedusa vaillanti</i> *	R / G	<i>Pyrrhulina</i> sp.	Pisces	Magnusson and Hero, 1991
<i>Pseudacris clarkii</i> *	Q / G	<i>Gambusia affinis</i>	Pisces	Grubb, 1972
<i>Pseudacris clarkii</i> *	Q / G	<i>Notropis lutrensis</i>	Pisces	Grubb, 1972
<i>Pseudacris crucifer</i>	Q / G	<i>Notophthalmus perstriatus</i>	Urodela	Christman, 1973

<i>Pseudacris nigrita</i> *	Q / G	<i>Ambystoma opacum</i>	Urodela	Walters, 1975
<i>Pseudacris regilla</i>	Q / G	<i>Taricha granulosa</i>	Urodela	White, 1977; Evenden, 1948
<i>Pseudacris regilla</i>	Q / G	<i>Taricha torosa</i>	Urodela	White, 1977; Evenden, 1948
<i>Pseudacris regilla</i> *	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969
	(oocytes)			
<i>Pseudacris regilla</i> *	Q / G	<i>Desserobdella picta</i>	Hirudinea	Chivers <i>et al.</i> , 2001
<i>Scinax boulengeri</i> *	Q / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Asyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Scinax boulengeri</i> *	Q / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Rhamdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Asyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Scinax elaeochroa</i> *	Q / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Scinax fuscomarginatus</i>	Q / G	<i>Leptodactylus labyrinthicus</i>	Tadpole	Shepard and Caldwell, 2005
<i>Tlalocohyla loquax</i> *	Q / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994

<i>Tlalocohyla loquax</i> *	Q / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Rhambdia guatemalensis</i>	Pisces	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Astyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Tlalocohyla loquax</i> *	Q / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<u>HYPEROLIIDAE</u> (11 spp.)				
<i>Afraxalus formasini</i>	R / G	<i>Afraxalus formasini</i>	Anura	Drewes and Altig, 1996
<i>Hyperolius chlorosteus</i>	R / G	<i>Cercocebus torquatus atys</i>	Primates	Mark-Oliver <i>et al.</i> , 2002
<i>Hyperolius cinnamomeoventris</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	Vonesh, 2000
<i>Hyperolius kivuensis</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	Vonesh, 2000
<i>Hyperolius kivuensis</i>	R / G	Phoridae	Diptera	Vonesh, 2000
<i>Hyperolius lateralis</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	Vonesh, 2000
<i>Hyperolius lateralis</i>	R / G	Phoridae	Diptera	Vonesh, 2000
<i>Hyperolius mitchelli</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	J. Vonesh, unpubl. data
<i>Hyperolius mitchelli</i>	R / G	<i>Afraxalus formasini</i>	Anura	J. Vonesh, unpubl. data
<i>Hyperolius platyceps</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	Vonesh, 2000
<i>Hyperolius platyceps</i>	R / G	Phoridae	Diptera	Vonesh, 2000
<i>Hyperolius puncticulatus</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	J. Vonesh, unpubl. data
<i>Hyperolius puncticulatus</i>	R / G	<i>Afraxalus formasini</i>	Anura	J. Vonesh, unpubl. data
<i>Hyperolius spinigularis</i>	R / G	<i>Afraxalus formasini</i>	Anura	Vonesh, 2005; Vonesh and Bolker, 2005
<i>Hyperolius spinigularis</i>	R / G	<i>Typopsilopa</i> sp.	Diptera	Vonesh, 2005; Vonesh and Bolker, 2005
<i>Hyperolius sylvaticus</i>	R / G	<i>Cercocebus torquatus atys</i>	Primates	Mark-Oliver <i>et al.</i> , 2002
<i>Hyperolius tuberilinguis</i>	R / G	<i>Afraxalus formasini</i>	Anura	Drewes and Altig, 1996
<u>LEIUPERIDAE</u> (8 spp.)				
<i>Engystomops pustulosus</i>	Q / F	<i>Agalychnis callidryas</i>	Tadpole	Ryan, 1985
<i>Engystomops pustulosus</i>	Q / F	<i>Chaunus marinus</i>	Tadpole	Downie, 1988; 1990
<i>Engystomops pustulosus</i>	Q / F	<i>Leptodactylus fuscus</i>	Tadpole	Downie, 1988; 1990
<i>Engystomops pustulosus</i>	Q / F	<i>Odonate nymphs</i>	Odonata	Downie, 1988; 1990
<i>Eupemphix nattereri</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Physalaemus centralis</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Physalaemus cf. marmoratus</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Physalaemus cuvieri</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003

<i>Physalaemus cuvieri</i>	Q / F	<i>Gastrops niger</i>	Diptera	Bokermann, 1957
<i>Physalaemus cuvieri</i>	Q / F	<i>Solenopsis</i> sp.	Hymenoptera	Sazima, 1957
<i>Physalaemus</i> aff. <i>gracilis</i>	Q / F	<i>Solenopsis</i> sp.	Hymenoptera	Lingnau and Di-Bernardo, 2006
<i>Pleurodema bufonina</i>	Q / F	<i>Pleurodema bufonina</i>	Tadpole	Jara, 2005
<i>Pleurodema thaul</i>	Q / F	<i>Pleurodema thaul</i>	Tadpole	Jara, 2005
<u>LEPTODACTYLIDAE</u> (10 spp.)				
<i>Leptodactylus fumarius</i>	S / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Leptodactylus fuscus</i>	S / F	<i>Megaselia nidanurae</i>	Diptera	Downie <i>et al.</i> , 1995
<i>Leptodactylus fuscus</i> *	S / F	<i>Camponotus</i> sp.	Hymenoptera	Arzabe and Prado, 2006
<i>Leptodactylus knudseni</i> *	T / F	<i>Leptodactylus rhodomystax</i>	Tadpole	Magnusson and Hero, 1991
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Dendropsophus minutus</i>	Anura	Silva <i>et al.</i> , 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Physalaemus</i> cf. <i>fuscumaculatus</i>	Anura	Silva <i>et al.</i> , 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Chrysocyon brachyurus</i>	Canidae	Prado <i>et al.</i> , 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Silva <i>et al.</i> , 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Camponotus rufipes</i>	Hymenoptera	Prado <i>et al.</i> , 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Leptodactylus labyrinthicus</i>	Tadpole	Prado <i>et al.</i> , 2005; Silva <i>et al.</i> , 2005; Shepard and Caldwell, 2005
<i>Leptodactylus labyrinthicus</i>	Q / F	<i>Physalaemus cuvieri</i>	Tadpole	Silva <i>et al.</i> , 2005
<i>Leptodactylus latinasus</i>	S / F	<i>Lycosa pampeana</i>	Arachnid	Villa <i>et al.</i> , 1982
<i>Leptodactylus mystacinus</i>	S / F	<i>Camponotus</i> sp.	Hymenoptera	Arzabe and Prado, 2006
<i>Leptodactylus ocellatus</i>	Q / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<i>Leptodactylus ocellatus</i>	Q / F	<i>Liophis miliaris</i>	Serpentes	Lingnau and Di-Bernardo, 2006
<i>Leptodactylus pentadactylus</i>	Q / F	<i>Gastrops willistoni</i>	Diptera	Villa <i>et al.</i> , 1982
<i>Leptodactylus pentadactylus</i>	Q / F	<i>Angiopolybia pallens</i>	Hymenoptera	Villa <i>et al.</i> , 1982; Lacey, 1979
<i>Leptodactylus plaumani</i>	S / F	<i>Liophis jaegeri</i>	Serpentes	Solé and Kwet, 2003
<i>Leptodactylus</i> sp.	S / F	<i>Beckeriella niger</i>	Diptera	Menin and Giaretta, 2003
<u>LIMNODYNASTIDAE</u> (1 sp.)				
<i>Lechriodus fletcheri</i>	Q / F	<i>Lechriodus fletcheri</i>	Tadpole	Polis and Myers, 1985
<u>MICROHYLIDAE</u> (3 spp.)				
<i>Chiasmocleis leucosticta</i>	Q / G	<i>Patagoniobdella variabilis</i>	Hirudinea	Haddad and Hödl, 1997
<i>Gastrophne olivacea</i> *	Q / G	<i>Gambusia affinis</i>	Pisces	Grubb, 1972

<i>Hoplophryne rogersi</i>	R / G	<i>Hoplophryne rogersi</i>	Anura	Polis and Myers, 1985
<u>PELOBATIDAE</u> (1 sp.)				
<i>Pelobates cultripes</i>	Q / G	<i>Triturus marmoratus</i>	Urodela	Martinez-Solano, 2000
<u>RANIDAE</u> (13 spp.)				
<i>Lithobates areolatus</i> *	Q / G	<i>Lepomis macrochirus</i>	Pisces	Werschul and Christensen, 1977
<i>Lithobates catesbeianus</i>	Q / G	<i>Macrobella decora</i>	Hirudinea	Howard, 1978
<i>Lithobates catesbeianus</i>	Q / G	<i>Lithobates catesbeianus</i>	Anura	Stuart and Painter, 1993
<i>Lithobates catesbeianus</i> *	Q / G	<i>Notophthalmus viridescens</i>	Urodela	Walters, 1975
<i>Lithobates catesbeianus</i> *	Q / G	<i>Ambystoma gracile</i>	Urodela larvae	Licht, 1969
<i>Lithobates catesbeianus</i> *	Q / G	<i>Gasterosteus aculeatus</i>	Pisces	Licht, 1969
<i>Lithobates catesbeianus</i> *	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969
<i>Lithobates clamitans</i> *	Q / G	<i>Ambystoma maculatum</i>	Urodela	Walters, 1975
<i>Lithobates clamitans</i> *	Q / G	<i>Ambystoma opacum</i>	Urodela	Walters, 1975
<i>Lithobates clamitans</i> *	Q / G	<i>Notophthalmus viridescens</i>	Urodela	Walters, 1975
<i>Lithobates clamitans</i> *	Q / G	<i>Ambystoma gracile</i>	Urodela larvae	Licht, 1969
<i>Lithobates clamitans</i> *	Q / G	<i>Gasterosteus aculeatus</i>	Pisces	Licht, 1969
<i>Lithobates clamitans</i> *	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969
<i>Lithobates maculatus</i>	Q / G	Not identified	Platyhelminthes	Kluge, 1981
<i>Lithobates palmipes</i> *	Q / G	<i>Kinosternon leucostomum</i>	Testudines	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Rhinoclemmys funerea</i>	Testudines	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Leptodactylus pentadactylus</i>	Tadpole	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Agalychnis callidryas</i>	Tadpole	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Agalychnis calcarifer</i>	Tadpole	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Dendropsophus ebraccatus</i>	Tadpole	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Rivulus isthmensis</i>	Pisces	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Rhania guatemalensis</i>	Pisces	Roberts, 1994
<i>Lithobates palmipes</i> *	Q / G	<i>Astyanax fasciatus</i>	Pisces	Roberts, 1994
<i>Lithobates pipiens</i>	Q / G	<i>Pholis gilli</i>	Pisces	Roberts, 1994
<i>Lithobates pipiens</i>	Q / G	<i>Ambystoma opacum</i>	Urodela	Walters, 1975
<i>Lithobates pipiens</i>	Q / G	<i>Ambystoma gracile</i>	Urodela larvae	Licht, 1969
<i>Lithobates pipiens</i>	Q / G	<i>Gasterosteus aculeatus</i>	Pisces	Licht, 1969
<i>Lithobates pipiens</i>	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969

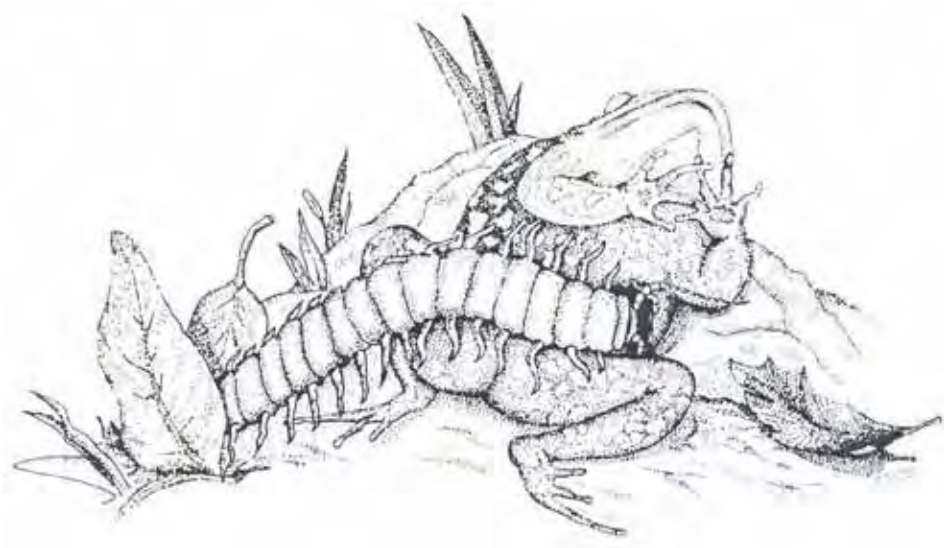
<i>Lithobates</i> sp.*	Q / G	<i>Haemopsis</i> sp.	Hirudinea	Licht, 1969
<i>Rana arvalis</i> *	Q / G	<i>Aeshna</i> sp.	Odonata	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Corixa dentipes</i>	Hemiptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Cymatia bondsdorffi</i>	Hemiptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Dysticus lapponicus</i>	Coleoptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Glaenocorista propinqua</i>	Hemiptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Leucorrhinia dubia</i>	Odonata	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Notonecta glauca</i>	Hemiptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Rhantus exoletus</i>	Coleoptera	Henrickson, 1990
<i>Rana arvalis</i> *	Q / G	<i>Triturus vulgaris</i>	Urodela	Henrickson, 1990
<i>Rana aurora</i>	Q / G	<i>Taricha</i> sp.	Urodela	Rathbun, 1998
<i>Rana aurora</i> *	Q / G	<i>Ambystoma gracile</i>	Urodela larvae	Licht, 1969
<i>Rana aurora</i> *	Q / G	<i>Gasterosteus aculeatus</i>	Pisces	Licht, 1969
<i>Rana aurora</i> *	Q / G	<i>Salmo clarkii</i>	Pisces	Licht, 1969
<i>Rana boylei</i>	Q / G	<i>Pacifastacus leniusculus</i>	Crustacea	Rombough and Hayes, 2005; Wiseman <i>et al.</i> , 2005
<i>Rana boylei</i>	Q / G	<i>Dicosmoecus gilvipes</i>	Tricoptera	Rombough and Hayes, 2005
<i>Rana boylei</i>	Q / G	<i>Rhinichthys osculus</i>	Pisces	Rombough and Hayes, 2005
<i>Rana boylei</i>	Q / G	<i>Cottus perplexus</i>	Pisces	Rombough and Hayes, 2005
<i>Rana boylei</i>	Q / G	<i>Ptychocheilus oregonensis</i>	Pisces	Rombough and Hayes, 2005
<i>Rana boylei</i>	Q / G	<i>Richardsonius balteatus</i>	Pisces	Rombough and Hayes, 2005
<i>Rana boylei</i>	Q / G	<i>Taricha granulosa</i>	Urodela	White, 1977; Evenden, 1948
<i>Rana boylei</i>	Q / G	<i>Taricha torosa</i>	Urodela	White, 1977; Evenden, 1948
<i>Rana cascadae</i>	Q / G	<i>Desserobdella picta</i>	Hirudinea	Chivers <i>et al.</i> , 2001
<i>Rana muscosa</i>	Q / G	<i>Rana muscosa</i>	Tadpole	Vredenburgh, 2000
<i>Rana temporaria</i> *	Q / G	<i>Rana temporaria</i>	Tadpole	Heusser, 1970
<i>Rana temporaria</i> *	Q / G	<i>Lissotriton helveticus</i>	Urodela	Denton and Beebe, 1991
<i>Rana temporaria</i> *	Q / G	<i>Lissotriton vulgaris</i>	Urodela	Denton and Beebe, 1991
RHACOPHORIDAE (5 spp.)				
<i>Chiromantis rufescens</i>	R / F	<i>Cercoebus torquatus atys</i>	Primates	Mark-Oliver <i>et al.</i> , 2002
<i>Chiromantis rufescens</i>	R / F	<i>Cercopithecus diana diana</i>	Primates	Mark-Oliver <i>et al.</i> , 2002
<i>Chiromantis xerampelina</i>	R / F	<i>Afraxalus fornasini</i>	Anura	Drewes and Altig, 1996

<i>Kurixalus eiffingeri</i>	R / F	<i>Kurixalus eiffingeri</i>	Tadpole	Kam <i>et al.</i> , 1996
<i>Polypedates leucomystax</i>	Q / F	<i>Lucilia</i> sp.	Diptera	Yorke 1983
<i>Rhacophorus viridis</i>	R / F	<i>Rhacophorus viridis</i>	Tadpole	Tanaka and Nishihira, 1987
<u>SCAPHIOPODIDAE</u> (1 sp.)				
<i>Scaphiopus couchi</i>	Q / G	<i>Gambusia affinis</i>	Pisces	Gurbb, 1972

CAPÍTULO 2

PREDAÇÃO DE ANUROS JUVENIS E ADULTOS POR INVERTEBRADOS: CONHECIMENTO ATUAL E PERSPECTIVAS

Luís Felipe Toledo



Carpenter & Gillingham, 1984

CAPÍTULO 2

PREDATION OF JUVENILE AND ADULT ANURANS BY INVERTEBRATES: CURRENT KNOWLEDGE AND PERSPECTIVES

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Anuran amphibians are preyed on by vertebrates, invertebrates, and even carnivorous plants (Duellman and Trueb 1994). Most of these reports on predation are anecdotal (Fitch 1987; Greene 1993) and do not provide data other than a short description of the predatory event (e.g., Boistel and Pauwels 2002; Brandão and Garda 2000; Del-Grande and Moura 1997; Mitchell 1990). The scattered information on the subject makes it difficult to identify patterns. Additionally, McCormick and Polis (1982) pointed out the lack of quantitative data evaluating the impact of arthropod predators upon vertebrates. This is particularly true for predation by invertebrates upon post-metamorphic (generally adult) anurans. For example, reports on this subject usually state that few cases of invertebrate predation upon anurans are recorded (e.g., Bastos et al. 1994; Bernarde et al. 1999; Del-Grande and Moura 1997; Hinshaw and Sullivan 1990; Mitchell 1990), when, in fact, a considerable amount of information is generally available (e.g., McCormick and Polis 1982). Therefore, I review the subject in an attempt to depict our current knowledge, add unpublished data, and provide a background to which new reports may be added.

By reviewing published information on the subject I collected data on a wide range of taxa, i.e., at least 68 post-metamorphic (juvenile to adult) anuran species preyed upon by at least 57 invertebrate species, including arachnids, crabs, leeches, and various insect groups (Tables 1 and 2). Besides the species listed (Table 2), there exists indirect evidence and laboratory studies that add other potential invertebrate predators to the list, such as spiders (*Oilos antaguensis*, *Stasina portoricensis*, and *Avicularia latea*), amblypygids (*Phrynus longipes*), and forest crabs (*Epilobocera situatifrons*) (Formanowicz et al. 1981; Stewart 1995). Laboratory studies using pipid and hyperoliid frogs report pisaurid spiders as additional potential predators upon previously unreported anuran families (Table 2).

It appears that many anuran species can be preyed upon by invertebrate predators, independent of prey body size/age (see discussion in McCormick and Polis 1982), phylogeny, or recognized presence of an elevated quantity of biologically active skin secretions (Duellman and Trueb 1994) (Table 2). However, the risk of predation by invertebrates seems to be greater in two crucial periods of the anurans life cycle: 1) during the breeding season, when most species enter the water and consequently are in contact with potential aquatic predators (e.g., Bastos et al. 1994; Haddad and Bastos

1997; Toledo 2003); and 2) when the recently-metamorphosed frogs are about to leave or actually leave the water (Fig. 1), thus facing both aquatic and terrestrial invertebrates (e.g., Clerke and Williamson 1992; Hirai and Hidaka 2002; Robertson 1989; Toledo 2003). Almost 90% of the observations that provide descriptions of the frog behavior before the predation were recorded during these two stages.

Table 1. Invertebrate predators and number of species reported to prey upon post-metamorphic anuran amphibians.

Class	Order	Family	Common name	Abbreviation	Number of species	
Hirudinea	Arhynchobdellida	Hirudinidae	Leeches	Ah	1	
Chilopoda	Scolopendromorpha	Scolopendridae	Giant centipedes	Gc	1	
Arachnida	Scorpiones	Buthidae	Scorpions	Sc	1	
		Uropygi	Thelyphonidae	Vinegaroons	Ut	1
	Amblypygi	Amblypygidae	Amblypygids	Am	1	
		Araneae	Araneidae	Orb weavers	Aa	3
	Ctenidae		Wandering spiders	Ac	2	
	Ctenizidae		Trapdoor spiders	Az	1	
	Dipluridae		Tarantulas	Ad	1	
	Lycosidae		Wolf spiders	Al	6	
	Pisauridae		Fishing spiders	Ap	10	
	Sparassidae		Crab spiders	As	1	
	Theraphosidae	Tarantulas	At	6		
	Malacostraca	Decapoda	Coenobitidae	Crabs	Dc	1
	Hexapoda	Coleoptera	Carabidae	Ground beetles	Cb	3
Cicindelidae			Tiger beetles	Cc	1	
Dytiscidae			Diving beetles	Cd	1	
Tabanidae			Horse flies	Di	1	
Hemiptera		Belostomatidae	Water bugs	Hb	8	
		Nepidae	Water scorpions	Hn	1	
		Formicidae	Ants	Hf	4	
Mantodea		Mantidae	Preying mantis	Mm	1	
Neuroptera		Corydalidae	Hellgrammites	Ch	1	

Table 2. Post-metamorphic (juvenile to adult) anurans (15 families; at least 68 species) reported as prey of invertebrates (22 families; at least 57 species) and the microhabitat where the predation occurred. Anuran specific names follow Frost (2004), and thus some genera and species are updated. Predators' abbreviations are in table 1. An asterisk (*) after the anuran names indicates the recognized presence of a high amount of biologically active skin secretions.

Anurans (Prey)	Invertebrates (Predators)	Predation microhabitat	References
<u>Ascaphidae</u>			
<i>Ascaphus truei</i>	Hellgrammite – unidentified (Mh)	Pool in the stream	Jones and Raphael, 1998
<u>Bufonidae</u>			
<i>Bufo bufo</i> *	<i>Formica rufa</i> (Hf)	Lake margin	Zuffi, 2001
<i>Bufo crucifer</i> *	<i>Lethocerus grandis</i> (Hb)	Temporary pond	Haddad and Bastos, 1997
<i>Bufo houstonensis</i> *	<i>Solenopsis invicta</i> (Hf)	Litter	Thomas and Allen, 1997
<i>Bufo marinus</i> *	<i>Iridomyrmex purpureus</i> (Hf)	Pond margin	Clerke and Williamson, 1992
<i>Bufo marinus</i> *	<i>Scolopendra alternans</i> (Gc)	Leaf litter	Carpenter and Gillingham, 1984
<i>Bufo terrestris</i> *	<i>Lethocerus</i> sp. (Hb)	Temporary pond	McCoy, 2003
<u>Centrolenidae</u>			
<i>Centrolene prosoblepon</i>	<i>Cupiennus</i> sp. (Ac)	Over rocks, near the water	Hayes, 1983
<i>Hyalinobatrachium fleischmanni</i>	<i>Cupiennus</i> sp. (Ac)	Over leaf	Hayes, 1983
<u>Dendrobatidae</u>			
<i>Colostethus inguinalis</i>	Freshwater crab – unidentified (Dc)	Not provided	Duellman and Trueb, 1994
<i>Dendrobates auratus</i> *	<i>Sericopelma rubronitens</i> (At)	Litter	Summers, 1999
<i>Dendrobates pumilio</i> *	<i>Paraponera clavata</i> (Hf)	Litter	Fritz et al., 1981
<u>Hylidae</u>			
<i>Acris crepitans</i>	<i>Hogna helluo</i> (Al)	Semi-permanent wetland	Blackburn et al., 2002
<i>Acris gryllus</i>	<i>Dolomedes</i> sp. (Ap)	Edges of water body	Goin, 1943
<i>Hyla albomarginata</i>	<i>Belostoma</i> sp. (Hb)	Temporary pond	Froehlich, 2001
<i>Hyla albosignata</i>	Tarantula – unidentified (At)	Vegetation over water	A. Antunes, unpubl. data
<i>Hyla cinerea</i>	<i>Dolomedes okefnokensis</i> (Ap)	Vegetation over water	Jeffery et al., 2004
<i>Hyla cinerea</i>	<i>Acanthepeira stellata</i> (Aa)	Not provided	Lockley, 1990
<i>Hyla crepitans</i>	<i>Belostoma</i> sp. (Hb)	Permanent pool	Mijares-Urrita et al., 1997
<i>Hyla ebraccata</i>	<i>Cupiennius coccineus</i> (Ac)	Swamp	Szelistowski, 1985

<i>Hyla japonica</i>	<i>Diplonychus japonicus</i> (Hb)	Flooded rice field	T. Hirai, unpubl. data
<i>Hyla japonica</i>	<i>Dolomedes sulfurous</i> (Ap)	Flooded rice field	T. Hirai, unpubl. data
<i>Hyla japonica</i>	<i>Laccotrepes japonensis</i> (Hn)	Flooded rice field	T. Hirai, unpubl. data
<i>Hyla japonica</i>	<i>Lethocerus deyrollei</i> (Hb)	Flooded rice field	Hirai and Hidaka, 2002
<i>Hyla jimi</i>	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<i>Hyla minuta</i>	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<i>Hyla minuta</i>	<i>Lethocerus delponteii</i> (Hb)	Permanent pond	Bastos et al., 1994
<i>Hyla minuta</i>	<i>Dolomedes</i> sp. (Ap)	Permanent pond	Bastos et al., 1994
<i>Hyla minuta</i>	<i>Ancylometes vulpes</i> (Ap)	Permanent pond	Bernarde et al., 1999
<i>Hyla minuta</i>	<i>Ancylometes gigas</i> (Ap)	Permanent pond	Bernarde et al., 1999
<i>Hyla miotypanum</i>	<i>Abedus</i> sp. (Hb)	Permanent stream	Pineda, 2003
<i>Hyla nana</i>	<i>Thaumasia</i> sp. (Ap)	Swamp	Pramuk and Alamillo, 2002
<i>Hyla sanborni</i>	<i>Diapontia</i> cf. <i>uruguayensis</i> (Al)	Web over pond	Del-Grande and Moura, 1997
<i>Hyla versicolor</i>	<i>Argiope aurantia</i> (Aa)	Web near pond	Steehouder, 1992
<i>Hyla versicolor</i>	<i>Lethocerus americanus</i> (Hb)	Pond	Hinshaw and Sullivan, 1990
<i>Litoria caerulea</i>	<i>Hierodula werneri</i> (Mm)	Not provided	Ridpath, 1977
<i>Litoria caerulea</i>	<i>Atrax formidabilis</i> (Ad)	Not provided	McCormick and Polis, 1982
<i>Litoria ewingi</i>	<i>Catadromus lacordairei</i> (Cb)	Not provided	LittleJohn and Wainer, 1978
<i>Litoria lesueurii</i>	<i>Lycosa lapidosa</i> (Al)	On the rocks of a creek bed	Raven, 1990
<i>Litoria raniformis</i>	<i>Archimantis latistyla</i> (Mm)	Not provided	Ridpath, 1977
<i>Pseudacris crucifer</i>	Diving beetle – unidentified (Cd)	Temporary pond	Hinshaw and Sullivan, 1990
<i>Pseudacris fertarum</i>	<i>Dolomedes triton</i> (Ap)	Temporary pond	Mitchell, 1990
<i>Pseudacris ocularis</i>	<i>Lycosa</i> sp. (Al)	Ground, near water body	Owen and Johnson, 1997
<i>Scinax alter</i>	<i>Ancylometes rufus</i> (Ap)	Over aquatic vegetation	Prado and Borgo, 2003
<i>Scinax alter</i>	<i>Thaumasia</i> sp. (Ap)	Water surface	Marra et al., 2003
<i>Scinax cruentommus</i>	Wolf spider – unidentified (Al)	Vegetation over ground	Aucone and Card, 2002
<i>Scinax elaeochroa</i>	<i>Cupiennius coccineus</i> (Ac)	Swamp	Szelistowski, 1985
<i>Scinax fuscomarginatus</i>	<i>Oxyuptychus brasiliensis</i> (Ah)	Vegetation over pond	Brandão and Garda, 2000
<i>Scinax fuscomarginatus</i>	Tarantula – unidentified (At)	Temporary pond	L. F. Toledo, unpubl. data
<i>Scinax fuscomarginatus</i>	Water bug – unidentified (Hb)	Temporary pond	L. F. Toledo, unpubl. data
<i>Scinax ruber</i>	Preying mantis - unidentified (Mm)	Over vegetation	J. L. Guillaumet, unpubl. data

<i>Scinax squalirostris</i>	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<i>Scinax</i> sp. (aff. <i>similis</i>)	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<u>Hyperoliidae</u>			
<i>Hyperolius marmoratus</i>	<i>Thalassius fimbriatus</i> (Ap)	Laboratory situation	McCormick and Polis, 1982
<u>Leptodactylidae</u>			
<i>Eleutherodactylus coqui</i>	<i>Olios</i> sp. (As)	Above ground	Formanowicz Jr. et al., 1981
<i>Eleutherodactylus coqui</i>	<i>Oligoctenus ottlei</i> (Al)	Not provided	Formanowicz Jr. et al., 1981
<i>Eleutherodactylus coqui</i>	<i>Phrynus palmatus</i> (Am)	Not provided	Formanowicz Jr. et al., 1981
<i>Eleutherodactylus coqui</i>	<i>Tityus obtusus</i> (Sc)	Vegetation over ground	Villanueva-Rivera et al., 2000
<i>Eleutherodactylus zugi</i>	<i>Ctenus vernalis</i> (Ac)	Ground inside cave	Novo et al., 1985
<i>Eleutherodactylus</i> sp.	<i>Paraponera clavata</i> (Hf)	Litter	Fritz et al., 1981
<i>Eleutherodactylus</i> spp.	<i>Cupiennius coccineus</i> (Ac)	Experimental condition	Szelistowski, 1985
<i>Hylodes phyllodes</i>	<i>Trachalea keyserlingi</i> (Ap)	Leaf litter next to a stream	Schiesari et al., 1995
<i>Leptodactylus Knudseni</i> *	<i>Theraphosa leboni</i> (At)	Not provided	Boistel and Pauwels, 2002
<i>Leptodactylus labyrinthicus</i> *	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<i>Leptodactylus ocellatus</i>	<i>Lethocerus annulipes</i> (Hb)	Not provided	Lima, 1940
<i>Physalaemus cuvieri</i>	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003, Brasileiro et al., 2003
<i>Physalaemus fuscomaculatus</i> *	<i>Belostoma elongatum</i> (Hb)	Temporary pond	Toledo, 2003
<i>Physalaemus</i> cf. <i>fuscomaculatus</i> *	<i>Lethocerus</i> sp. (Hb)	Temporary pond	Giaretta and Menin, 2004
<i>Physalaemus pustulosus</i>	<i>Sericopelma rubronitens</i> (At)	Leaf litter	Gray et al., 1999
<i>Physalaemus spiniger</i>	Wolf spider – unidentified (Al)	Temporary pond	L. M. Giasson, unpubl. data
<u>Limnodynastidae</u>			
<i>Limnodynastes tasmaniensis</i>	<i>Catadromus lacordairei</i> (Cb)	Not provided	LittleJohn and Wainer, 1978
<i>Neobatrachus centralis</i>	<i>Selenotypus</i> sp. (At)	Not provided	Raven, 1990
<i>Neobatrachus centralis</i>	<i>Selenocosmia crassipes</i> (At)	Not provided	McCormick and Polis, 1982
<u>Microhylidae</u>			
<i>Microhyla ornata</i>	<i>Lycosa carmichaeli</i> (Al)	Not provided	McCormick and Polis, 1982
<u>Myobatrachidae</u>			
<i>Crinia pseudinsignifera</i>	<i>Aganippe raphiduca</i> (Az)	Ground, near spider burrow	Butler and Main, 1959
<i>Crinia signifera</i>	<i>Chlaenius darlingensis</i> (Cb)	Margin of pond	Robertson, 1989
<i>Uperoleia laevigata</i>	<i>Chlaenius darlingensis</i> (Cb)	Margin of pond	Robertson, 1989

<u>Pelobatidae</u>					
<i>Spea multiplicata</i>	<i>Tabanus punctifer</i> (Di)	Mud margin of pond	Jackman et al., 1983		
<i>Spea multiplicata</i>	<i>Cicindela sedecimpunctata</i> (Cc)	Not provided	McCormick and Polis, 1982		
<u>Pipidae</u>					
<i>Xenopus laevis</i> *	<i>Dolomedes triton</i> (Ap)	Laboratory situation	Rogers, 1996		
<u>Racophoridae</u>					
<i>Rhacophorus arboreus</i>	<i>Cybister japonicus</i> (Cd)	Flooded rice field	T. Hirai, unpubl. data		
<i>Rhacophorus schlegelii</i>	<i>Laccotrepes japonensis</i> (Hn)	Flooded rice field	T. Hirai, unpubl. data		
<i>Rhacophorus schlegelii</i>	<i>Lethocerus deyrollei</i> (Hb)	Flooded rice field	Hirai and Hidaka, 2002		
<u>Ranidae</u>					
<i>Euphlyctis cf. cyanophlyctis</i>	<i>Lycosa barmanica</i> (Al)	Not provided	McCormick and Polis, 1982		
<i>Fejervarya limnocharis</i>	<i>Lethocerus deyrollei</i> (Hb)	Flooded rice field	Hirai and Hidaka, 2002		
<i>Rana cascade</i>	<i>Lethocerus</i> sp. (Hb)	Lake	Nauman and Dettlaff, 1999		
<i>Rana clamitans</i>	Wolf Spider – unidentified (Al)	Grass field	Neil, 1948		
<i>Rana nigromaculata</i>	<i>Epomis nigricans</i> (Cb)	Flooded rice field	T. Hirai, unpubl. data		
<i>Rana nigromaculata</i>	<i>Lethocerus deyrollei</i> (Hb)	Flooded rice field	Hirai and Hidaka, 2002		
<i>Rana porosa</i>	<i>Lethocerus deyrollei</i> (Hb)	Irrigation ditch (rice field)	T. Hirai, unpubl. data		
<i>Rana rugosa</i>	<i>Lethocerus deyrollei</i> (Hb)	Flooded rice field	T. Hirai, unpubl. data		
<u>Unidentified anurans</u>					
Frog	<i>Grammostola</i> sp. (At)	Not provided	McCormick and Polis, 1982		
Frog	<i>Lasidora</i> sp. (At)	Not provided	McCormick and Polis, 1982		
Frog	<i>Birgus latro</i> (Dc)	Not provided	McCormick and Polis, 1982		
Frogs and toads	<i>Mastigoproctus giganteus</i> (Ut)	Not provided	McCormick and Polis, 1982		
Green Frog	<i>Nephila plumipes</i> (Aa)	Not provided	McCormick and Polis, 1982		
Green Tree Frog	<i>Nephila plumipes</i> (Aa)	Not provided	McCormick and Polis, 1982		
Leptodactylidae Brown Frogs	Wolf Spider – unidentified (Al)	Not provided	McCormick and Polis, 1982		
Tree Frog	<i>Dolomedes okefenokensis</i> (Ap)	Not provided	McCormick and Polis, 1982		



Figure 1. Juvenile *Hyla albosignata* being preyed upon by a tarantula on vegetation near a stream in a forested area, Municipality of Pilar do Sul, State of São Paulo, Brazil. Photograph by André Antunes.

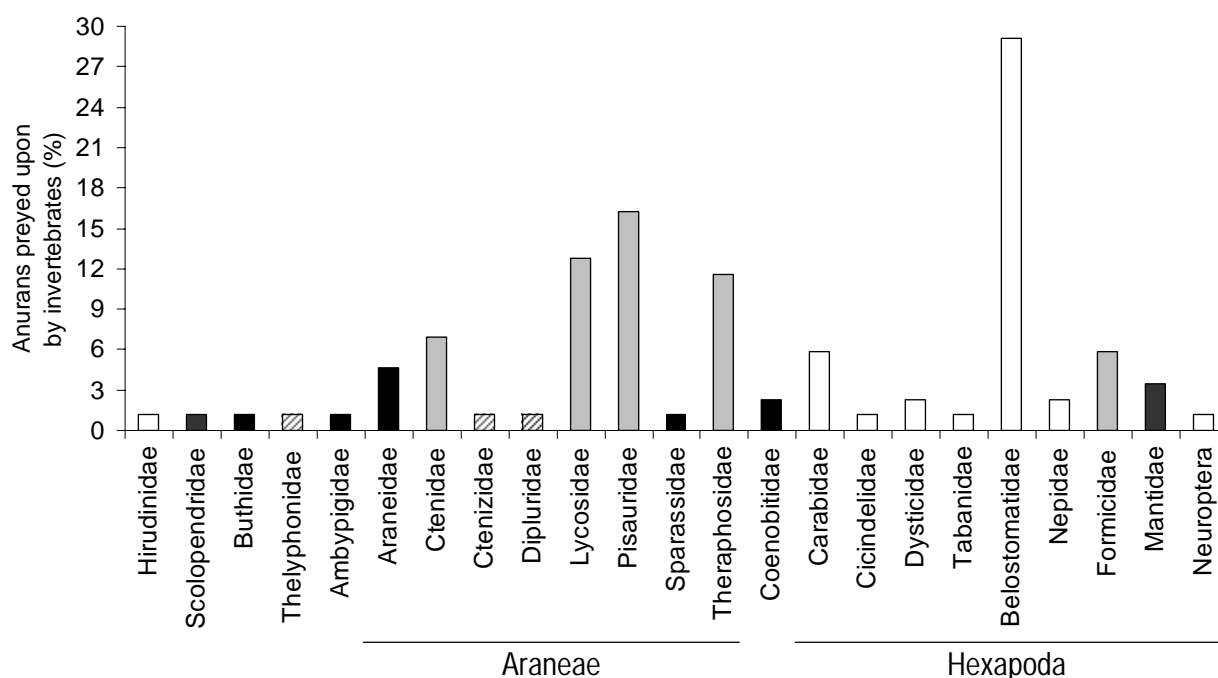


Figure 2. Percentage of different anuran species that were preyed upon by different invertebrate families based on references listed in table 2 ($N_{\text{total}} = 89$ accounts). White bars indicate predation events reported to occur in the water; dark bars indicate predation events out of the water; gray bars indicate predation events both in and out of the water; and striped bars represent lack of information on the microhabitat which the predation occurred.

Predation events occurred both in and out of the water and about 73% of them involved water bugs (approximately 25%) and spiders (approximately 48%) as anuran predators (Fig. 2). This may reflect the high density of these animals in nature, (DuBois and Gobin 2001; Formanowicz et al. 1981; McCormick and Polis 1982; and references therein). Additionally, it could indicate that spiders and water bugs may be significant predators of anuran populations (Formanowicz et al. 1981; Toledo 2003), though, few studies have determined actual predation rates on adult anurans (e.g., Haddad and Bastos 1997; Hinshaw and Sullivan 1990).

In reviewing the subject I was able to identify a few cases of incorrect or repeated data. For example, Nauman and Dettlaff (1999) reported “the first published record of a giant water bug preying on an adult frog”; however, at least three reports on giant water bugs preying on adult frogs were already available by that time (Bastos et al. 1994; Haddad and Bastos 1997; Hinshaw and Sullivan 1990). Additionally, both Toledo (2003) and Brasileiro et al. (2003) provided duplicate reports of the predation of *Physalaemus cuvieri* by the same water bug species (*Belostoma elongatum*) at the same study site. Nevertheless, repeated records may be beneficial as they provide more evidence for an actual predator-prey relationship, and may help determine if any geographic variation occurs in the predator-prey relationship.

Despite the considerable number of reports much more information is likely to appear in the next few years. However, the simple descriptions of a predatory event without providing further details (e.g., microhabitat and prey activity before predation - data that should generally be available to the observers) make future discussions and predictions difficult (see Greene 1993). Therefore, even reports on simple interactions between predator and prey (particularly in the context discussed here) should provide more detailed accounts whenever possible (see complementary discussions in Greene 1986; 1993).

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CAPÍTULO 3

ANUROS COMO PRESA: UMA ANÁLISE EXPLORATÓRIA E AS RELAÇÕES DE TAMANHO ENTRE OS PREDADORES E SUAS PRESAS

Luís Felipe Toledo, Ricardo S. Ribeiro & Célio F. B. Haddad



Antoine Hercule Romuald Florence (1804 – 1879)

Desenhista, inventor da fotografia (veja a primeira fotografia do mundo tirada em Campinas) e precursor do registro de sons de animais. Francês, mas radicado no Brasil, não é reconhecido atualmente apesar de sua relevância. Esta tese não seria possível sem registros fotográficos e gravações das vocalizações dos anuros.

CAPÍTULO 3

ANURANS AS PREY: AN EXPLORATORY ANALYSIS AND THE SIZE RELATIONSHIPS BETWEEN PREDATORS AND THEIR PREYS

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Abstract

The vertebrate predators of post-metamorphic anurans were quantified and the predator-prey relationship investigated by analyzing the relative size of invertebrate predators and anurans. More than 100 vertebrate predators were identified (in more than 200 reports) and classified as opportunistic, convenience, temporary specialized, and specialized predators. Invertebrate predators were classified as solitary non-venomous, venomous, and social foragers according to the 333 reviewed reports. Each of these categories of invertebrate predators were compared to the relative size of the anurans, showing an increase in relative size of the prey when predators used special predatory tactics. The number of species and number of families of anurans that were preyed upon did not vary with the size of the predator suggesting that the prey selection was not arbitrary and energetic constrains must be involved in this choice. The relatively low predation pressure upon brachycephalids was related to the presence of some defensive strategies of its species. This compounding review can be used as the foundation for future advances in vertebrates' predator-prey interactions.

Introduction

Anurans exhibit a great diversity of defensive strategies (e.g., Dodd Jr., 1976), which could include, alone or in combination, ecological, morphological, physiological, or behavioural features (Duellman & Trueb, 1994; Toledo & Jared, 1995). The whole defensive repertoire of a population or a species may have been evolved due to the strong and continuously selective pressure wielded by its natural predators (Greene, 1997; Vamosi, 2005). Moreover, predators may also have been coevolved to suppress these defensive strategies, generating a predator-prey arms race (Brodie III & Brodie Jr., 1999*a*; 1999*b*; Geffeney, Brodie Jr. & Brodie III, 2002). Anurans are known to be preyed upon by so many predators that it has been stated that “practically anything will eat an amphibian” (Porter, 1972 *apud* Duellman & Trueb, 1994 p. 244). In spite of this, there is no data compilation about the actual anurans predators. Most of the reports are anecdotic, just reporting the predation events (see comments in Toledo, 2005), and few articles can give substantial contributions, e.g., by giving information on predation rates (Olson, 1989; Hinshaw & Sullivan, 1989; Martins, Sazima & Egler, 1993), inferring on the risks of predation (e.g., Ryan, 1985; Haddad & Bastos, 1997), or revising the subject (e.g., McCormick & Polis, 1982; Toledo, 2005).

It is suggested that relatively larger predators generally subdue their prey without having to use special tactics (Hespenheide, 1973). On the other hand, in order to capture larger or equal size prey, it is possible that predators make use of specialized tactics such as poisoning, trapping, or social foraging (Hespenheide, 1973; McCormick & Polis, 1982; McNab, 1983; Pough, Heiser & McFarland, 1990; Menin, Rodrigues & Azevedo, 2005). Again, these theories have not been tested jointly for anurans. Therefore, in the present study we carried out a qualified and quantified review of the main vertebrate predators of post-metamorphic anurans, verifying the relationship between relative predator-prey sizes. We have also considered the use of specialized predation tactics in relation to relative size of prey.

Methods

Vertebrate predators

Given the large amount of available reports on post-metamorphic anurans as prey of vertebrates (invertebrate predators were reviewed elsewhere: Toledo, 2005),

only unpublished data, articles, and natural history notes published in *Herpetological Review* (since the first number in the late 1960's up to the last number of 2005) were considered. Additional references were only considered when they provided relative significant contributions, for example, when referring to an unreported family (or even a higher taxa) of prey and/or predator. Furthermore, we only considered articles that identified to the specific level both the prey (anurans) and predators (vertebrates). Predation attempts in the field, laboratory experiments, and captivity observations were also not considered. Specific names are in agreement to online databases: amphibians follow Frost (2004) complemented by Faivovich et al. (2005), Nascimento et al. (2005) and Frost et al. (2006), reptiles follow Uetz *et al.* (2005), fishes follow Froese & Pauly (2004), birds follow Lepage (2005), and mammals follow Wilson & Reeder (1993). To assert that our review is representative over the anuran phylogenetic groups we made a linear regression analysis between number of species in the family and number of predation reports, including data from invertebrates (based on Toledo, 2005) and vertebrates (present study) and expected to find a positive significance fixing α in 99 %.

Size relationships and predation tactics

The predator-prey size relationship was verified from the analysis of 333 accounts of invertebrate predation upon anurans (see Table 2 in Toledo, 2005), taking into account the relative size of the prey in relation to predators [R_s = snout-vent length of anuran (SVL) / total length of invertebrate (TL)] and the presence or absence of specialized predatory tactics, such as use of traps (e.g., webs), poison, social foraging, or any association between them. Values of R_s are presented as mean \pm standard deviation (range). Vertebrate predators were not included in this analysis, because, in the great majority of the circumstances, they were many times larger than anurans complicating the visualization of the results (see discussion).

For R_s comparisons among predator groups a Mann-Whitney (t) test was used. Predator size was correlated with anuran size using linear correlation. The same analysis was used when correlating the size classes of the invertebrates and number of families of anurans that were preyed upon. Significant values were considered when $P < 0.001$.

Results

Our databases, including invertebrate and vertebrate predators, comprised 21 anuran families. We found a positive relation between species of anurans in the families and number of reports of predation (adjusted $r^2 = 0.46$; $F = 17.86$; $P = 0.0005$; $n = 21$; Fig. 1). The only group who was found out of the 95 % prediction interval ellipse was the family Brachycephalidae. Out of the 95 % confidence interval were the Leiopelmatidae, Leptodactylidae, Microhylidae, Pipidae, Racophoridae, and Scaphiopodidae families. Among these families microhylid was the one that have differentiated the most (Fig. 1).

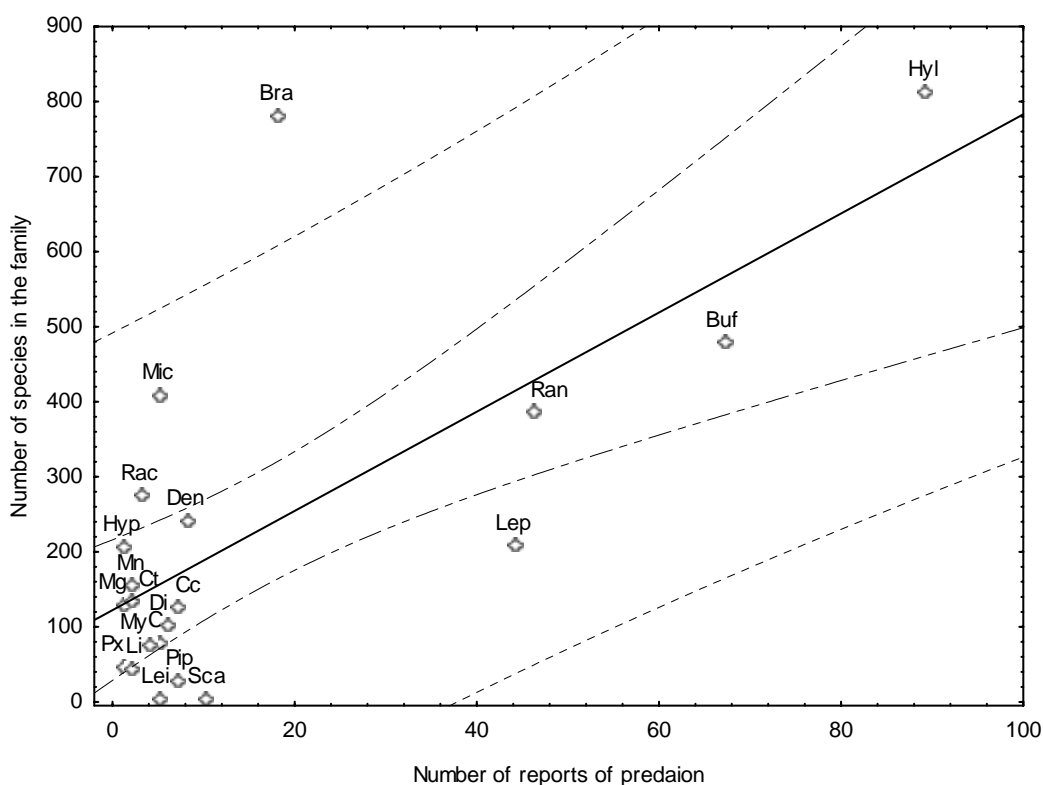


Fig. 1. Linear regression, 95 % of confidence interval, and 95 % prediction interval ellipse between the number of reports of predation by invertebrates and vertebrates upon post-metamorphic anurans and the number of species in the anuran families. The labels refer to the names of the families: Brachycephalidae (Bra), Bufonidae (Buf), Ceratophryidae (C), Centrolenidae (Ct), Cycloramphidae (Cc), Dendrobatidae (Den), Dicroglossidae (Di), Hylidae (Hyl), Hyperoliidae (Hyp), Leptodactylidae (Lep), Leiopelmatidae (Lei), Limnodynastidae (Li), Mantellidae (Mn), Megophryidae (Mg), Microhylidae (Mic), Myobatrachidae (My), Pipidae (Pip), Pyxicephalidae (Px), Ranidae (Ran), Racophoridae (Rac), and Scaphiopodidae (Sca).

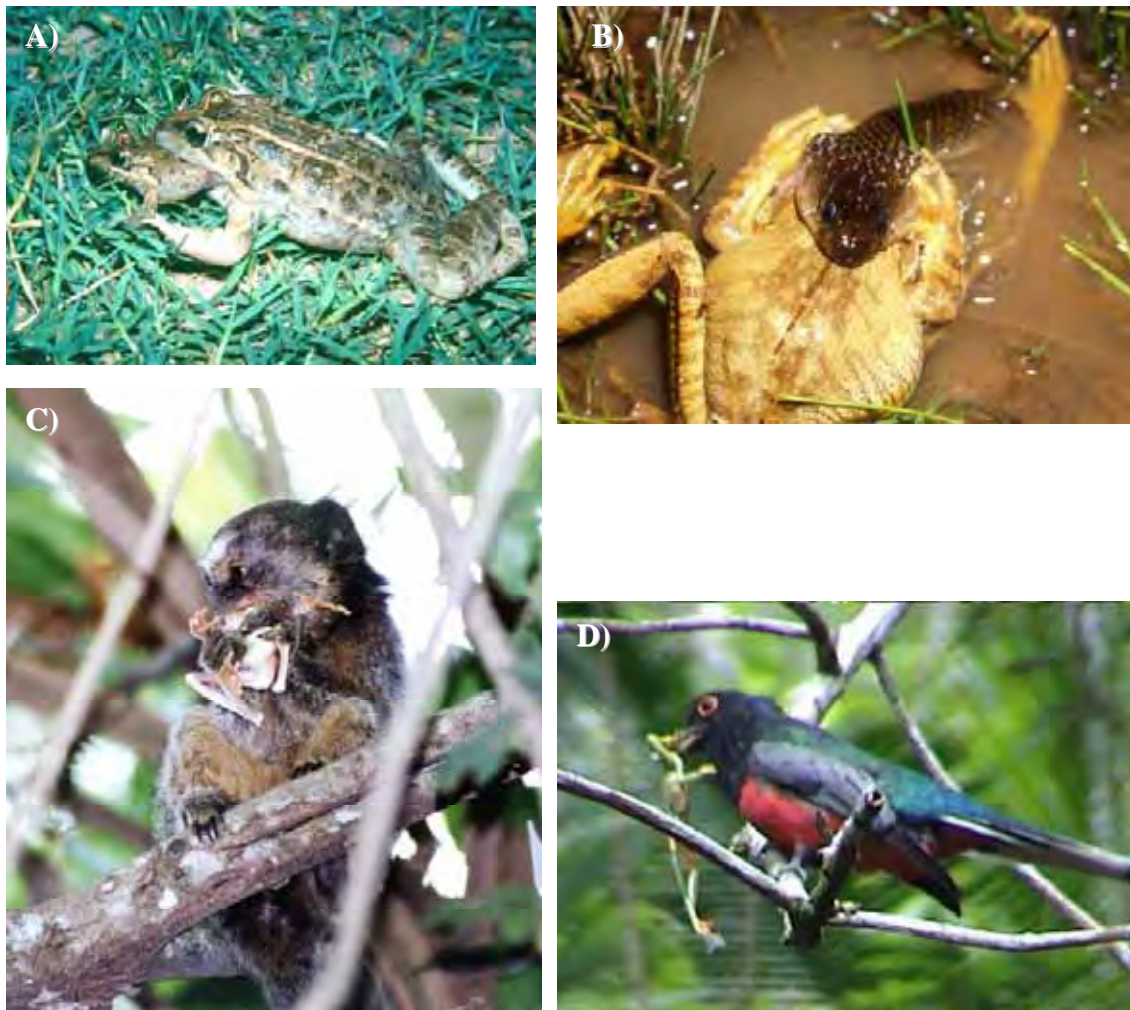


Fig. 2. Post-metamorphic anurans preyed by vertebrates. A) Adult *Leptodactylus* cf. *ocellatus* preying upon a conspecific juvenile; B) Adult *Liophis miliaris* preying upon an adult male *Hypsiboas faber*; C) a *Calitryx penicilata* eating an adult *Hypsiboas lundii*; and D) an adult *Trogon surrucura* preying upon an adult *Hypsiboas albomarginatus*.

Vertebrate predators

More than one hundred anuran species ($n = 137$), belonging to 16 families (Brachycephalidae, Bufonidae, Ceratophryidae, Cycloramphidae, Dendrobatidae, Dicroglossidae, Hylidae, Leiopelmatidae, Leptodactylidae, Mantellidae, Megophryidae, Microhylidae, Pipidae, Pyxicephalidae, Ranidae, and Scaphiopodidae) were reported as prey of 136 species from all main groups of vertebrates (Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia) (Fig. 2; Appendix I). Among them, snakes were the most representative group, being referred to in about 45 % of the reports (Fig. 3).

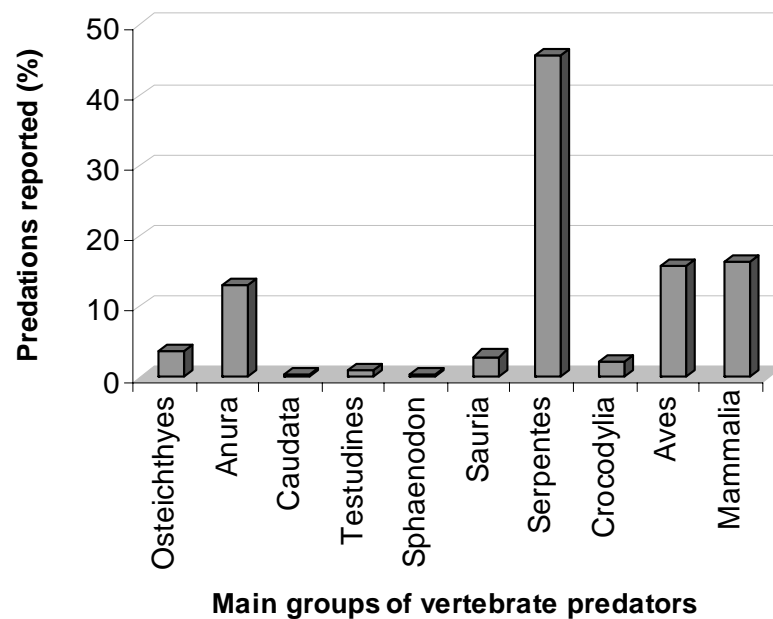


Fig. 3. Percentage of the main vertebrate groups reported as post-metamorphic anuran predators (data source = Appendix 1; N = 243).

We were able to divide the vertebrate predators into four categories:

I) Opportunistic predators: the ones who feed on anurans occasionally and opportunistically. These predators are diet-generalist and prey on anurans when, once in a while, they encounter them in nature. This is the largest group and made up about 42 % of the reports and is formed by fishes, salamanders, turtles, lizards, crocodylians, and some species of birds and mammals (see also Poulin *et al.*, 2001; Bueno *et al.*, 2002; Seamark & Bogdanowicz, 2002) (Fig. 2).

II) Convenience predators: they are not predators specialized on anurans, but feed on them with regularity. In this case, the most representative predators are those who exhibit similar habits to the anurans, facilitating their (predator-prey) encounters. Examples are the anurans themselves (about 25 % of the reports; Fig. 2) and some bird species (e.g., *Geranospiza caerulescens*) that forage in areas where the chances of encountering anurans is greatly enhanced, such as margins of water bodies, gaps on tree trunks, axils of bromeliads, and holes in the ground (e.g., Bokermann, 1978).

III) Temporary specialized predators: those who look specifically for anurans in a determined phase of their life cycle or for a determined purpose. In this case we included some snakes, such as some species of *Bothrops* that feed exclusively or

primarily on anurans when they are juveniles (Sazima, 1992; Hartmann *et al.*, 2003; Nogueira *et al.*, 2003). Another example are some bird species, e.g., *Trogon surrucura* and *Pitangus sulphuratus* that hunt for anurans to feed their nestlings (Toledo *et al.*, 2005; Fig. 2) or males of *Baryphthengus martii* that provide colourful anurans (dendrobatids) to females as a courtship signal (Master, 1999). A third possibility in this group is represented by those vertebrates that prey upon anurans in order to use their skin toxins in their own defence (Brodie Jr., 1977). This is the smallest group, making up less than 1 % of the reports.

IV) Specialized predators: this group is basically formed by some bat species, e.g., *Cardioderma cor* and *Megaderma* spp., but mainly *Trachops cirrhosus* (Tuttle *et al.*, 1982; Tandler *et al.*, 1996), and several snake species specialized in hunting anurans, e.g., *Chironius* spp. and *Liophis* spp. (Duellman, 1978; Michaud & Dixon, 1989; Martins & Oliveira, 1999; Marques *et al.*, 2001) (Fig. 2). Indeed, some snake species exhibit preferences, occasionally together with morphological specializations, for hunting species within a genus or a family. For example, the snakes *Causus rhombeatus*, *Waglerophis merremi*, and *Xenodon newiedii* are specialized to hunt *Chaunus* spp. or other bufonids that they may face (Vanzolini *et al.*, 1980; Duellman & Trueb, 1994; Marques *et al.*, 2001). This category comprises approximately 31 % of the reports.

Size relationships and predation tactics

In all reported predation events the vertebrate predators were larger than anurans. Anurans were preyed even when they had a great amount of skin toxins (for example, bufonids, *Leptodactylus labyrinthicus*, and *L. pentadactylus*) or highly toxic skin secretions (e.g., *Atelopus varius*, *Dendrobates auratus*, *Eupemphix nattereri*, and *Phyllobates terribilis*) (Appendix I).

Out of the 333 reported predations by invertebrates upon post-metamorphic anurans, 34 were made by predators that did not use specialized tactics [$R_s = 0.92 \pm 0.31$ (0.29 – 1.78)] and 299 by predators with specialized tactics [$R_s = 1.52 \pm 0.79$ (0.30 – 5.00)]. These groups differed significantly between their R_s ($t = 3,585.5$; $P < 0.0001$), suggesting that when the invertebrates exhibited specialized tactics they were practically the same size as their preys (venomous predators) or smaller than their preys (social

foragers). On the other hand, when they were solitary non-venomous predators they were relatively larger than their preys (Fig. 4).

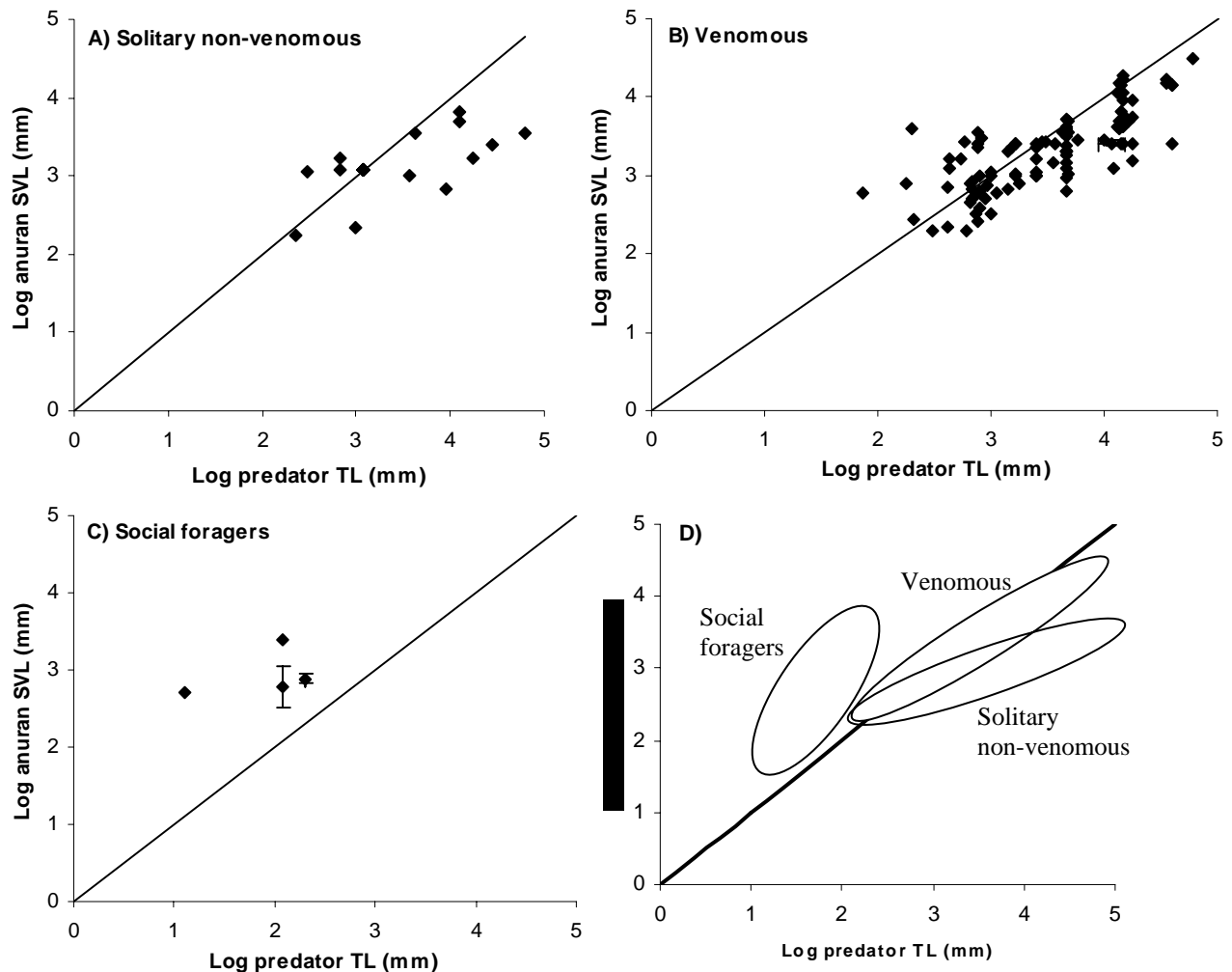


Fig. 4. Relationship between anuran snout-vent length (SVL) and the total length (TL) of their respective invertebrate predators (data from Toledo, 2005). Predators are divided into the following categories: A) solitary non-venomous ($N = 34$), B) venomous ($N = 132$), and C) social foragers ($N = 167$). D) A schematic synthesis of the relationships among all categories of invertebrate predator sizes and anuran sizes.

Only 34.11 % of the invertebrates were larger than their victims. The SVL of the anurans was positively correlated with the TL of the solitary non-venomous ($r = 0.64$; $P < 0.001$; $n = 34$) and venomous predators ($r = 0.78$; $P < 0.001$; $n = 132$), but not with the social foragers ($r = 0.13$; $P = 0.08$; $n = 167$). Excluding the social foragers, the larger the invertebrate, the smaller was the relative size of the captured prey (Fig. 3). We did not find a significant correlation between the TL categories and the number of

families of anurans ($r = -0.09$; $P = 0.83$; $n = 8$) or the number of species that were preyed upon ($r = -0.41$; $P = 0.31$; $n = 8$) (Table 1).

Table 1. Invertebrate total length (TL) classes and the respective number of anuran families and species that were preyed upon.

TL classes in mm (N)	Number of anuran families	Number of anuran species
3 to 10 (172)	3	8
11 a 20 (32)	5	20
21 a 30 (36)	5	13
31 a 40 (30)	6	15
41 a 50 (4)	2	2
51 a 60 (15)	3	6
61 a 70 (35)	6	13
85 a 200 (9)	3	6

Discussion

Size relationships and predation tactics

McCormick & Polis (1982) observed, to a certain extent, a similar proportion (45 %; $n = 134$) to that calculated in the present study (34 %; $n = 333$) of invertebrate predators that were larger than their vertebrate preys. Besides this, accordingly with our observations, it has also been reported an increase of the relative prey size with the sociality level of the predator (for invertebrates see: McCormick & Polis, 1982; for vertebrates see: McNab, 1983). Coincident observations among different predators and prey groups (from small invertebrates to large vertebrates) suggest that these relationships must be widespread in natural communities.

Without considering the social foragers, we observed that the larger the invertebrate predator, the smaller is the relative prey size. This fact can be related to an ontogenetic variation in the diet of the invertebrates (e.g., Cisneros & Rosenheim, 1997; Koperski, 1997), which could be focused on more energetically valuable items in terms of accessibility and/or subjugation facility (MacArthur & Pianka, 1966; Bennett, 1986). That is, the larger the anuran, the larger its capacity to escape from a predator (Formanowicz Jr. *et al.*, 1981). Therefore, these predators would have a higher energetic cost implied for searching, stalking, striking, and subduing (including killing and

ingesting) relatively larger prey. Another possibility would be an alteration in the encounter rate of predators and preys in the wild due to differences of habits and density among classes of size, both of the invertebrates and anurans (MacArthur & Pianka, 1966). Therefore, it would be more advantageous, in energetic terms, to hunt for relatively smaller (Enders, 1975) and/or more accessible prey (Begon *et al.*, 1990). Nonetheless, as larger the anuran, the lower is the risk of invertebrate predation (present study), and at a certain moment the anuran can become the predator of the invertebrate (see discussion below).

Vertebrate predators were not included in this analysis; however, their inclusion would only reinforce our correlations and comparisons since vertebrates that prey on anurans are many times larger than their preys, are solitary hunters, and do not use traps or poison (with only the exception of venomous snakes).

For hunting preys that are larger than they are, predators are commonly reported to make use of specialized tactics (Hespenheide, 1973; Enders, 1975; McCormick & Polis, 1982; present study). However, this does not exclude the availability of relatively smaller prey to these predators (Enders, 1975). Consequently, predators that use these tactics may capture a broader array of prey (with regard to size) when compared to solitary non-venomous predators. Consecutively, it is possible that an increase in the amplitude of prey sizes could allow a diversification (with regard to richness) of items that could be captured. However, our results do not sustain these hypotheses, i.e., we neither observed an increase in the amplitude of sizes of anurans that were captured (Fig. 3b; 3c), nor an increase in the richness of dietary items (Table 1) with the increment of predator body size (length). Therefore, we suggest that invertebrates could be selecting their prey due to energetic restrictions involved in the predatory process of searching, stalking, striking, or subduing (including killing and ingesting) (e.g., Brooks & Dodson, 1965; Griffiths, 1975; 1980; Bennett, 1986).

Predators and defence

Studying snakes and their predators, Greene (1997) suggested that, since endothermic predators (birds and mammals) have higher metabolic rates than ectothermic ones (Randall *et al.*, 2002), endothermic predators must ingest their prey at a higher rate. Therefore, birds and mammals must input a greater selective pressure over

the defensive strategies than ectothermic predators, such as snakes. Even though it could be true for anurans and their predators (it has never been tested), another factor must be considered in this relation. Although snakes do not feed at the same rate that the endothermics do, for example a single adult hawk is able to eat up to 18 adult anurans in a four hour period (Bokermann, 1978), there is a much larger number of species and individuals (independent of the species) of snakes that hunt occasionally, preferentially, or specifically for anurans. In contrast, birds and mammals are occasional predators, usually much more generalists (present study). Hence, if the relative abundance of snakes is higher than that of other predators (e.g., birds and mammals), in a determined area, in a determined time (the relative abundance of a predator group varies within latitudinal ranges and within biomes: Greene, 1988), snakes should be considered the main anuran predators. As a consequence, it is possible that snakes have been (or are being) driving the diversification of the anuran defensive strategies (see discussion in Vamosi, 2005). Similarly, spiders may play a significant role if invertebrates are taken into account (see Toledo, 2005).

Another aspect that seems to influence the divergence and maintenance of a specific defensive behaviour is the success in escaping from predators (Greene, 1988). I.e., predators that have commonly hunted anuran species, except anurans who present successful defences, are those who are driving the evolution of such mechanisms (Greene, 1988). This hypothesis is intuitive when considering anuran communities, since we have few experimental and field approaches that corroborate or reject it (e.g., Formanowicz Jr. *et al.*, 1981; Heinen, 1995; Heinen & Hammond, 1997; Leary & Razafindratsita, 1998). However, if it is truth for anurans, not all snakes and spiders species are those who are driving the evolution of defensive mechanisms in anurans, but some of them, or even other group of species. All these suggestions still need clarification by means of field observations, experimentation, and broader analysis.

Most of the *Eleutherodactylus* and *Craugastor* species (which represents the majority of the species in the family Brachycephalidae) occurs spread on the forest floor (persn. obs.), have cryptic colorations, and are very polymorphic (Hoffman & Boulin, 2000; Sander *et al.*, 2003). In contrast, aposematic and toxic *Brachycephalus* species can be found in very high densities distributed in a patch pattern on the forest floor. Some of the cryptic species of *Brachycephalus*, such as *B. nodoterga*, can be found

spread on the forest floor like *Eleutherodactylus* spp. and *Craugastor* spp. (persn. obs.). Hence, these morpho-ecological characteristics may efficiently prevent individuals of this family to be preyed. However, we do not exclude the possibility of their cryptic and distributional characteristics to difficult field observations of predation. Microhylids were also preyed less than expected. Most of microhylids are fossorial and explosive breeders, emerging from their galleries few days a year (Duellman & Trueb, 1994). Therefore, it would again explain the few numbers of predation accounts. The scenery for the other families that were not included in the confidence interval may change with additional predation reports and species descriptions.

Cross predation, cannibalism, and threats

Although anurans are preyed on by practically any kind of animal, we observed countless reports that leads us to suggest status inversion, i.e., from being prey they become predators when the size relationship becomes more favourable for the anurans. Stomach content studies provide many examples of anurans feeding primarily on small invertebrates (Pough *et al.*, 1998). Nevertheless, large-sized anurans, such as *Conraua goliath*, *Ceratophrys*, some *Leptodactylus*, *Pyxicephalus*, and *Lithobates* spp. can prey upon several types of vertebrates (Duellman and Trueb, 1994). *Lithobates catesbeianus*, for example, has already been reported feeding on fish (Cross & Gerstenberger, 2002), turtles (Graham, 1984), snakes (Carpenter *et al.*, 2002; Rorabaugh & Humphrey, 2002), birds (Black, 1974), bats (Kirkpatrick, 1982), mice, minks (Beringer & Johnson, 1995), and other anurans, including conspecific individuals (references in Appendix I; Fig. 2a). Cannibalism is reported essentially among species of *Lithobates* (Stuart & Painter, 1993; Rombough *et al.*, 2003; Appendix I), yet there is no evidence that conspecifics are able to recognize themselves, being cannibalism only an opportunistic form of predation (Duellman & Trueb, 1994). In this way, alien populations of *Lithobates catesbeianus*, introduced generally by frog farms, represent a strong threat to native vertebrate populations, but primarily for anuran populations (Batista, 2002; Borges-Martins & Di-Bernardo, 2002; Kats & Ferrer, 2003), since they are highly voracious convenience predators (*sensu* present study).

Another important anuran predator is the human being. Although the effects of hunting are relatively unknown, there is evidence of human impact over some

populations or species (Schlaepfer *et al.*, 2005), leading some of them to noticeable decline or even to extinction (Beebee, 1996; Collins & Storfer, 2003). Humans hunt for anurans essentially with three objectives: I) for exhibitions and pets, II) science or education, and III) for skin and meat supply. The latter is most intense over large anurans, occurs all over the world, and should be the most impacting (Beebee, 1996). As examples of species that have been hunted for human feeding we can list: *Conraua goliath* (Africa), *Rana draytonii*, *Lithobates catesbeianus* (North America), *Leptodactylus fallax*, *L. labyrinthicus*, *L. ocellatus*, *L. pentadactylus* (Central and South America), *Hoplobatrachus rugulosus* (Asia), and *Rana temporaria* (Europe) (Beebee, 1996; Collins & Storfer, 2003; AmphibiaWeb, 2005; Zina & Haddad, 2005; L. F. Toledo & C. F. B. Haddad, unpubl. data).

Finally, we believe that our study, rather than a closing review of the subject must be considered as a starting point for future research clarifying several aspects of natural history of vertebrates (specially anurans), mainly aspects related to predation, defence and conservation. Our results may also help in studies of communities of predators, specially those involving size-relationship analyses.

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Appendix I. Vertebrate predators (136 species; 50 families) and their respective prey: post-metamorphic anurans (137 species; 16 families) reviewed from 243 reports (including unpublished observations).

Vertebrate Predator		Anuran Prey		Reference
Higher Taxa	species	Family	species	
Osteichthyes				
Anguillidae	<i>Anguilla reinhardtii</i>	Hylidae	<i>Litoria lesueurii</i>	Harvey <i>et al.</i> , 1999
Centrarchidae	<i>Lepomis cyanellus</i>	Hylidae	<i>Pseudacris cadaverina</i>	Ervin <i>et al.</i> , 2000
	<i>Micropterus salmoides</i>	Hylidae	<i>Pseudacris cadaverina</i>	Hovey & Ervin, 2005
	<i>Micropterus salmoides</i>	Ranidae	<i>Lithobates pipiens</i>	Cochran, 1982
	<i>Micropterus salmoides</i>	Ranidae	<i>Lithobates sylvaticus</i>	Cochran, 1999
Characidae	<i>Brycon guatemalensis</i>	Dendrobatidae	<i>Dendrobates auratus</i>	Hedstrom & Bolaños, 1986
Erythrinidae	<i>Hoplias cf. malabaricus</i>	Bufoinidae	<i>Chaunus ornatus</i>	Haddad & Bastos, 1997
Salmonidae	<i>Salmo trutta</i>	Hylidae	<i>Pseudacris crucifer</i>	Cochran & Cochran, 2003
	<i>Salmo trutta</i>	Ranidae	<i>Rana cascadae</i>	Simons, 1998
Amphibia				
Anura				
Bufonidae	<i>Anaxyrus terrestris</i>	Ranidae	<i>Lithobates heckscheri</i>	Beane & Pusser, 2005
Ceratophryidae	<i>Chaunus jimi</i>	Bufoinidae	<i>Chaunus granulatus</i>	Guix, 1993
	<i>Ceratophrys aurita</i>	Bufoinidae	<i>Chaunus scheneideri</i>	R. P. Bastos, unpubl. data
	<i>Ceratophrys cranwelli</i>	Leptodactylidae	<i>Physalaemus biligonigerus</i>	Wild, 2001
	<i>Ceratophrys cranwelli</i>	Microhylidae	<i>Dermatonotus muelleri</i>	Wild, 2001
Hylidae	<i>Hypsiboas faber</i>	Hylidae	<i>Scinax granulatus</i>	Solé <i>et al.</i> , 2004
Leptodactylidae	<i>Leptodactylus labyrinthicus</i>	Hylidae	<i>Hypsiboas albopunctatus</i>	L. F. Toledo & O. G. S. Araújo, unpubl. data
	<i>Leptodactylus labyrinthicus</i>	Hylidae	<i>Hypsiboas faber</i>	C. F. B. Haddad, unpubl. data
	<i>Leptodactylus labyrinthicus</i>	Leptodactylidae	<i>Eupemphix nattereri</i>	Silva <i>et al.</i> , 2003
	<i>Leptodactylus ocellatus</i>	Hylidae	<i>Hypsiboas albomarginatus</i>	C. F. B. Haddad, unpubl. data
	<i>Leptodactylus ocellatus</i>	Hylidae	<i>Hypsiboas faber</i>	Haddad & Sazima, 1992
	<i>Leptodactylus ocellatus</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Kokubum & Rodrigues, 2005
	<i>Leptodactylus ocellatus</i>	Leptodactylidae	<i>Eupemphix nattereri</i>	Rodrigues & Filho, 2004
	<i>Leptodactylus pentadactylus</i>	Leptodactylidae	<i>Hypsiboas rosenbergi</i>	Kluge, 1981
	<i>Leptodactylus podicipinus</i>	Bufoinidae	<i>Chaunus granulatus</i>	Guimarães <i>et al.</i> , 2004
	<i>Litoria aurea</i>	Leiopelmatidae	<i>Leiopelma archeyi</i>	Thurley & Bell, 1994
	<i>Ptychoadena mascareniensis</i>	Mantellidae	<i>Mantidactylus wittei</i>	McIntyre & Ramanamanjato, 1999

	<i>Rana aurora</i>	Hylidae	<i>Pseudacris regilla</i>	Arnold & Halliday, 1986
	<i>Lithobates blairi</i>	Hylidae	<i>Pseudacris triseriata</i>	Bolek & Janvy Jr., 2004
	<i>Rana cascade</i>	Ranidae	<i>Rana cascadeae</i>	Rombough <i>et al.</i> , 2003
	<i>Lithobates catesbeianus</i>	Bufonidae	<i>Anaxyrus californicus</i>	Griffin & Case, 2002
	<i>Lithobates catesbeianus</i>	Bufonidae	<i>Anaxyrus fowleri</i>	Smith & Green, 2002
	<i>Lithobates catesbeianus</i>	Bufonidae	<i>Anaxyrus nelsoni</i>	Jones <i>et al.</i> , 2003
	<i>Lithobates catesbeianus</i>	Hylidae	<i>Pseudacris triseriata</i>	Bolek & Janvy Jr., 2004
	<i>Lithobates catesbeianus</i>	Ranidae	<i>Rana aurora</i>	Cook, 2002
	<i>Lithobates catesbeianus</i>	Ranidae	<i>Rana boylei</i>	Crayon, 1998
	<i>Lithobates catesbeianus</i>	Ranidae	<i>Lithobates catesbeianus</i>	Stuart & Painter, 1993
	<i>Lithobates catesbeianus</i>	Scaphiropodidae	<i>Scaphiopus hammondi</i>	Hays & Warner, 1985
	<i>Rana luteiventris</i>	Bufonidae	<i>Anaxyrus boreas</i>	Pearl, 2000
	<i>Rana luteiventris</i>	Ranidae	<i>Rana luteiventris</i>	Pilliod, 1999
	<i>Rana pretiosa</i>	Ranidae	<i>Rana pretiosa</i>	Pilliod, 1999
	<i>Lithobates vaillanti</i>	Hylidae	<i>Agalychnis callidryas</i>	Vaughan, 2003
Caudata				
Ambystomatidae	<i>Dicamptodon copei</i>	Leiopelmatidae	<i>Ascaphus truei</i>	Aresco & Reed, 1998
Reptilia				
Crocodylia				
Alligatorinae				
	<i>Caiman crocodilus</i>	Bufonidae	<i>Chaunus granulosis</i>	Gorzula, 1977
	<i>Caiman crocodilus</i>	Leptodactylidae	<i>Pleuroderma brachyops</i>	Gorzula, 1977
	<i>Caiman crocodilus</i>	Microhylidae	<i>Elachistocleis ovalis</i>	Gorzula, 1977
	<i>Caiman yacare</i>	Hylidae	<i>Pseudis paradoxa</i>	Santos <i>et al.</i> 1996
	<i>Paleosuchus palpebrosus</i>	Bufonidae	<i>Chaunus scheneideri</i>	L. F. Toledo, unpubl. data
Rynchocephalia				
Sphenodontidae	<i>Sphenodon punctatus</i>	Leiopelmatidae	<i>Leiopelma hamiltoni</i>	Newman, 1977
Sauria				
Gekkonidae	<i>Thecadactylus rapicauda</i>	Brachycephalidae	<i>Eleutherodactylus johnstonei</i>	Henderson & Berg, 2005
Gerrhosauridae	<i>Zonosaurus madagascariensis</i>	Mantellidae	<i>Mantella laevigata</i>	Heying, 2001
Teiidae	<i>Ameiva festiva</i>	Leptodactylidae	<i>Leptodactylus poecilochilus</i>	Toral, 2004
	<i>Crocodilus amazonicus</i>	Bufonidae	<i>Chaunus marinus</i>	Costa <i>et al.</i> , 2005
	<i>Tupinambis merianae</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Silva & Hillesheim, 2004
	<i>Tupinambis merianae</i>	Bufonidae	<i>Chaunus schneideri</i>	L. F. Toledo, unpubl. data
	<i>Tupinambis teguixim</i>	Leptodactylidae	<i>Leptodactylus mystaceus</i>	Souza <i>et al.</i> , 2002

Serpentes

Boidae					Caudell <i>et al.</i> , 2000
Colubridae	<i>Boiga irregularis</i>	Bufonidae	<i>Chaunus marinus</i>		Rodríguez-Robles & Leal, 1993
	<i>Alsophis portoricensis</i>	Brachycephalidae	<i>Eleutherodactylus antillensis</i>		Rodríguez-Robles & Leal, 1993
	<i>Alsophis portoricensis</i>	Brachycephalidae	<i>Eleutherodactylus coqui</i>		Fong, 2004
	<i>Antillophis andreae</i>	Bufonidae	<i>Peltophryne peltoccephalus</i>		Fong, 2004
	<i>Antillophis andreae</i>	Brachycephalidae	<i>Euhyas dimidiatus</i>		Castanho, 1996
	<i>Chironius exoletus</i>	Hylidae	<i>Phyllomedusa distincta</i>		Rocha <i>et al.</i> , 1999
	<i>Chironius multiventris</i>	Hylidae	<i>Bokermannohyla circumdata</i>		Rocha <i>et al.</i> , 1999
	<i>Chironius multiventris</i>	Cycloramphidae	<i>Proceratophrys appendiculata</i>		Prado, 2003
	<i>Clelia bicolor</i>	Hylidae	<i>Trachycephalus venulosus</i>		Pauwels, 2002
	<i>Dendrelaphis pictus</i>	Dicroglossidae	<i>Ferjevaria limnocharis</i>		Pauwels, 2002
	<i>Enhydryis plumbea</i>	Dicroglossidae	<i>Ferjevaria limnocharis</i>		Silva Jr. <i>et al.</i> , 2003
	<i>Helicops angulatus</i>	Hylidae	<i>Hypsiboas crepitans</i>		Feltrim & Cechin, 2000
	<i>Helicops infrataeniatus</i>	Hylidae	<i>Phyllomedusa iheringii</i>		Martins & Duarte, 2003
	<i>Helicops infrataeniatus</i>	Leptodactylidae	<i>Eupemphix nattereri</i>		Tucker, 2000
	<i>Heterodon platirhinos</i>	Bufonidae	<i>Anaxyrus fowleri</i>		Bakkegard & Greene, 2002
	<i>Heterodon platirhinos</i>	Ranidae	<i>Lithobates pipiens</i>		Myers <i>et al.</i> , 1978.
	<i>Leimadophis epinephelus</i>	Dendrobatidae	<i>Phyllobates territorialis</i>		Kluge, 1981
	<i>Leptodeira annulata</i>	Hylidae	<i>Hypsiboas rosenbergi</i>		Mora, 1999
	<i>Leptodeira annulata</i>	Ranidae	<i>Lithobates vaillanti</i>		Russell <i>et al.</i> , 1999
	<i>Leptodeira septentrionalis</i>	Hylidae	<i>Scinax elaeochroa</i>		Albuquerque & Di-Bernardo, 2005
	<i>Leptophis ahaetulla</i>	Hylidae	<i>Trachycephalus venulosus</i>		Lopez <i>et al.</i> , 2003
	<i>Leptophis ahaetulla</i>	Hylidae	<i>Dendropsophus nanus</i>		Lopez <i>et al.</i> , 2003
	<i>Leptophis ahaetulla</i>	Hylidae	<i>Scinax cf. acuminatus</i>		Lopez <i>et al.</i> , 2003
	<i>Leptophis ahaetulla</i>	Hylidae	<i>Scinax nasicus</i>		Michaud & Dixon, 1989
	<i>Liophis anomalus</i>	Bufonidae	<i>Chaunus arenarum</i>		Michaud & Dixon, 1989
	<i>Liophis anomalus</i>	Bufonidae	<i>Chaunus dorbignyi</i>		Michaud & Dixon, 1989
	<i>Liophis anomalus</i>	Bufonidae	<i>Chaunus granulosus</i>		Michaud & Dixon, 1989
	<i>Liophis anomalus</i>	Ceratophryidae	<i>Ceratophrys ornata</i>		Michaud & Dixon, 1989
	<i>Liophis anomalus</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>		Michaud & Dixon, 1989
	<i>Liophis cobella</i>	Dendrobatidae	<i>Mannophryne trinitatis</i>		Michaud & Dixon, 1989
	<i>Liophis dilepis</i>	Leptodactylidae	<i>Leptodactylus fuscus</i>		Michaud & Dixon, 1989
	<i>Liophis dilepis</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>		Michaud & Dixon, 1989
	<i>Liophis dilepis</i>	Leptodactylidae	<i>Physalaemus cuvieri</i>		Michaud & Dixon, 1989

<i>Liophis epinephelus</i>	Bufonidae	<i>Atelopus varius</i>	Greene, 1997
<i>Liophis epinephelus</i>	Bufonidae	<i>Chaunus marinus</i>	Michaud & Dixon, 1989
<i>Liophis epinephelus</i>	Bufonidae	<i>Rhinella margaritifera</i>	Michaud & Dixon, 1989
<i>Liophis epinephelus</i>	Brachycephalidae	<i>Craugastor fitzingeri</i>	Michaud & Dixon, 1989
<i>Liophis lineatus</i>	Hylidae	<i>Scinax ruber</i>	Michaud & Dixon, 1989
<i>Liophis lineatus</i>	Leptodactylidae	<i>Leptodactylus fuscus</i>	Michaud & Dixon, 1989
<i>Liophis melanotus</i>	Bufonidae	<i>Chaunus granulosis</i>	Michaud & Dixon, 1989
<i>Liophis meridionalis</i>	Leptodactylidae	<i>Leptodactylus fuscus</i>	Kokubum & Giaretta, 2002
<i>Liophis miliaris</i>	Bufonidae	<i>Chaunus granulosis</i>	Michaud & Dixon, 1989
<i>Liophis miliaris</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Michaud & Dixon, 1989
<i>Liophis miliaris</i>	Microhylidae	<i>Elachistocleis bicolor</i>	Michaud & Dixon, 1989
<i>Liophis miliaris</i>	Pipidae	<i>Pipa carvalhoi</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Bufonidae	<i>Chaunus arenarum</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Bufonidae	<i>Chaunus dorbignyi</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Bufonidae	<i>Chaunus granulosis</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Hylidae	<i>Hypsiboas multifasciatus</i>	Silva Jr. <i>et al.</i> , 2003
<i>Liophis poecilogyrus</i>	Hylidae	<i>Hypsiboas pulchellus</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Hylidae	<i>Trachycephalus venulosus</i>	Silva Jr. <i>et al.</i> , 2003
<i>Liophis poecilogyrus</i>	Hylidae	<i>Scinax ruber</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Cycloramphidae	<i>Odontophrynus americanus</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Leptodactylidae	<i>Physalaemus cuvieri</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Leptodactylidae	<i>Physalaemus fernandezae</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Leptodactylidae	<i>Physalaemus gracilis</i>	Michaud & Dixon, 1989
<i>Liophis poecilogyrus</i>	Pipidae	<i>Pipa carvalhoi</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Bufonidae	<i>Rhinella margaritifera</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Dendrobatidae	<i>Mannophryne trinitatis</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Hylidae	<i>Scinax ruber</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Brachycephalidae	<i>Craugastor biporcatus</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Brachycephalidae	<i>Eleutherodactylus terraebolivaris</i>	Michaud & Dixon, 1989
<i>Liophis reginae</i>	Leptodactylidae	<i>Leptodactylus wagneri</i>	Michaud & Dixon, 1989
<i>Liophis sagittifer</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Michaud & Dixon, 1989
<i>Liophis typhlus</i>	Leptodactylidae	<i>Leptodactylus mystacinus</i>	Michaud & Dixon, 1989

<i>Liophis viridis</i>	Hylidae	<i>Scinax ruber</i>	Michaud & Dixon, 1989
<i>Liophis viridis</i>	Leptodactylidae	<i>Physalaemus cuvieri</i>	Michaud & Dixon, 1989
<i>Masticophis flagellum</i>	Scaphiropodidae	<i>Scaphiopus couchii</i>	Ryberg & Dayton, 2004
<i>Nerodia fasciata</i>	Ranidae	<i>Lithobates capito</i>	Jensen, 2000
<i>Nerodia fasciata</i>	Scaphiropodidae	<i>Scaphiopus holbrookii</i>	Palis, 2000
<i>Nerodia valida</i>	Bufonidae	<i>Anaxyrus punctatus</i>	Blazquez, 1996
<i>Philodryas patagoniensis</i>	Bufonidae	<i>Chaunus granulatus</i>	Lopez, 2003
<i>Philodryas patagoniensis</i>	Leptodactylidae	<i>Leptodactylus gracilis</i>	Lopez, 2003
<i>Pliocercus euryzonus</i>	Brachycephalidae	<i>Eleutherodactylus</i> sp.	Greene, 1997
<i>Ptyas korros</i>	Dicroglossidae	<i>Fejervaria limnocharis</i>	Pauwels, 2002
<i>Rhabdophis murudensis</i>	Megophryidae	<i>Megophrys kobayashii</i>	Das & Tuen, 2005
<i>Thamnodynastes strigatus</i>	Hylidae	<i>Dendropsophus minutus</i>	C. F. B. Haddad, unpubl. data
<i>Thamnodynastes strigatus</i>	Hylidae	<i>Hypsiboas faber</i>	Souza <i>et al.</i> , 2003
<i>Thamnodynastes strigatus</i>	Cycloramphidae	<i>Crossodactylus</i> cf. <i>bokermanni</i>	Kopp & Wachlevski, 2005
<i>Thamnodynastes strigatus</i>	Cycloramphidae	<i>Odontophrynus americanus</i>	Souza <i>et al.</i> , 2003
<i>Thamnodynastes strigatus</i>	Ranidae	<i>Lithobates catesbeianus</i>	Souza <i>et al.</i> , 2003
<i>Thamnophis atratus</i>	Ranidae	<i>Rana cascadae</i>	Garwood & Welsh Jr., 2005
<i>Thamnophis cyrtopsis</i>	Bufonidae	<i>Cranopsis occidentalis</i>	Abbadí-Bisogno <i>et al.</i> , 2003
<i>Thamnophis elegans</i>	Ranidae	<i>Rana pretiosa</i>	Reaser & Dexter, 1996
<i>Thamnophis hammondi</i>	Bufonidae	<i>Anaxyrus californicus</i>	Griffin & Case, 2002
<i>Thamnophis hammondi</i>	Hylidae	<i>Pseudacris regilla</i>	Ervin & Fisher, 2001
<i>Thamnophis hammondi</i>	Pipidae	<i>Xenopus laevis</i>	Ervin & Fisher, 2001
<i>Thamnophis hammondi</i>	Scaphiropodidae	<i>Spea hammondi</i>	Ervin & Fisher, 2001
<i>Thamnophis sauritus</i>	Hylidae	<i>Osteopilus septentrionalis</i>	Love, 1995
<i>Thamnophis scalaris</i>	Ranidae	<i>Lithobates neovolcanica</i>	Romero <i>et al.</i> , 2003
<i>Thamnophis sirtalis</i>	Leiopelmatidae	<i>Ascaphus truei</i>	Karraker, 2001
<i>Thamnophis sirtalis</i>	Hylidae	<i>Osteopilus septentrionalis</i>	Jansen, 1997
<i>Thamnophis sirtalis</i>	Ranidae	<i>Rana cascadae</i>	Garwood & Welsh Jr., 2005
<i>Thamnophis sirtalis</i>	Ranidae	<i>Rana muscosa</i>	Feldman & Wilkinson, 2000
<i>Thamnophis sirtalis</i>	Ranidae	<i>Rana aurora</i>	Maclay <i>et al.</i> , 2004
<i>Thamnophis valida</i>	Scaphiropodidae	<i>Scaphiopus couchii</i>	Grismer, 2000
<i>Xenochrophis flavopunctatus</i>	Dicroglossidae	<i>Fejervaria limnocharis</i>	Pauwels, 2002
<i>Xenoxylbelis argenteus</i>	Bufonidae	<i>Rhinella proboscidea</i>	Menin, 2005
<i>Xenodon neuwiedii</i>	Hylidae	<i>Bokermannohyla hylax</i>	Silva & Rodrigues, 2001

Hidrophiidae	<i>Pseudechis porphyriacus</i>	Bufonidae	<i>Chaunus marinus</i>	Fearn, 2003
Viperidae	<i>Agkistrodon piscivorus</i>	Ranidae	<i>Lithobates clamitans</i>	Cross, 2002
	<i>Agkistrodon piscivorus</i>	Ranidae	<i>Lithobates sphenoccephala</i>	Cross, 2002
	<i>Bothrops ammodytoides</i>	Cycloramphidae	<i>Odontophrynus occidentalis</i>	Avila & Morando, 1998
	<i>Bothrops asper</i>	Brachycephalidae	<i>Eleutherodactylus</i> sp.	Greene, 1997
	<i>Bothrops atrox</i>	Leptodactylidae	<i>Leptodactylus fuscus</i>	Macedo-Bernarde & Bernarde, 2005
	<i>Bothrops jararaca</i>	Cycloramphidae	<i>Cycloramphus boraceiensis</i>	Giaretta & Nunes, 1997
	<i>Porthidium nasutum</i>	Brachycephalidae	<i>Eleutherodactylus</i> sp.	Greene, 1997
	<i>Porthidium nasutum</i>	Ranidae	<i>Lithobates warszewitschii</i>	Warner & Kolbe, 2003
Testudines				
Kinosternidae	<i>Kinosternon sonoriense</i>	Bufonidae	<i>Anaxyrus punctatus</i>	Ligon & Stone, 2003
Testudinidae	<i>Gopherus polyphemus</i>	Ranidae	<i>Lithobates sevoxa</i>	Braid <i>et al.</i> , 2000
Aves				
Accipitridae	<i>Haliaeetus leucocephalus</i>	Ranidae	<i>Lithobates catesbeianus</i>	Applegate, 1990
	<i>Haliaeetus leucocephalus</i>	Ranidae	<i>Lithobates palustris</i>	Applegate, 1990
Anatidae	<i>Buteo jamaicensis</i>	Bufonidae	<i>Anaxyrus boreas</i>	Jones & Stiles, 2000
	<i>Buteo magnirostris</i>	Leptodactylidae	<i>Leptodactylus ocellatus</i>	Souza <i>et al.</i> , 2003
	<i>Anas platyrhynchos</i>	Ranidae	<i>Rana aurora</i>	Hayes & Rombough, 2004
	<i>Anas platyrhynchos</i>	Ranidae	<i>Rana boylei</i>	Bombough <i>et al.</i> , 2005
	<i>Anas platyrhynchos</i>	Ranidae	<i>Rana temporaria</i>	Bombough <i>et al.</i> , 2005
	<i>Anas platyrhynchos</i>	Ranidae	<i>Lithobates sylvaticus</i>	Bombough <i>et al.</i> , 2005
	<i>Oxyura ferruginea</i>	Ceratophryidae	<i>Atelognathus patagonicus</i>	Cuello <i>et al.</i> , 2005
Ardeidae	<i>Ardea herodias</i>	Pipidae	<i>Xenopus laevis</i>	Crayon & Hothem, 1998
	<i>Ardea herodias</i>	Ranidae	<i>Rana aurora</i>	Fellers & Wood, 2004
	<i>Nycticorax nycticorax</i>	Pipidae	<i>Xenopus laevis</i>	Crayon & Hothem, 1998
	<i>Tigrisoma lineatum</i>	Hylidae	<i>Pseudis paradoxa</i>	Prado, 2003
	<i>Tigrisoma lineatum</i>	Leptodactylidae	<i>Leptodactylus chaquensis</i>	Prado, 2003
Corvidae	<i>Corvus macrorhynchos</i>	Bufonidae	<i>Bufo parietalis</i>	Krishna & Vijayalaxmi, 2004
Cracidae	<i>Penelope superciliosus</i>	Brachycephalidae	<i>Brachycephalus ephippium</i>	Carvalho, 1941
Cuculidae	<i>Guirra guirra</i>	Leptodactylidae	<i>Physalaemus cf. fuscumaculatus</i>	Kokubum & Zacca, 2003
	<i>Piaya cayana</i>	Hylidae	<i>Osteocephalus taurinus</i>	Cintra & Sanaïotti, 1990
Falconidae	<i>Polyborus plancus</i>	Hylidae	<i>Bokermannohyla alvarengai</i>	Machado & Galdino, 2005
Icteridae	<i>Quiscalus quiscula</i>	Scaphiopodidae	<i>Scaphiopus holbrookii</i>	Palis, 2000
Laridae	<i>Larus delawarensis</i>	Bufonidae	<i>Anaxyrus fowleri</i>	Smith & Green, 2005

	<i>Larus maculipennis</i>	Ceratophryidae	<i>Atelognathus patagonicus</i>	Cuello <i>et al.</i> , 2005
Momotidae	<i>Barythengus martii</i>	Dendrobatidae	<i>Dendrobates auratus</i>	Master, 1998
Odontophoridae	<i>Colinus virginianus</i>	Scaphiropodidae	<i>Scaphiopus hurterii</i>	McCoid <i>et al.</i> , 1999
Phalacrocoracidae	<i>Phalacrocorax carbo</i>	Pipidae	<i>Xenopus laevis</i>	Kopij, 1998
Podicipedidae	<i>Phalacrocorax carbo</i>	Pyxicephalidae	<i>Amietia angolensis</i>	Kopij, 1998
	<i>Podiceps occipitalis</i>	Ceratophryidae	<i>Atelognathus patagonicus</i>	Cuello <i>et al.</i> , 2005
	<i>Podiceps rolland</i>	Ceratophryidae	<i>Atelognathus patagonicus</i>	Cuello <i>et al.</i> , 2005
Sturnidae	<i>Sturnus vulgaris</i>	Scaphiropodidae	<i>Scaphiopus holbrookii</i>	Palis, 2000
Threskiornithidae	<i>Theristicus caudatus</i>	Bufonidae	<i>Chaunus granulatus</i>	Carvalho, 1941
	<i>Theristicus caudatus</i>	Microhylidae	<i>Elachistocleis cf. ovalis</i>	Carvalho, 1941
Tinamidae	<i>Tinamus solitarius</i>	Brachycephalidae	<i>Brachycephalus ephippium</i>	Carvalho, 1941
Trogonidae	<i>Trogon surrucura</i>	Hylidae	<i>Hypisiboas albomarginatus</i>	Toledo <i>et al.</i> , 2005
	<i>Trogon surrucura</i>	Hylidae	<i>Hypsiboas bischoffi</i>	Toledo <i>et al.</i> , 2005
	<i>Trogon surrucura</i>	Hylidae	<i>Phyllomedusa distincta</i>	Toledo <i>et al.</i> , 2005
Tyranidae	<i>Pitangus sulphuratus</i>	Hylidae	<i>Scinax nasicus</i>	Toledo <i>et al.</i> , 2005
Tytonidae	<i>Tyto alba</i>	Leptodactylidae	<i>Eupemphix nattereri</i>	Toledo <i>et al.</i> , 2005; Ávila, 2005
	<i>Tyto alba</i>	Ranidae	<i>Lithobates sphenoccephalus</i>	C. F. B. Haddad, unpubl. data
				Briggler, 2000
Mammalia				
Carnivora				
Canidae	<i>Cerdocyon thous</i>	Leptodactylidae	<i>Eupemphix nattereri</i>	Bezerra, 1998
	<i>Chrysocyon brachyurus</i>	Bufonidae	<i>Chaunus ictericus</i>	Guix, 1993
	<i>Chrysocyon brachyurus</i>	Leptodactylidae	<i>Leptodactylus labyrinthicus</i>	Prado <i>et al.</i> , 2005
	<i>Vulpes vulpes</i>	Bufonidae	<i>Anaxyrus boreas</i>	Jones <i>et al.</i> , 1999
Mustelidae	<i>Galictis vittata</i>	Bufonidae	<i>Chaunus marinus</i>	Cintra, 1988
	<i>Lontra canadensis</i>	Ranidae	<i>Rana pretiosa</i>	Hayes <i>et al.</i> , 2005
	<i>Lutra longicaudis</i>	Leptodactylidae	<i>Leptodactylus pentadactylus</i>	Roberts, 1997A
	<i>Lutra longicaudis</i>	Ranidae	<i>Rana pretiosa</i>	Roberts, 1997B
	<i>Mustela putorius</i>	Bufonidae	<i>Bufo bufo</i>	Lodé, 1996
	<i>Mustela putorius</i>	Ranidae	<i>Rana dalmatina</i>	Lodé, 1996
	<i>Mustela putorius</i>	Ranidae	<i>Pelophylax esculentus</i>	Lodé, 1996
	<i>Mustela vison</i>	Ranidae	<i>Lithobates palustris</i>	Beane, 1990
Procyonidae	<i>Procyon lotor</i>	Bufonidae	<i>Anaxyrus boreas</i>	Jones <i>et al.</i> , 1999
	<i>Procyon cancrivorus</i>	Bufonidae	<i>Chaunus ictericus</i>	Guix, 1993
Chiroptera				

Phyllostomatidae	<i>Trachops cirrhosus</i>	Leptodactylidae	<i>Engystomops pustulosus</i>	Tuttle <i>et al.</i> , 1982
Insectivora				
Erinaceidae	<i>Atelerix pruneri</i>	Bufo	<i>Bufo alvarius</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Anaxyrus americanus</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Anaxyrus boreas</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Chaunus marinus</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Anaxyrus quercicus</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Amietophrynus regularis</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Anaxyrus terrestris</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Bufo	<i>Anaxyrus woodhousii</i>	Brodie Jr., 1977
	<i>Atelerix pruneri</i>	Rana	<i>Lithobates catesbeianus</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Bufo alvarius</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Anaxyrus americanus</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Anaxyrus boreas</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Chaunus marinus</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Anaxyrus quercicus</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Amietophrynus regularis</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Anaxyrus terrestris</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Bufo	<i>Anaxyrus woodhousii</i>	Brodie Jr., 1977
	<i>Hemiechinus auritus</i>	Rana	<i>Lithobates catesbeianus</i>	Brodie Jr., 1977
Soricidae	<i>Blarina brevicauda</i>	Hyla	<i>Hyla versicolor</i>	Brodie Jr. & Formanowicz Jr., 1981
Marsupialia				
Didelphidae	<i>Didelphis marsupialis</i>	Bufo	<i>Chaunus marinus</i>	Garrett & Boyer, 1993
	<i>Philander opossum</i>	Hyla	<i>Hypsiboas rosenbergi</i>	Kluge, 1981
Primates				
Callitrichidae	<i>Callithrix penicillata</i>	Hyla	<i>Hypsiboas lundii</i>	Canale & Lingnau, 2003
Rodentia				
Muridae	<i>Rattus rattus</i>	Leopelmatidae	<i>Leiopelma archeyi</i>	Thurley & Bell, 1994

CAPÍTULO 4

QUANDO OS SAPOS GRITAM! UMA REVISÃO DAS VOCALIZAÇÕES DEFENSIVAS DOS ANUROS

Luís Felipe Toledo & Célio F. B. Haddad



Jean-Luc Perret, 1961

CAPÍTULO 4

WHEN FROGS SCREAM! A REVIEW OF ANURAN DEFENSIVE VOCALIZATIONS

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ABSTRACT

The most common defensive vocalization in anurans is the distress call. Additionally, two other types of defensive vocalizations (alarm and warning calls) have been recognized and several species have been reported to behave defensively when using them. Our knowledge about these acoustic features is fragmented and relies on scattered information available generally from short notes in the literature. We, therefore, reviewed the subject, added new data, and included a phylogenetic approach. We described the defensive calls of 31 anuran species and made correlations between anuran size and the physical structure of their calls (sound pressure level, dominant frequency, and call duration). We also grouped data from the literature and from unrecorded individuals on 77 anuran species that are known to emit defensive calls, in 15 families widespread throughout the Anura clade. Defensive calls are most likely an ancestral character in anurans and a positive relationship may exist between the physical characteristics of distress calls and chances of avoiding predation. This review strengthens our knowledge about defensive vocalizations in anurans and will hopefully instigate new challenges for future research.

Key words: Vocalization; Distress call; Warning call; Alarm call; Defensive behavior; Anurans

INTRODUCTION

Among several facets of the social behavior of anurans, their calling abilities attain a great interest among scientists. The most common vocalization is the advertisement call, emitted by males, mainly to attract reproductive females and to maintain the spatial distribution among neighboring males in a chorus (Duellman & Trueb, 1994). However, anurans have a wide acoustic repertoire; some species are known to emit several types of vocalizations, such as territorial calls, fighting calls, or courtship calls (Duellman & Trueb, 1994). Besides these, we are able to recognize other defensive vocalizations, the most frequent of which is the distress call, which is emitted not only by males, but even by females and juveniles (Bogert, 1960; Sazima, 1975; Toledo *et al.*, 2005). This type of call, probably described for the first time at the end of the 19th century (Boulenger, 1897), is characterized by a high pitched whistle, generally emitted with the mouth open (see exceptions in Hoff & Moss, 1974; Webber, 1978), a conspicuous difference that readily distinguishes this from other non-defensive vocalizations (e.g., Hödl & Gollmann, 1986; Duellman & Trueb, 1994).

Several functions have been hypothesized for defensive vocalizations, of which the most common and accepted one is to repel predators when the frogs are being subdued (e.g., Sazima, 1975). Additionally, some other functions have been suggested, in some cases depending on the context of the emission (e.g., Leary & Razafindratsita, 1998). Consequently, several other types of calls have been designated, such as the warning call or alarm call. However, the function and effectiveness of defensive vocalizations are debated issues and several discussions have been triggered on the subject (e.g., Staton, 1978; Högstedt, 1983; Gorzula, 1985; Hödl & Gollmann, 1986; Leary & Razafindratsita, 1998). For example, if the defensive vocalizations of different species are similar, could a distress call from one individual be recognized and interpreted by another individual from the same or different species (e.g., Yerks, 1903; Smith, 1977; Leary & Razafindratsita, 1998)? These discussions have remained stagnated due to lack of information about this defensive behavior. Hence, for a better understanding of this subject, we present new data, review the subject, and include a phylogenetic approach in the analysis of anuran defensive vocalizations.

MATERIAL AND METHODS

The major available herpetological journals (e.g., *Amphibia-Reptilia*, *Copeia*, *Herpetologica*, *Herpetological Bulletin*, *Herpetological Journal*, *Herpetological Review*, and *Journal of Herpetology*) were analyzed and reports on defensive vocalizations were compiled. Both natural and experimental conditions were considered.

Additional vocalizations were obtained by human handling in the laboratory or in the field, from several localities in Brazil (FIG. 1). Human handling stimuli was performed in three forms: I) by unexpectedly grasping the frog by its hind limbs while it was resting or emitting advertisement calls in the field; II) by shaking the frog by its hind limbs, eventually piercing its leg with the researcher's fingernails (making sure not to harm the individual); or III) by letting the frog escape from the researcher and then grasping its hind legs firmly from time to time. If the animal did not emit a defensive vocalization, it was released or the handling sequences were repeated one or two days later (in the case of collected animals). All handled animals were measured (snout-vent length: SVL) with a caliper to the nearest 0.01 mm.

We recorded vocalizations with a Marantz cassette tape recorder (PMD222), equipped with an external directional microphone (Audiotecnica AT835b) positioned approximately 50 cm from the frog. Vocalizations were recorded on chrome cassette tapes at 4.75 cm/s. We analyzed the calls using Raven 1.2.1 software at 16 bits of resolution, 44 kHz of frequency sampling, FFT and frame length of 256 samples. The terminology used in the descriptions is presented in Toledo & Haddad (2005). Composed series of distress calls were considered when more than one call was emitted in an interval shorter than one second.



FIG. 1.—The 13 Brazilian states (Paraíba, Alagoas, Sergipe, Bahia, Espírito Santo, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul, Minas Gerais, Mato Grosso do Sul, Goiás, and Acre) where anurans have been tested for the emission of defensive vocalizations.

RESULTS

Reports of 72 species, in 15 families, were revised from the literature (Appendix A: Anurans reported to emit distress calls). Besides this, 850 individuals from 111 anuran species, in 13 families, were tested for the emission of defensive vocalizations (Appendix B: Anurans tested for the emission of distress calls). Among these, defensive vocalizations were emitted by 86 individuals of 33 species from Brazil and one from

Panama (TABLE 1). Most of the individuals that emitted defensive calls had SVL between 31 and 60 mm (FIG. 2). Distress calls of *Hypsiboas albopunctatus* and *Leptodactylus chaquensis* were not recorded.

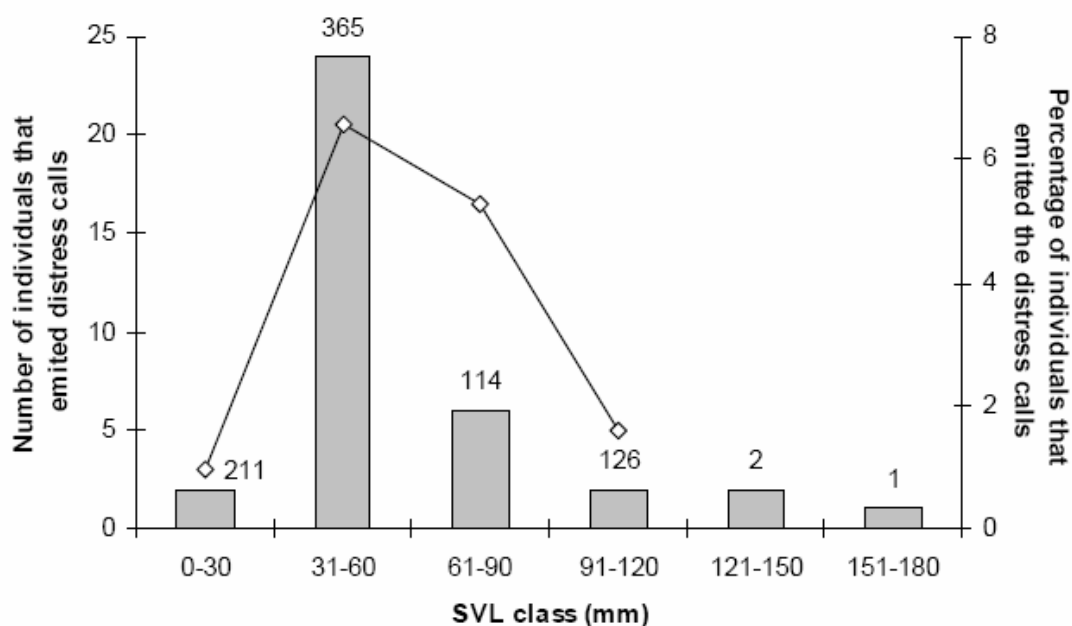


FIG. 2.—Number of individuals that emitted defensive calls per size class (bars and left axis) and percentage of defensive calls emitted per size class (line and right axis); the line is not presented in the last two size classes, because all individuals tested emitted defensive calls (i.e., 100 %). The number above the bars represents the number of individuals tested in each size class.

Descriptions

The major characteristics of the vocalizations are shown in TABLE 1. When a specific vocalization was very different from another (in the same species, sex, and age) it was placed on a new row in the table. We observed that all individuals and species (with the exception of two females of *Leptodactylus mystaceus*, which could not be observed) emitted the distress or warning calls with their mouth open (FIG. 3). Brief descriptions and any other special characteristics or remarks are presented below. Almost all calls presented repeated ascending and decreasing modulations.

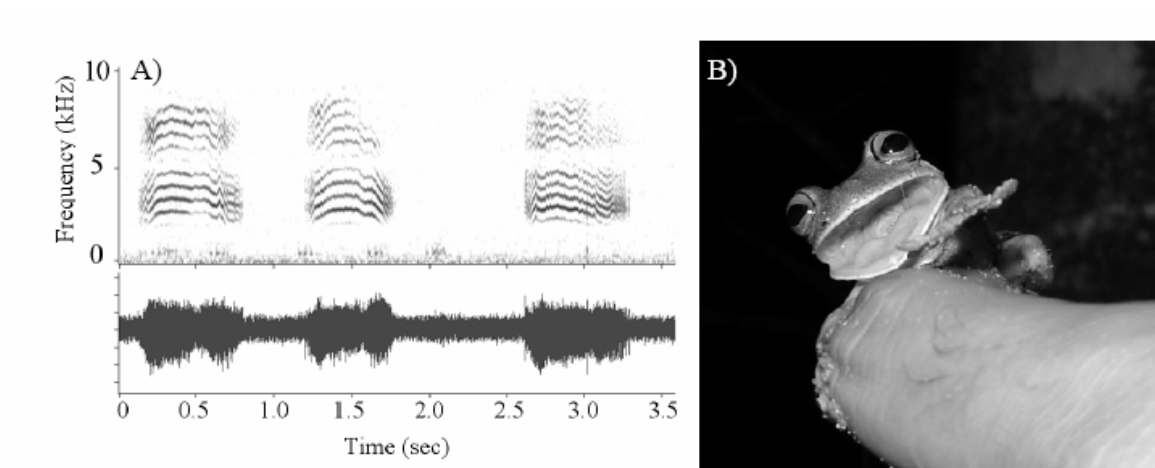


FIG. 3.—A) Spectrogram (above) and waveform (below) of a series of three distress calls of the endangered *Bokermannohyla izecksohni* and B) the adult male during handling and the emission of distress calls.

Brachycephalidae

Eleutherodactylus binotatus

Out of 11 individuals handled (8 males and 3 females), only four (1 male and 3 females) emitted distress calls. Only one male (SVL = 45 mm) was recorded. The distress calls of this species are very high-pitched; the minimum frequency is about 5 kHz and the maximum could not be determined at this moment as there are ultra-sound components in this call and the conventional equipment does not allow us to record frequencies above 22 kHz. The call is descending modulated and presents, at least, three harmonics. The first (N = 7) varies in mean between 5.17 ± 0.44 kHz (range: 4.65 – 5.73) and 10.54 ± 1.08 kHz (range: 9.1 – 11.79); the second (N = 7) varies between 12.48 ± 0.79 kHz (range: 11.39 – 13.88) and 19.09 ± 1.20 kHz (range: 16.98 – 20.0 or more not registered due to software limitations); the third (N = 1) varies between 15.9 kHz and 17.52 kHz (TABLE 1; FIG. 4).

Ceratophryidae

Ceratophrys joazeirensis

Two individuals of *Ceratophrys joazeirensis*, one male (SVL = 81 mm) and one female (SVL = 104 mm) were recorded. These individuals emitted warning calls when we approached them, and distress calls when handled. Although there is a difference in

the circumstances, there is no physical difference between the two types of calls. These calls can be divided into two parts. In the first it is possible to recognize harmonics between about 0.3 kHz and 15 kHz. Above 15 kHz weak harmonics can be observed. The second part of the call does not present harmonic structure (TABLE 1; FIG. 4).

Cycloramphidae

Cycloramphus sp. (aff. *bolitoglossus*)

Two females of *Cycloramphus* sp. (aff. *bolitoglossus*) (SVL = 29.38 and 31.50 mm) were recorded in laboratory conditions. The distress calls of these individuals were short in duration (less than 0.32 seconds), high-pitched (sometimes exceeding 20 kHz) and can be divided into two parts; the first being differentiated from the second by having well defined harmonics and higher amplitude of frequencies (TABLE 1; FIG. 4).

Hylidae

Aplastodiscus albosignatus

The distress call of one female *A. albosignatus* (SVL = 47.9 mm) was recorded. It is quite long (exceeding 1.5 seconds of duration), high-pitched (reaching almost 20 kHz), and is entirely formed by harmonic structure (TABLE 1; FIG. 4).

Aplastodiscus arildae

One adult male *A. arildae* (SVL = 39.19 mm) emitted three distress calls that were recorded. The call of this species is short (about 0.4 seconds of duration) and is entirely formed by harmonic structure (TABLE 1; FIG. 4).

Aplastodiscus cochranæ

One adult male of *A. cochranæ* (SVL = 43.5 mm) was recorded. The distress calls were analyzed only in the most intense portion of the calls (between ca. 3 and 10 kHz), because, although they have bands below and above these frequencies, they are too weak and are probably side bands (TABLE 1; FIG. 4).

Aplastodiscus leucopygius

The distress calls of this species were recorded from two males (SVL = 41.5 and 42.3 mm). It is a short call in duration, generally less than 0.5 seconds long that can reach up to ca. 11 kHz, and has about 11 harmonic bands (TABLE 1; FIG. 5).

Aplastodiscus perviridis

The distress calls of this species have a harmonic structure, both in the calls recorded from a male and from a female (mean SVL = 39.9 and 41.0 mm). However, the harmonic bands of the female recording were hard to distinguish and, therefore, not analyzed. In the recording of the male it was possible to identify up to 23 harmonic bands (TABLE 1; FIG. 5).

Bokermannohyla circumdata

Three females of *B. circumdata* (mean SVL = 66.5 mm) were recorded in the field after handling. Their distress calls presented harmonic bands and were not too high-pitched, reaching about 12 kHz in maximum frequencies. In one of the recordings, it was possible to observe weak bands over these maximum frequencies; however they were not analyzed, as this could be an artifact resulting from recording saturation (TABLE 1; FIG. 5).

Bokermannohyla hylax

The distress calls of one male (SVL = 58.2 mm) were recorded in the field after handling. They presented harmonic bands and were not too high-pitched, reaching about 13 kHz in maximum frequencies. Bands can be observed above the eighth harmonics, but these were not analyzed as they were too weak and could represent side bands (TABLE 1; FIG. 5).

Bokermannohyla izecksohni

Seven distress calls of one male (SVL = 45 mm) were emitted in an interval of 12.5 seconds and were recorded in the field after handling. The vocalizations had from 10 to 12 harmonic bands, ranging from about 1.8 to 8.5 kHz (TABLE 1; FIG. 3).

Bokermannohyla luctuosa

The distress calls of one male (SVL = 49 mm) were recorded in the field after handling. The vocalizations presented a high number of harmonic bands (from 23 to 31) and reached about 18 kHz in maximum frequencies. Above about 11 kHz the harmonic bands lose energy but were still clear enough to be analyzed (TABLE 1; FIG. 5).

Dendropsophus minutus

Only one distress call from one adult female (SVL = 25.3 mm) was recorded. This call was very short (0.18 seconds of duration), presented six harmonic bands, and was high-pitched, reaching more than 16 kHz (TABLE 1; FIG. 5).

Hypsiboas albomarginatus

Recordings of distress calls of two males (SVL = 47.4 and 47.8 mm) were made in the field after handling. The initial and terminal portions of some of the calls seem to have harmonics, but they were not analyzed because they were hard to distinguish. The call is modulated with the highest frequencies in the central portion. There are no harmonic bands in this portion. Some of the distress calls are pulsed. The energy is concentrated mostly in the lower frequencies (TABLE 1; FIG. 6).

Hypsiboas bischoffi

Seven distress calls of one female (SVL = 37.14 mm) were recorded in the field after handling. The vocalizations were short (about 0.3 seconds in duration), presented harmonics (from 5 to 10), and were not too high-pitched, reaching up to about 13 kHz (TABLE 1; FIG. 6). An exceptional case involving this species was observed in the field. After we suddenly seized an adult male, which was emitting advertisement calls, he emitted a distress call. After that, all other calling males of the chorus stopped calling immediately. They remained in silence for about 2 minutes before starting to emit advertisement calls again.

Hypsiboas caingua

One male (SVL = 32.5 mm) of this species (found in the municipality of Pilar do Sul, state of São Paulo, Brazil) had two distress calls recorded. These calls seem to

present harmonics; however, they are difficult to distinguish and, therefore, not analyzed. Their calls had a mean duration of 0.55 seconds, were not too high-pitched, and reached about 10 kHz (TABLE 1; FIG. 7).

Hypsiboas faber

Several individuals of *H. faber* that were handled emitted distress calls, including juveniles, adult males and females. Some individuals emitted a group of these calls in a series, where, generally, the first call was the strongest and the longest. The longest calls were usually modulated with more than one peak of high frequencies. The number of harmonic bands varied from 9 to 25 and the maximum frequencies could reach more than 20 kHz (TABLE 1; FIG. 6).

Hypsiboas latistriatus

Only one adult female (SVL = 46.47 mm) was tested and emitted 11 distress calls that were recorded. The calls presented side bands (from 16 to 35) and were high-pitched, reaching more than 21 kHz (TABLE 1; FIG. 6).

Hypsiboas lundii

Both adult males and females, and a juvenile of *H. lundii* emitted distress calls. The recorded calls of one juvenile and one female presented harmonic bands and were pulsed. The recordings of the call of one male seemed to be saturated, showing visible harmonic bands (most of them in the central portion of the calls) (TABLE 1; FIG. 6).

Hypsiboas pardalis

Four adult males of *H. pardalis* (mean SVL = 60.2 mm) had their distress calls recorded in the field after handling. Their calls were short (0.35 seconds in mean duration), presented harmonics generally in the initial part of the call (from 17 to 24), and were not too high-pitched, reaching about 11 kHz in the maximum frequencies. The weak bands observed above about 11 kHz were not analyzed, because they are probably side bands. Some of the calls were pulsed, mainly in their final portion (TABLE 1; FIG. 6).

Hypsiboas raniceps

The distress calls of this species are short (about 0.35 seconds in duration), high-pitched, reaching more than 20 kHz, and can be divided into two parts: the initial, with mean maximum frequencies of 3.14 ± 0.17 kHz (range: 3.02 – 3.57 kHz) and mean duration of 178 ± 50.4 ms (range: 129 – 266 ms; $n = 9$ calls of one male and one female for both measurements); the final part of the call has mean maximum frequencies of 18.38 ± 0.96 kHz (range: 17.21 – 20.11 kHz) and mean duration of 187 ± 39.9 ms (range: 116 – 247 ms; $n = 9$ calls of one male and one female for both measurements) (TABLE 1; FIG. 7).

Pseudis cardosoi

Three distress calls of one adult male *P. cardosoi* (SVL = 48 mm) were recorded. These calls were short in duration (about 0.4 seconds), presented a large number of harmonic bands (from 24 to 28), and reached high frequencies (up to about 19 kHz) (TABLE 1; FIG. 7).

Pseudis paradoxa

Nineteen distress calls of three adult males of *P. paradoxa* were recorded (mean SVL = 45 mm). These calls were short in duration (about 0.4 seconds), presented a high number of harmonic bands (up to 23 harmonics), and did not reach very high frequencies (mean of 13.68 kHz) (TABLE 1; FIG. 7).

Leptodactylidae

Leptodactylus fuscus

One handled male (SVL = 40 mm) emitted five distress calls. They were short in duration (mean duration about 0.4 seconds), high pitched (about 17 kHz in the maximum frequencies), and had on average 18 harmonic bands (TABLE 1; FIG. 7).

Leptodactylus mystaceus

Two adult females (mean SVL of 46 mm) emitted distress calls and were recorded. These individuals only emitted the calls when running away from the

researcher (in both cases), or when running from a mouse that have been trapped in the same pitfall trap (in one case). In these two situations the individuals were in a plastic bucket. By usual handling none of these females and neither of the two tested males (also placed in a plastic bucket; see Appendix B) emitted distress calls. The distress calls were emitted isolated or in groups of two to seven similar calls. In the case of multiple calls, the mean interval between calls was 0.11 ± 0.06 ms (range: 0 – 0.25 ms) and the mean rate of emission was 0.30 ± 0.03 calls/second (range: 0.25 – 0.35; n = 8 series and 32 calls). The vocalizations were short in duration (about 0.2 seconds), could reach high frequencies (over 20 kHz), and presented from 6 to 12 harmonics (TABLE 1; FIG. 7).

Leptodactylus mystacinus

One adult male (SVL = 54.2 mm) emitted 10 distress calls when handled. These calls presented a low number of harmonics (from seven to nine), did not reach very high frequencies (less than 14 kHz), and were very short in duration (about 0.3 seconds) (TABLE 1; FIG. 8).

Leptodactylus pentadactylus

One adult female (SVL = 150 mm) emitted a series of 57 distress calls when handled in the field. Only seven out of these 57 calls were emitted isolated. The remaining were emitted in groups of 2 to 11 consecutive similar calls, interspaced by 0.16 ± 0.06 seconds on average (range: 0.03 – 0.25; n = 13) and with a mean rate of emission of 0.54 ± 0.11 calls/second (range: 0.43 – 0.75; n = 6 series and 28 calls). Seventeen out of 57 calls were analyzed. The calls were short in duration (0.4 seconds on average), low pitched (reaching less than 8 kHz), ascendant and descendant (successively) modulated, and presented an intermediate number of harmonic bands (from 6 to 14) (TABLE 1; FIG. 8).

Leptodactylus savagei

Twenty nine distress calls of an adult male *L. savagei* (SVL = 160 mm) were recorded in the field. These were emitted in eight groups from 3 to 5 short duration (about 0.35 seconds) calls. The mean interval between calls was 0.24 ± 0.04 seconds

(range: 0.17 – 0.34; n = 22) and the mean rate of emission was 0.52 ± 0.05 calls/second (range: 0.45 – 0.57; n = 7 series and 29 calls). However, the interval between calls inside the same group of calls was variable; the intervals gradually increased as more calls were added in the series (see TABLE 2). The calls were high pitched (reaching more than 20 kHz) and had a large number of harmonic bands (from 26 to 37) (TABLE 1; FIG. 8).

Table 2. Interval between calls (in milliseconds) in the grouped distress calls of *Leptodactylus savagei*. The asterisk “*” shows the only case where the second interval between notes is shorter than the first. In all other cases, the interval between notes increases successively.

Call intervals	Distress call groups							
	1	2	3	4	5	6	7	8
1	0.172	0.182	0.186	0.249	0.235	0.261	0.283	0.172
2	0.216	0.195	0.194	0.339	0.286	0.246*	0.293	0.216
3	0.238	0.199	0.208		0.312	0.272		0.238
4	0.247	0.239	0.244					0.247

Leptodactylus troglodytes

Two males (mean SVL = 44 mm) had their distress calls recorded in the field. The composed series had from 3 to 30 short duration (about 0.36 seconds) distress calls. The mean rate of emission in the series was 1.63 ± 0.11 calls/second (range: 1.56 – 1.64; n = 2 series and 51 calls). The calls were high pitched (reaching up to 18.3 kHz) and presented an intermediate number of harmonic bands (from 8 to 20) (TABLE 1; FIG. 8).

Leptodactylus vastus

One adult female (SVL = 140 mm) was recorded. The calls could be emitted isolated or in composed series containing 2 or 3 short duration (about 0.75 seconds) calls. The mean rate of emission was 0.99 ± 0.15 calls/second (range: 0.80 – 1.17; n = 5 series and 12 calls). These calls had 12 to 26 harmonic bands reaching less than 10 kHz (TABLE 1; FIG. 8).

Ranidae

Lithobates catesbeianus

Six out of 21 males of *Lithobates catesbeianus* kept in captivity emitted distress calls when handled. It was possible to recognize four types of calls (A, B, AB, and BA), composed by the combination of two different notes (A and B). These notes are different mostly in their duration (A being shorter than B), frequency amplitude (A having higher frequencies than B), and in number of harmonic bands (A having more than B). However, they are similar in the minimum (from 0.07 to 0.40 kHz) and dominant (from 2.12 to 3.50 kHz) frequencies. This call was the longest recorded in the present study, lasting more than seven seconds (TABLE 1; FIG. 8).

Table 1. Major characteristics of the distress calls of Neotropical anurans tested in the present study. Values presented as mean \pm standard deviation (range). SVL and temperature of the air are presented as a mean of the measured individuals and different days.

Species (N individuals / N calls)	SVL (mm)	Duration (sec)	Frequency (kHz)		Dominant	Harmonics		Temperature of the air (°C)
			Minimum	Maximum		N	Dominant	
Brachycephalidae								
<i>Eleutherodactylus bimotatus</i> (1 male / 7 calls)	45	0.58 \pm 0.16 (0.35 – 0.84)	5.22 \pm 0.45 (4.65 – 5.73)	> 22 (ultrasound)	7.80 \pm 0.53 (6.95 – 8.53)	2.14 \pm 0.37 (2 – 3)	1	17
Ceratophryidae								
<i>Ceratophrys jouzeirensis</i> (1 male / 10 calls)	81	2.49 \pm 0.90 (1.11 – 4.42)	0.30 \pm 0.13 (49.2 – 487)	13.29 \pm 2.34 (10.58 – 15.47)	2.90 \pm 0.48 (1.77 – 3.45)	25.25 \pm 4.84 (18 – 33)	5 – 7	25
<i>Ceratophrys jouzeirensis</i> (1 female / 2 calls)	104	1.88 – 3.16	0.26 – 0.30	14.53 – 17.48	1.98 – 2.15	24	4	25
Cycloramphidae								
<i>Cycloramphus</i> sp. (aff. <i>bolitoglossus</i>) (1 female / 4 calls)	29	0.28 \pm 0.03 (0.25 – 0.32)	0.42 \pm 0.28 (0.28 – 0.84)	20.61 \pm 0.29 (20.19 – 20.84)	1.51 \pm 0.27 (1.21 – 1.81)	10.67 \pm 0.58 (10 – 11)	1-2	24
<i>Cycloramphus</i> sp. (aff. <i>bolitoglossus</i>) (1 female / 2 calls)	31	0.18 – 0.20	1.04 – 1.14	19.67 – 20.91	11.28 – 13.78	11 – 12	7	24
Hylidae								
<i>Aplastodiscus albosignatus</i> (1 female / 3 calls)	47.9	1.11 \pm 0.63 (0.67 – 1.84)	0.61 \pm 0.11 (0.52 – 0.72)	18.15 \pm 1.04 (17.51 – 19.36)	6.43 \pm 0.69 (5.77 – 7.49)	16 \pm 1 (15 – 17)	5 – 6	18
<i>Aplastodiscus arildae</i> (1 male / 8 calls)	39.19	0.40 \pm 0.09 (0.29 – 0.53)	0.97 \pm 0.15 (0.81 – 1.28)	13.61 \pm 5.03 (8.46 – 19.68)	5.59 \pm 2.43 (1.46 – 7.72)	16.62 \pm 6.23 (10 – 24)	1 – 9	20
<i>Aplastodiscus cochranee</i> (1 male / 8 calls)	43.5	1.52 \pm 0.37 (1.09 – 2.17)	2.84 \pm 0.28 (2.66 – 3.48)	8.88 \pm 1.18 (7.96 – 11.61)	6.19 \pm 0.39 (5.60 – 6.55)	15.38 \pm 4.14 (11 – 22)	6 – 14	22

<i>Aplastodiscus leucopygius</i> (2 males / 17 calls)	41.09	0.44 ± 0.17 (0.21 – 0.86)	0.55 ± 0.09 (0.36 – 0.72)	9.07 ± 0.63 (7.87 – 10.64)	6.00 ± 0.68 (4.82 – 6.89)	11.18 ± 1.70 (9 – 16)	6 – 9	20
<i>Aplastodiscus perviridis</i> (1 male / 3 calls)	37.74	0.70 ± 0.23 (0.44 – 0.86)	0.21 ± 0.10 (0.10 – 0.31)	19.14 ± 0.72 (18.46 – 19.90)	4.22 ± 1.06 (3.45 – 5.43)	20.00 ± 2.65 (18 – 23)	4 – 6	–
<i>Aplastodiscus perviridis</i> (1 female / 4 calls)	43	0.76 ± 0.55 (0.34 – 1.55)	0.44 ± 0.28 (0.10 – 0.72)	20.04 ± 0.46 (19.58 – 20.61)	7.02 ± 1.80 (4.65 – 8.70)	–	–	–
<i>Bokermannohyla circumdata</i> (3 females / 17 calls)	66.5	0.94 ± 0.32 (0.44 – 1.40)	0.53 ± 0.11 (0.31 – 0.80)	9.70 ± 0.98 (8.78 – 12.45)	3.97 ± 1.22 (1.38 – 5.43)	13.71 ± 2.42 (10 – 18)	3 – 8	20
<i>Bokermannohyla hylax</i> (1 male / 10 calls)	58.2	1.17 ± 0.30 (0.71 – 1.64)	0.77 ± 0.18 (0.62 – 1.19)	12.52 ± 0.52 (11.66 – 13.23)	3.17 ± 0.99 (1.81 – 4.48)	20.56 ± 3.13 (15 – 24)	2 – 7	21
<i>Bokermannohyla izecksohni</i> (1 male / 7 calls)	45	0.79 ± 0.26 (0.55 – 1.28)	1.87 ± 0.11 (1.70 – 2.01)	8.59 ± 0.30 (8.24 – 9.07)	3.75 ± 1.61 (2.76 – 7.06)	10.86 ± 0.90 (10 – 12)	2 – 3	22
<i>Bokermannohyla luctuosa</i> (1 male / 8 calls)	49	1.01 ± 0.22 (0.82 – 1.36)	0.46 ± 0.15 (0.21 – 0.62)	17.57 ± 0.31 (17.00 – 18.03)	3.35 ± 0.31 (3.10 – 3.96)	26.50 ± 3.07 (23 – 31)	5 – 6	23.5
<i>Dendropsophus minutus</i> (1 female / 1 calls)	25.3	0.18	1.62	16.66	5.59	6	2	20
<i>Hypsiboas albomarginatus</i> (2 males / 19 calls)	47.6	0.39 ± 0.17 (0.22 – 0.75)	0.29 ± 0.09 (0.17 – 0.41)	15.43 ± 2.28 (8.42 – 18.27)	3.54 ± 2.05 (1.38 – 6.37)	–	–	–
<i>Hypsiboas bischoffi</i> (1 female / 7 calls)	37.14	0.29 ± 0.06 (0.21 – 0.37)	0.88 ± 0.48 (0.41 – 1.54)	10.96 ± 1.35 (9.13 – 13.13)	5.13 ± 2.33 (1.98 – 7.49)	8 ± 2.65 (5 – 10)	2 – 7	21
<i>Hypsiboas caingua</i> (1 male / 2 calls)	32.5	0.43 – 0.67	0.07 – 0.22	10.10 – 10.76	7.41 – 7.49	–	–	17

<i>Hypsiboas faber</i> (4 males / 29 calls)	92.6	0.70 ± 0.20 (0.44 – 1.23)	0.40 ± 0.15 (0.18 – 0.79)	10.54 ± 4.61 (5.78 – 19.69)	3.15 ± 0.72 (1.89 – 4.22)	15.48 ± 4.77 (9 – 25)	2 – 10	20.6
<i>Hypsiboas faber</i> (3 females / 17 calls)	83.3	1.83 ± 0.98 (1.09 – 4.74)	0.53 ± 0.17 (0.22 – 0.88)	9.04 ± 1.17 (6.43 – 10.94)	4.20 ± 0.52 (3.10 – 5.51)	15.47 ± 3.71 (11 – 23)	5 – 11	25
<i>Hypsiboas faber</i> (2 juveniles / 10 calls)	41	0.64 ± 0.36 (0.23 – 1.30)	0.69 ± 0.32 (0.29 – 1.33)	15.62 ± 3.44 (9.96 – 20.82)	4.37 ± 2.15 (1.89 – 7.75)	15.1 ± 2.77 (12 – 19)	1 – 6	20
<i>Hypsiboas latistriatus</i> (1 female / 11 calls)	46.47	0.57 ± 0.33 (0.25 – 1.17)	0.91 ± 0.21 (0.71 – 1.42)	19.62 ± 1.91 (14.84 – 21.34)	5.47 ± 1.25 (2.24 – 6.89)	23.9 ± 6.82 (16 – 35)	2 – 10	25
<i>Hypsiboas lundii</i> (1 male / 6 calls)	59	1.09 ± 0.35 (0.60 – 1.44)	0.32 ± 0.12 (0.20 – 0.51)	9.58 ± 1.47 (7.55 – 10.82)	0.89 ± 0.10 (0.78 – 1.03)	–	–	15
<i>Hypsiboas lundii</i> (1 female / 6 calls)	73	0.62 ± 0.16 (0.37 – 0.80)	0.59 ± 0.15 (0.36 – 0.80)	10.22 ± 0.60 (9.50 – 11.24)	4.38 ± 1.55 (2.15 – 6.37)	13.17 ± 1.60 (12 – 16)	3 – 7	–
<i>Hypsiboas lundii</i> (1 juvenile / 7 calls)	43.9	0.69 ± 0.11 (0.57 – 0.86)	0.46 ± 0.13 (0.22 – 0.58)	9.19 ± 1.10 (8.05 – 11.24)	1.98 ± 1.71 (1.12 – 5.86)	18.86 ± 4.49 (14 – 28)	2 – 16	15
<i>Hypsiboas pardalis</i> (4 males / 27 calls)	60.2	0.35 ± 0.16 (0.15 – 0.72)	0.43 ± 0.13 (0.14 – 0.65)	8.61 ± 0.92 (7.43 – 11.53)	1.14 ± 0.72 (0.69 – 4.65)	20.60 ± 2.27 (17 – 24)	1 – 2	24
<i>Hypsiboas raniceps</i> (1 male / 1 call)	67.7	0.33	0.36	17.21	0.95	25	1	–
<i>Hypsiboas raniceps</i> (1 female / 8 calls)	73.05	0.37 ± 0.05 (0.30 – 0.43)	0.46 ± 0.09 (0.31 – 0.61)	18.53 ± 0.91 (17.86 – 20.11)	1.04 ± 0.72 (0.95 – 1.12)	17.63 ± 2.77 (14 – 23)	1	–
<i>Pseudis cardosoi</i> (1 male / 3 calls)	48	0.40 ± 0.02 (0.38 – 0.42)	1.46 ± 0.47 (1.00 – 1.95)	19.26 ± 0.37 (19.0 – 19.7)	4.48 ± 0.89 (3.44 – 4.99)	26.33 ± 2.08 (24 – 28)	3 – 8	–
<i>Pseudis paradoxa</i>	45	0.40 ± 0.06	0.62 ± 0.17	13.68 ± 2.61	3.78 ± 0.60	18.66 ± 2.70	4 – 6	24

	(3 males / 19 calls)	(0.24 – 0.48)	(0.40 – 1.08)	(6.5 – 17.5)	(2.53 – 4.88)	(12 – 23)	
<u>Leptodactylidae</u>							
<i>Leptodactylus fuscus</i> (1 male / 5 calls)	40	0.42 ± 0.07 (0.36 – 0.54)	0.54 ± 0.12 (0.51 – 0.77)	17.31 ± 0.24 (17.08 – 17.68)	3.62 ± 1.08 (2.49 – 4.74)	18 ± 2.35 (13 – 19)	2 – 4 21
<i>Leptodactylus mystaceus</i> (2 females / 31 calls)	46	0.23 ± 0.08 (0.12 – 0.39)	0.73 ± 0.11 (0.51 – 1.03)	13.72 ± 4.90 (7.38 – 21.02)	6.02 ± 1.23 (1.29 – 8.10)	8.81 ± 1.76 (6 – 12)	1 – 5 25
<i>Leptodactylus mystacinus</i> (1 male / 10 calls)	54.2	0.33 ± 0.10 (0.20 – 0.52)	1.22 ± 0.28 (0.61 – 1.55)	13.11 ± 0.53 (12.33 – 13.95)	5.41 ± 0.44 (4.89 – 6.10)	7.9 ± 0.88 (7 – 9)	3 – 4 19
<i>Leptodactylus pentadactylus</i> (1 female / 17 calls)	150	0.40 ± 0.09 (0.25 – 0.58)	0.18 ± 0.07 (0.10 – 0.36)	6.15 ± 0.46 (5.44 – 7.33)	1.91 ± 0.42 (0.52 – 2.24)	10.71 ± 2.64 (6 – 14)	1 – 5 23
<i>Leptodactylus savagei</i> (1 male / 29 calls)	160	0.35 ± 0.07 (0.25 – 0.54)	0.21 ± 0.06 (0.09 – 0.38)	18.95 ± 1.50 (16.98 – 20.92)	2.07 ± 0.36 (1.55 – 2.58)	31.31 ± 3.29 (26 – 37)	3 – 4 18
<i>Leptodactylus troglodytes</i> (2 males / 17 calls)	44	0.36 ± 0.13 (0.23 – 0.70)	0.99 ± 0.27 (0.52 – 1.35)	15.56 ± 1.57 (13.35 – 18.32)	7.06 ± 0.96 (5.08 – 8.44)	11.88 ± 3.08 (8 – 20)	3 – 7 21
<i>Leptodactylus vastus</i> (1 female / 18 calls)	140	0.75 ± 0.23 (0.25 – 1.26)	0.17 ± 0.04 (0.12 – 0.22)	7.42 ± 1.07 (5.86 – 9.74)	1.64 ± 0.27 (1.21 – 2.15)	19.72 ± 3.88 (12 – 26)	4 – 6 –
<u>Ranidae</u>							
<i>Lithobates catesbeianus</i> type A (5 males / 10 calls)	115	2.24 ± 0.27 (1.90 – 2.79)	0.19 ± 0.08 (0.07 – 0.34)	9.49 ± 1.71 (6.81 – 12.13)	3.1 ± 0.17 (2.89 – 3.50)	16.6 ± 3.44 (10 – 22)	5 – 6 24
<i>Lithobates catesbeianus</i> type B (3 males / 5 calls)	110	3.20 ± 0.84 (2.30 – 4.18)	0.28 ± 0.12 (0.10 – 0.40)	5.45 ± 2.68 (2.09 – 8.76)	2.79 ± 0.46 (2.12 – 3.17)	3.0 ± 0.71 (2 – 4)	2 – 3 24
<i>Lithobates catesbeianus</i> type AB/BA (4 males / 4 calls)	117	5.22 ± 2.50 (2.20 – 7.39)	0.25 ± 0.08 (0.17 – 0.34)	9.19 ± 3.74 (4.65 – 13.81)	2.92 ± 0.59 (2.05 – 3.40)	14.75 ± 10.07 (3 – 25)	3 – 6 24

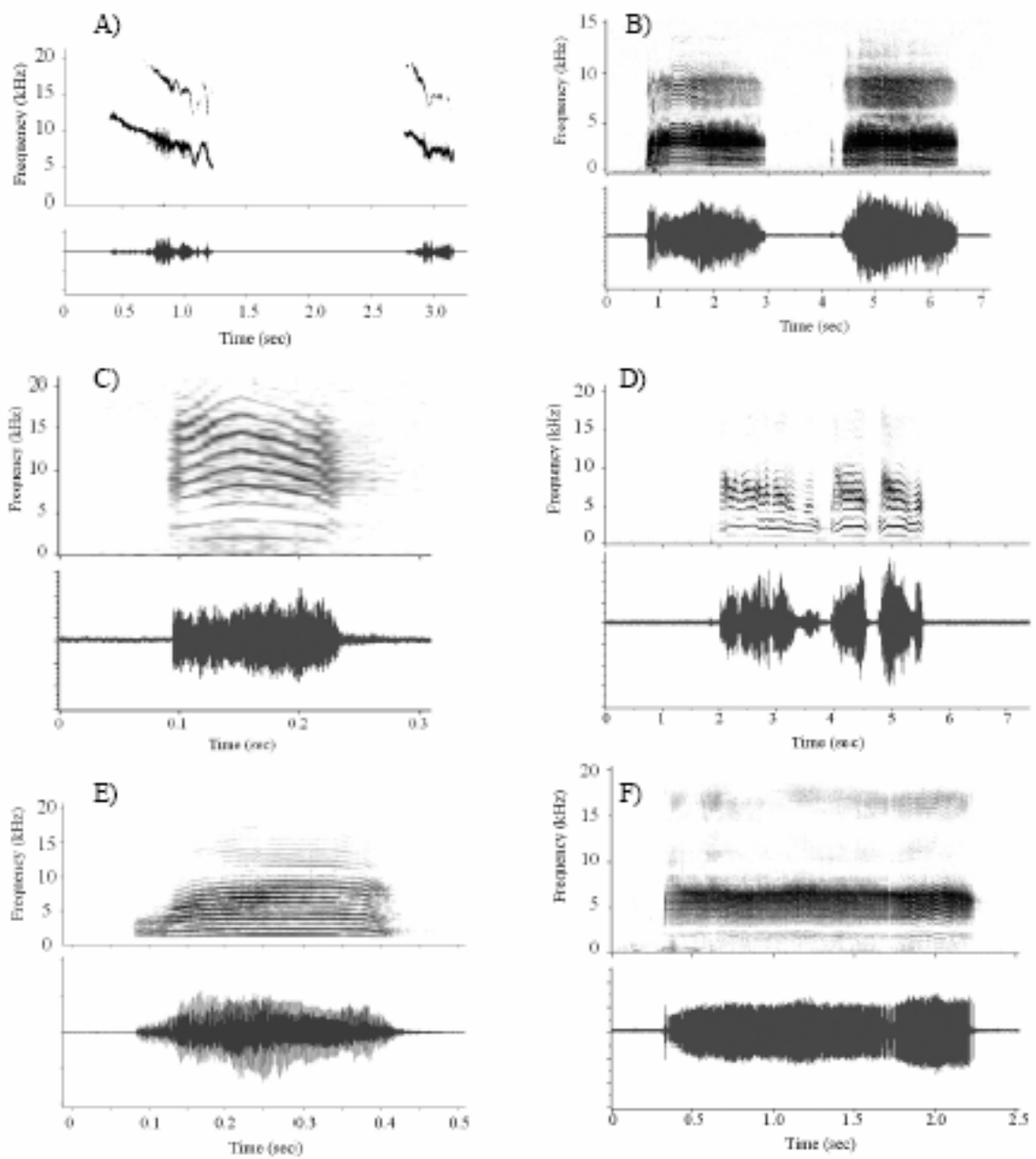


FIG. 4.—Spectrogram (above) and waveform (below) of the defensive vocalizations of: A) *Eletherodactylus binotatus*, B) adult male *Ceratophrys joazeirensis*, C) *Cycloramphus* sp. (aff. *bolitoglossus*), D) *Aplastodiscus albosignatus*, E) *A. arildae*, and F) *A. cochranae*.

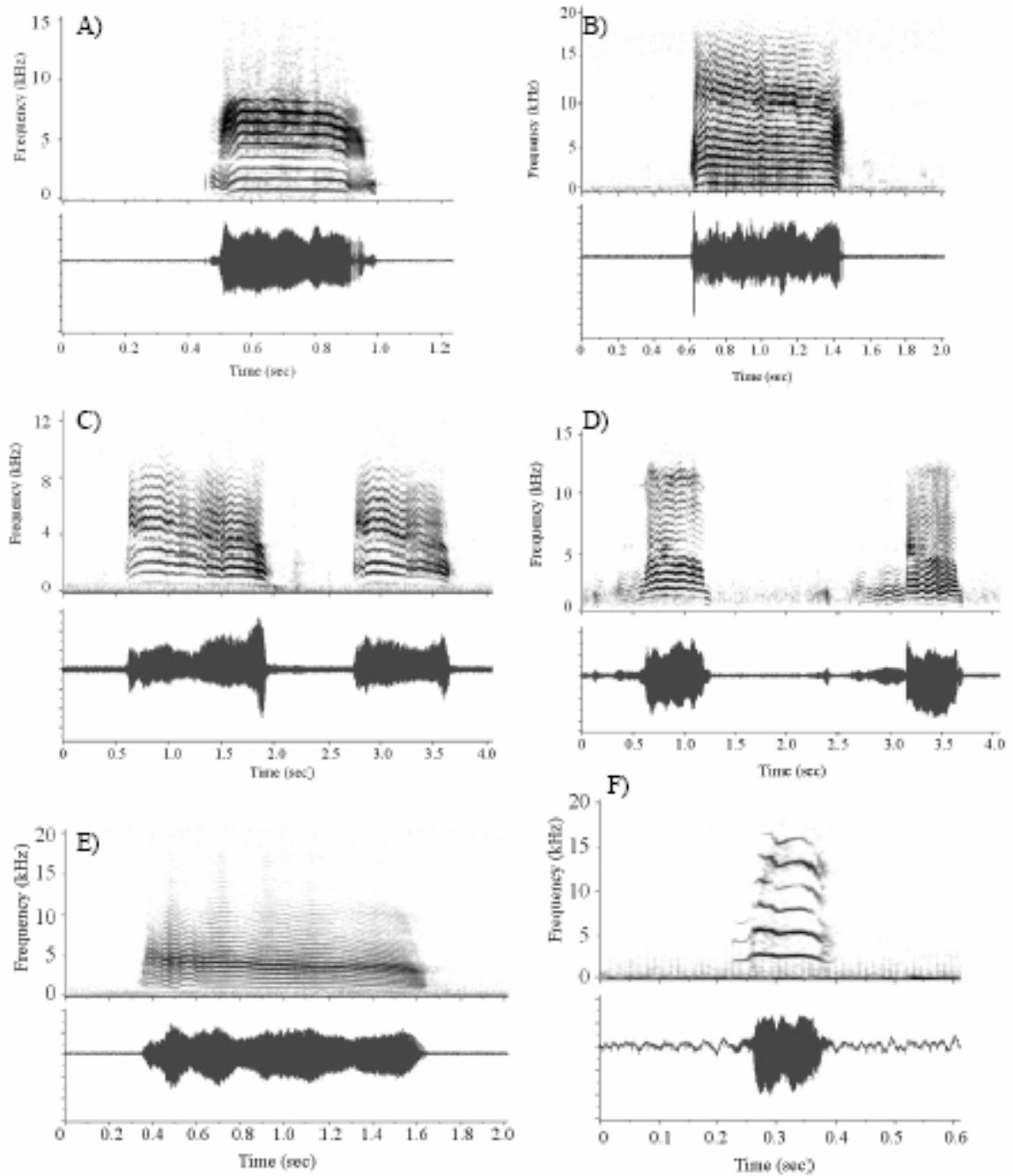


FIG. 5.—Spectrogram (above) and waveform (below) of the defensive vocalizations of: A) *Aplastodiscus leucopygius*, B) *A. perviridis*, C) *Bokermannohyla circumdata*, D) *B. hylax*, E) *B. luctuosa*, and F) *Dendropsophus minutus*.

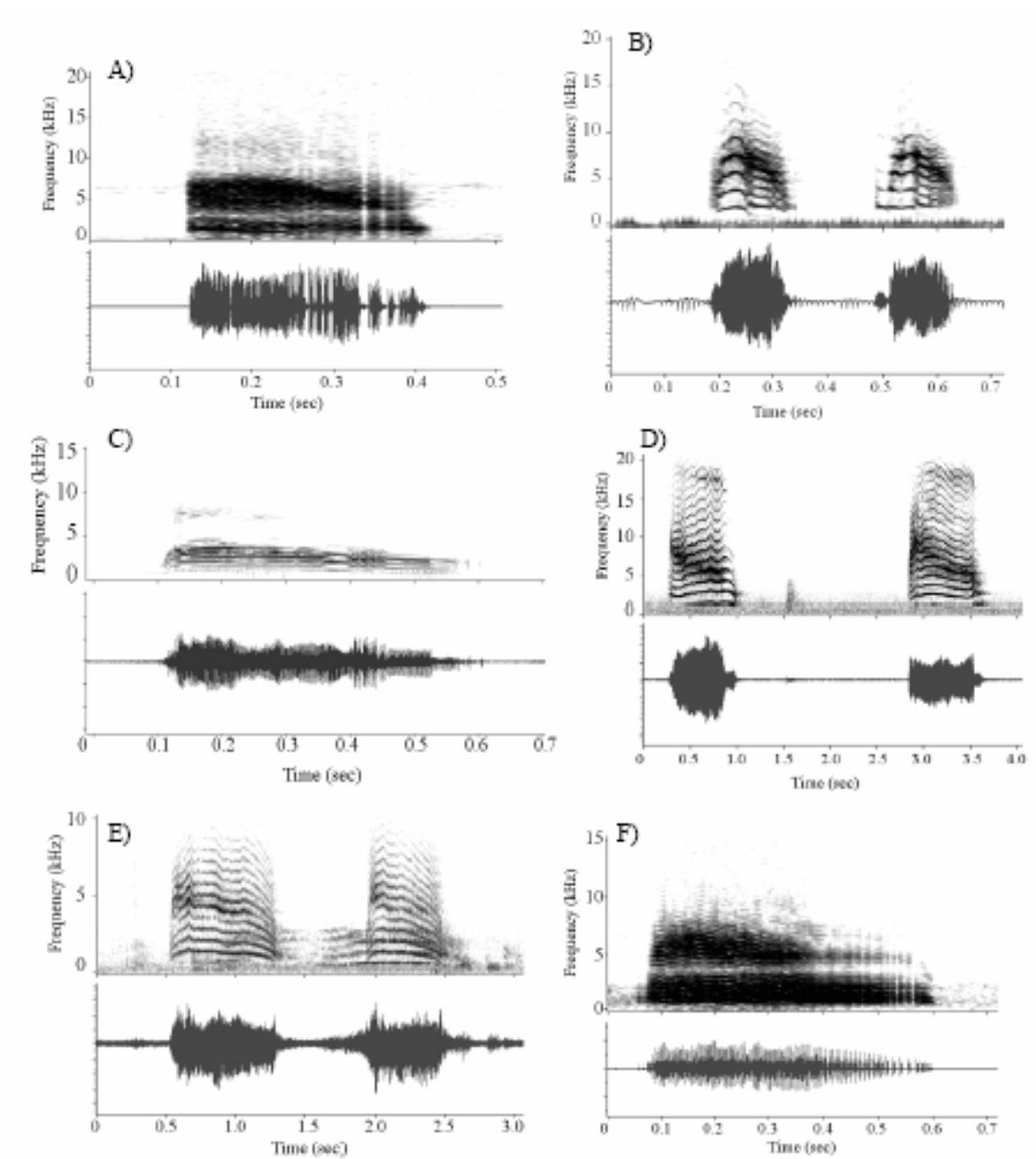


FIG. 6.—Spectrogram (above) and waveform (below) of the defensive vocalizations of: A) *Hypsiboas albomarginatus*, B) *H. bischoffi*, C) adult male *H. faber*, D) *H. latistriatus*, E) adult female *H. lundii*, and F) *H. pardalis*.

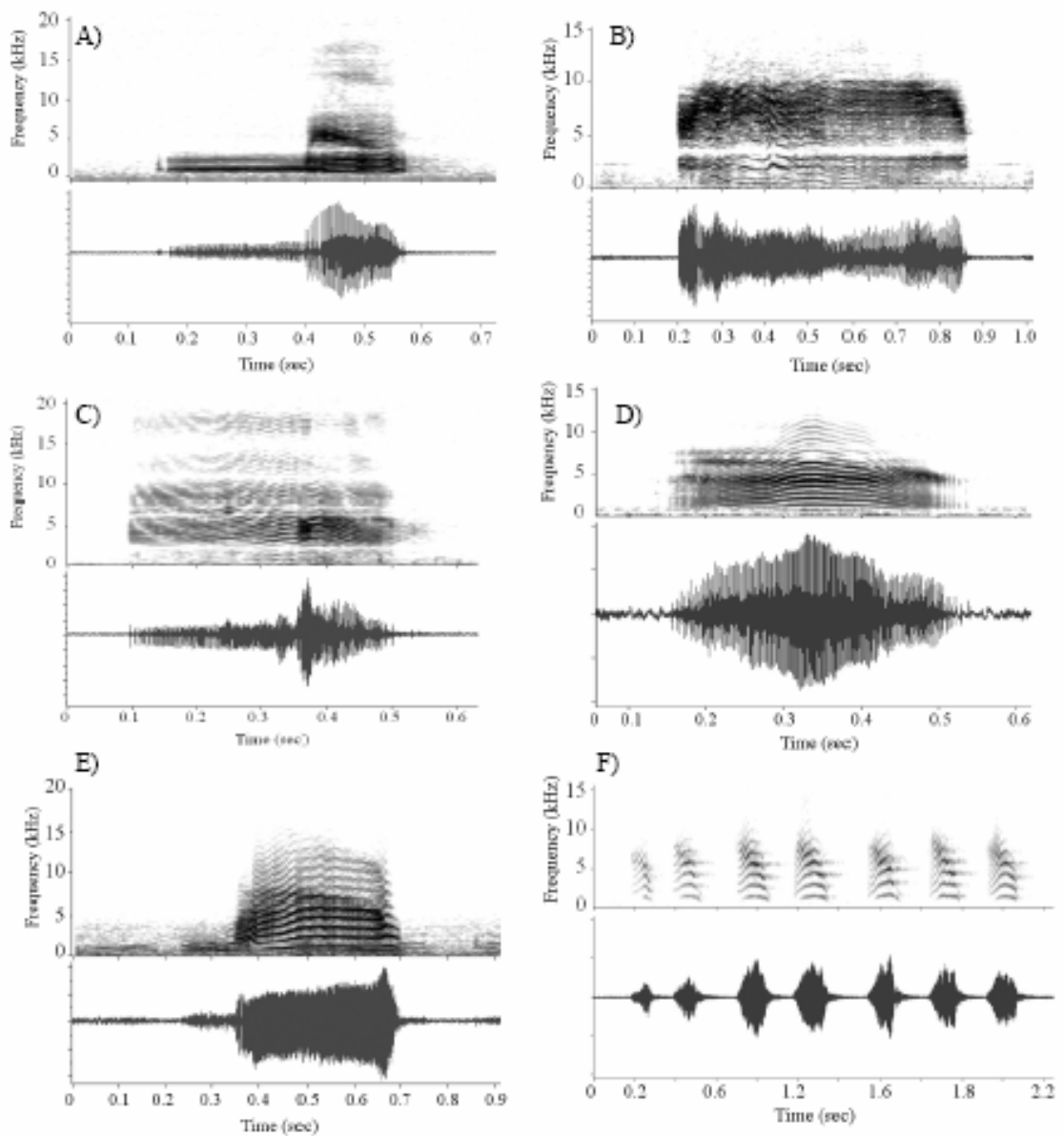


FIG. 7.—Spectrogram (above) and waveform (below) of the defensive vocalizations of: A) adult male *H. raniceps*, B) *Hypsiboas caingua*, C) *Pseudis cardosoi*, D) *P. paradoxa*, E) *Leptodactylus fuscus*, and F) *L. mystaceus*.

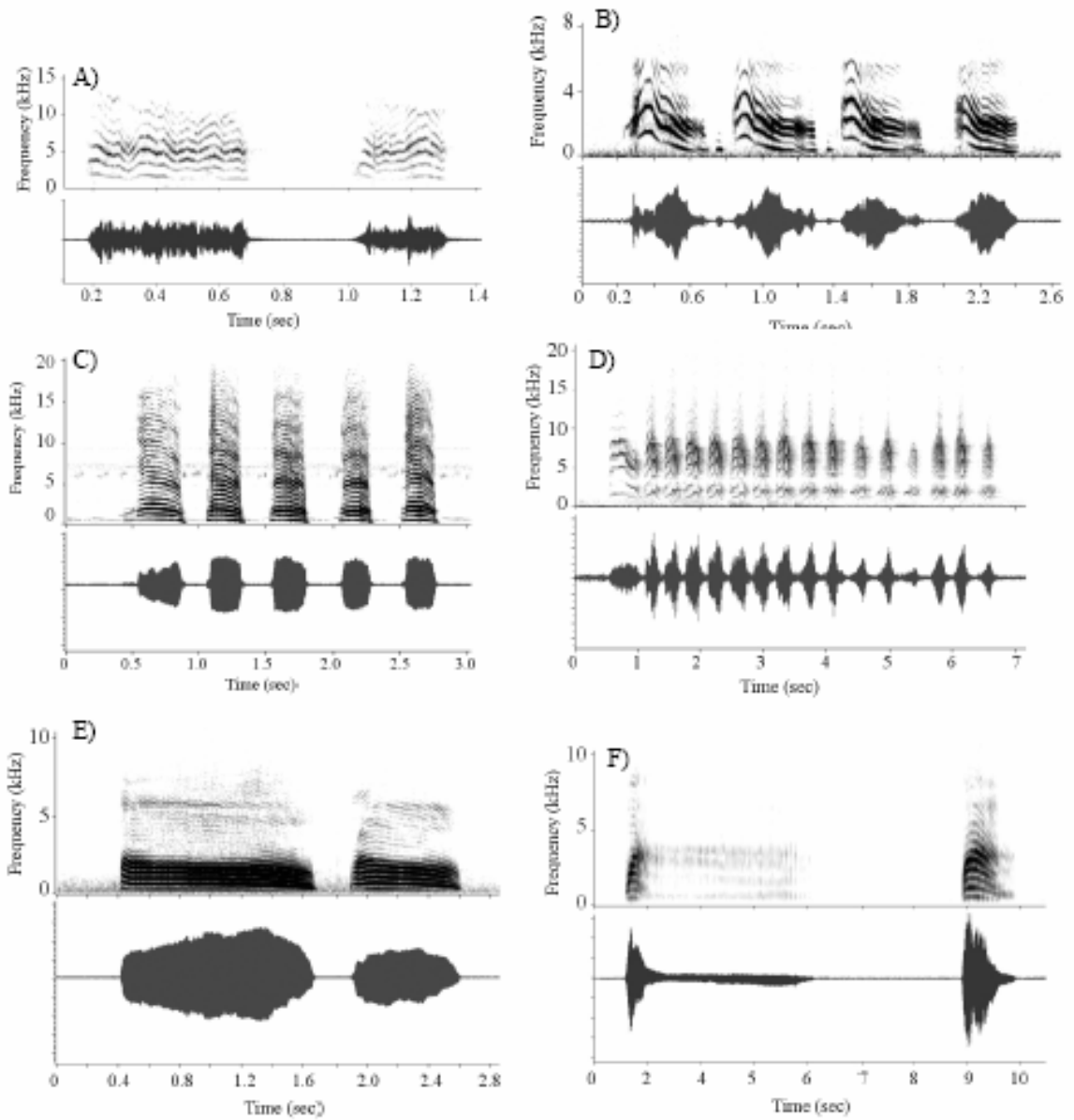


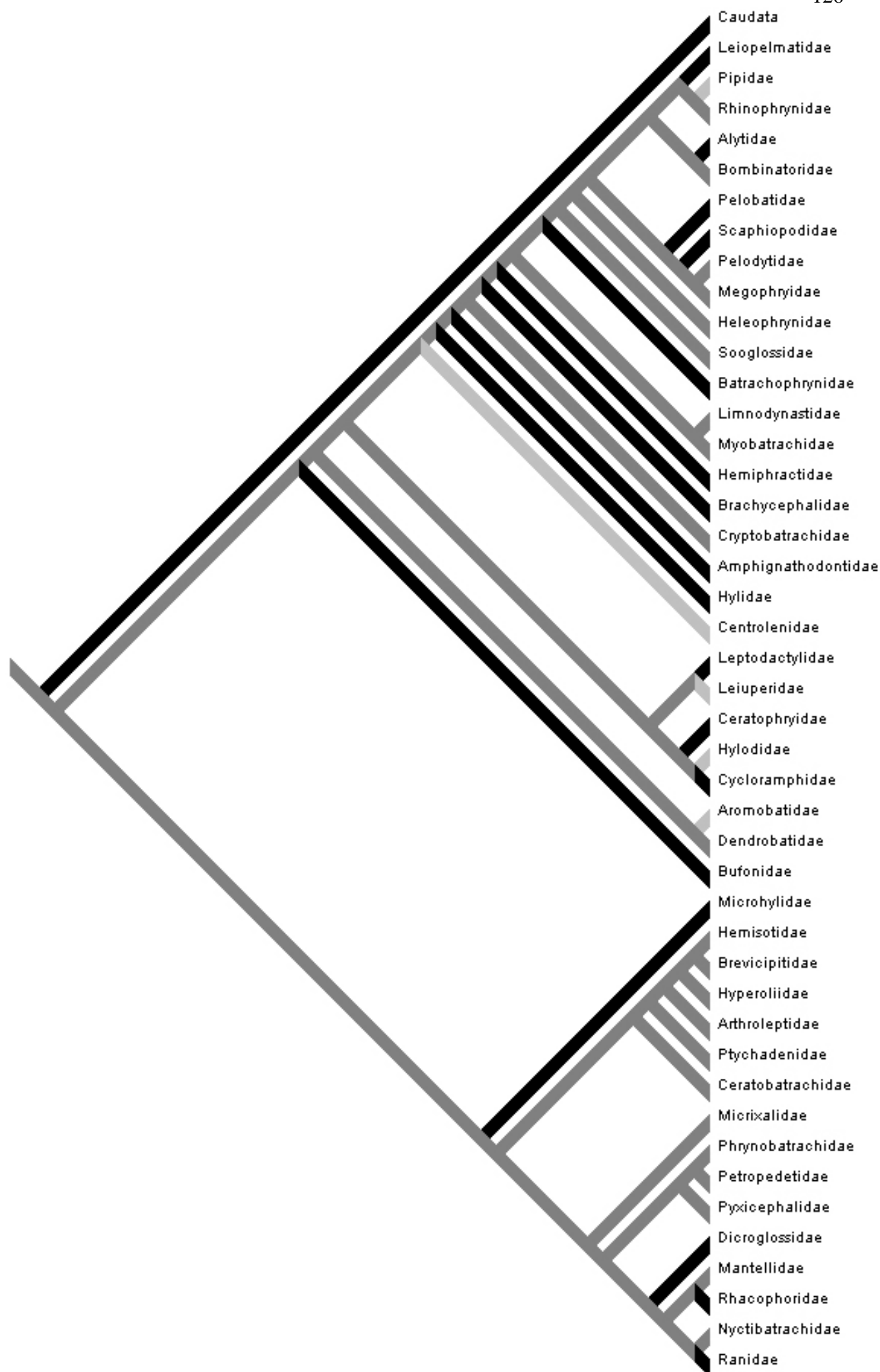
FIG. 8.—Spectrogram (above) and waveform (below) of the defensive vocalizations of: A) *Leptodactylus mystacinus*, B) *L. pentadactylus*, C) *L. savagei*, D) *L. troglodytes*, E) *L. vastus*, and F) *Lithobates catesbeianus*.
 Phylogeny

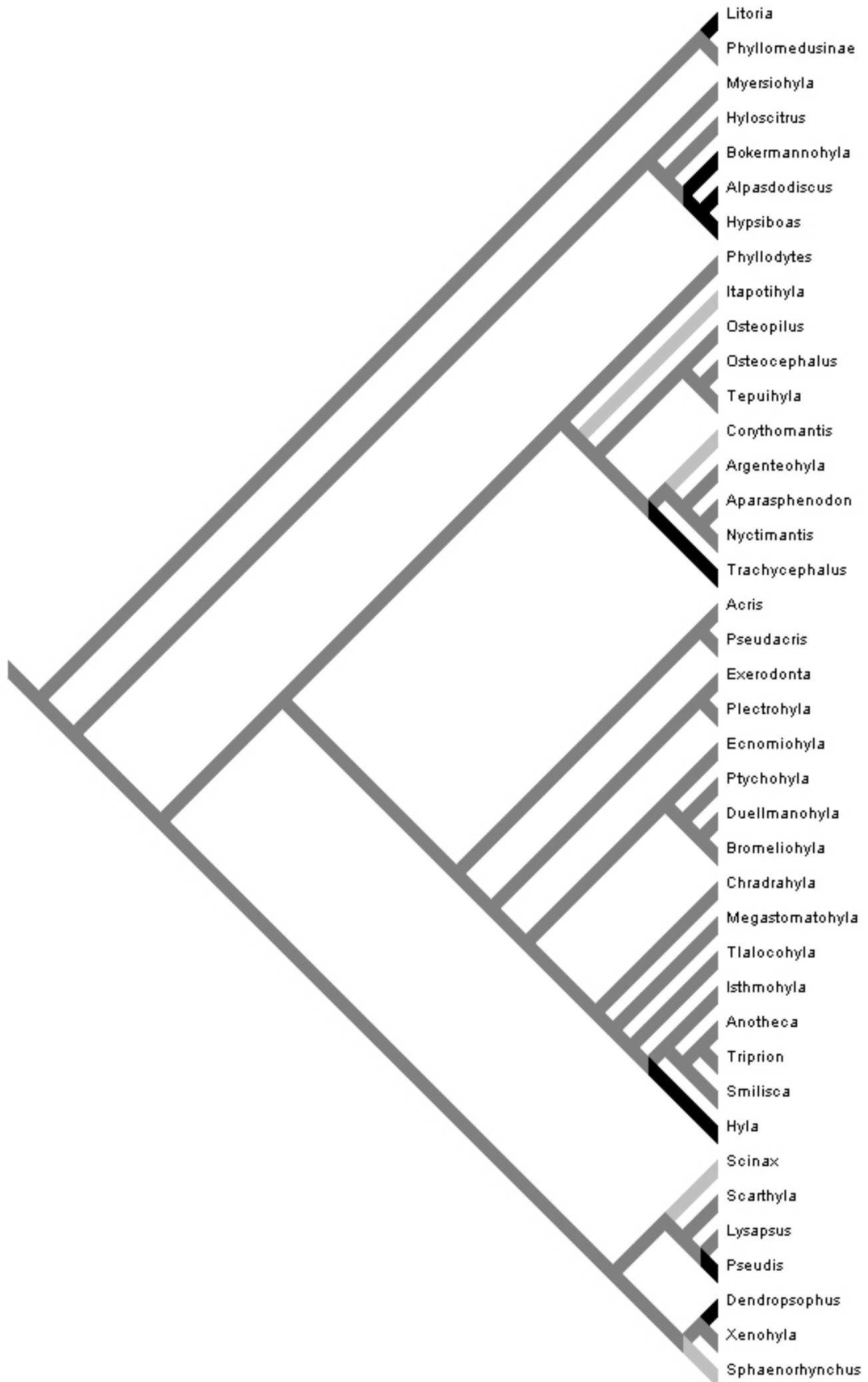
Distress and warning calls were recognized in about 38 % of the anuran families (17 out of 44), ranging from families considered to be the most basal to those considered to be the most derived, according to the recent systematic arrangement (see Grant *et al.*, 2006; Frost *et al.*, 2006) (FIG. 9). Among the hylids, distress calls are reported to occur in nine out of the 40 genera (about 23 %), again spread throughout the proposed phylogenetic tree (*sensu* Faivovich *et al.*, 2005) (FIG. 10).

CAPTIONS FOR THE NEXT FIGURES:

FIG. 9.—Phylogenetic tree of the anuran families, according to Grant *et al.* (2006) and Frost *et al.* (2006). The black branches show the families for which defensive vocalizations are reported, including distress, warning and alarm calls; the light gray branches show the negative results for the tested families (based on Appendixes I and II).

FIG. 10.—Phylogenetic tree of the hylid genera, according to Faivovich *et al.* (2006). The black branches show the genera for which the presence of defensive vocalizations is reported (including, distress, warning and alarm calls) and the light gray branches show the negative results for the tested genera (based on Appendixes I and II).





Size relationships

The snout-vent-length was positively correlated with the duration of the defensive calls ($r^2 = 0.16$; $P = 0.009$; $N = 41$; FIG. 11) and negatively correlated with the dominant frequency ($r^2 = 0.27$; $P = 0.0005$; $N = 41$; FIG. 12). The present study did not register the sound pressure levels (db) of the defensive vocalizations; however, based on data available in the study of Hödl & Gollmann (1986), we verified a positive logarithmic correlation between SVL and sound pressure levels ($r^2 = 0.65$; $P = 0.001$; $N = 16$) (FIG. 13).

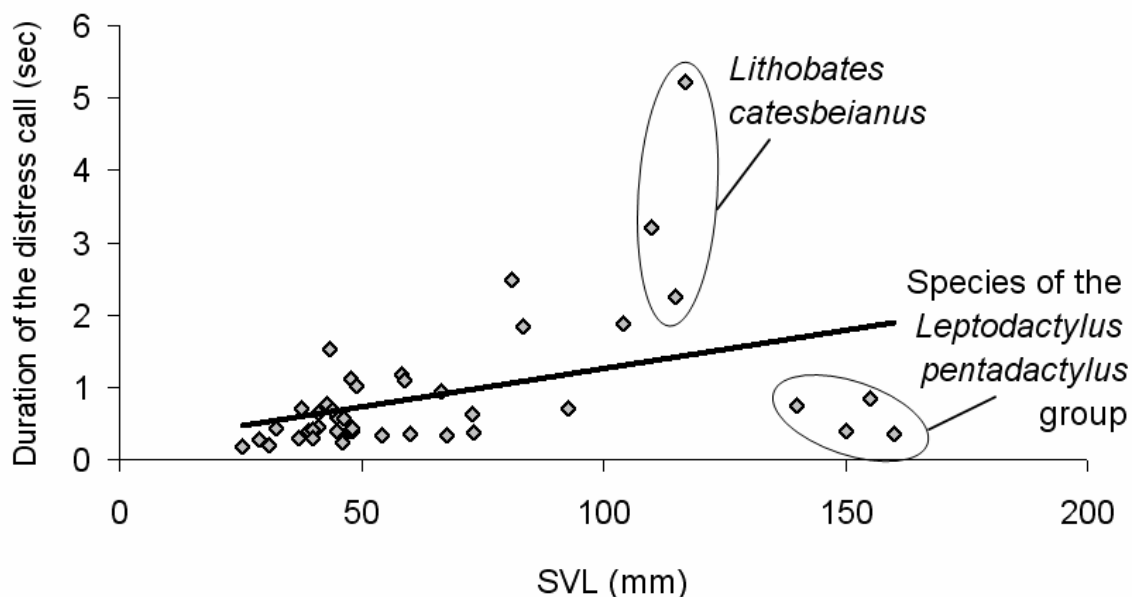


FIG. 11.—Linear regression between the snout-vent-length and the duration of the defensive vocalizations.

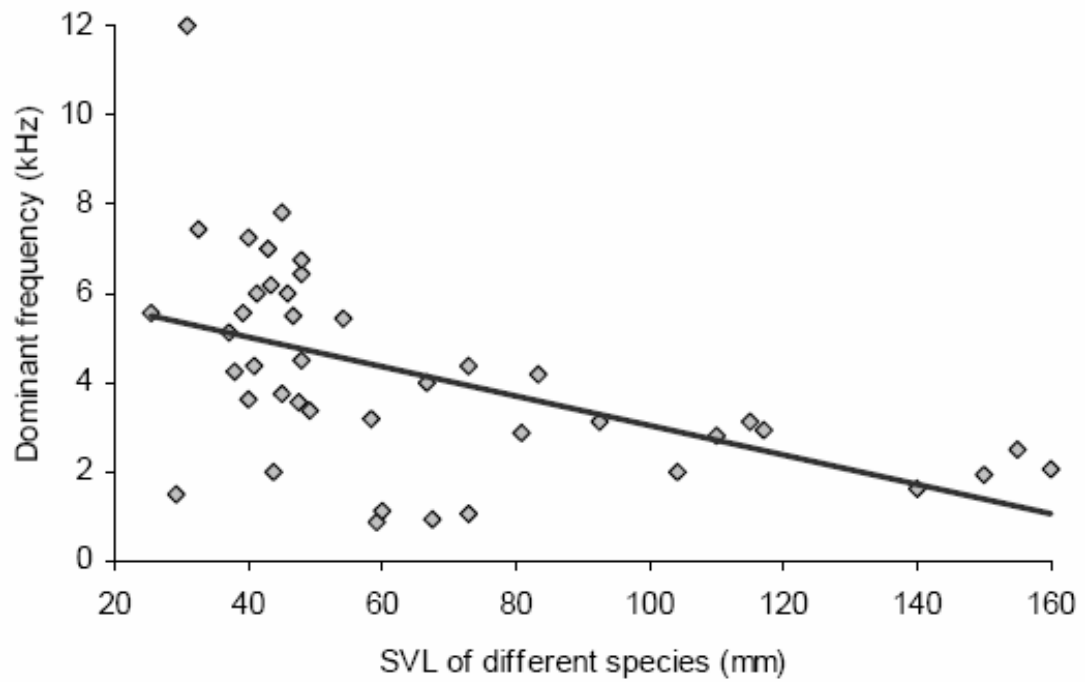


FIG. 12.—Linear regression between the snout-vent-length and the dominant frequency of the defensive vocalizations.

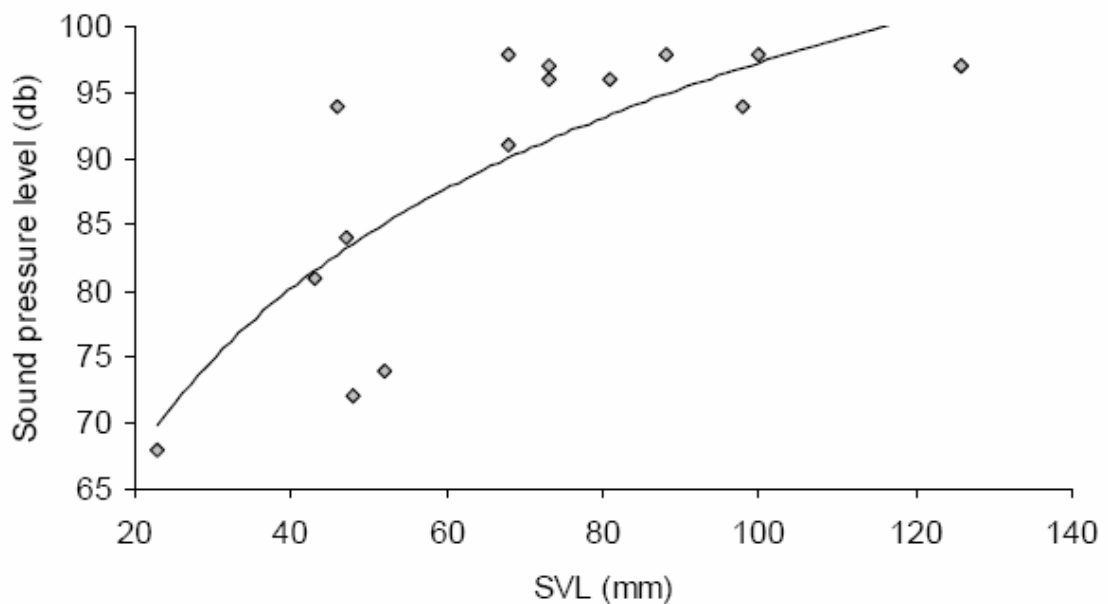


FIG. 13.—Logarithmic regression between the snout-vent-length (mm) and the sound pressure level (db) of the distress calls reported by Hödl & Gollmann (1986).

DISCUSSION

Methodology

Our handling technique seemed to work well, since many individuals emitted defensive vocalizations, and was certainly less stressful than other techniques previously used, such as electric discharges on the snout of the animals (see Capranica, 1968).

Physical characteristics and phylogenetic inferences

Despite the negative correlation between anuran size and the dominant frequency of the call, it is possible that no signal/information is transmitted to the receptors; i.e., up to the present moment, there is no information that supports the hypothesis that predators use distress call characteristics to evaluate the size of the anuran. In fact, this correlation may be directly related to the size of the anuran vocal cords, which affects the frequencies of the vocalizations (Martin, 1972), as is observed for advertisement calls (e.g., Bastos & Haddad, 2002; Toledo & Haddad, 2005). Equally, the duration and sound pressure levels of the defensive vocalizations, positively correlated to the size of the animals, may be due to some physical characteristic of the individuals. That is, the larger the anuran, the larger the lungs; therefore, the more air the animal can hold inside its lungs, the longer (Barrio, 1963; present study) and more powerful (in terms of sound pressure levels) the vocalization will be (present study). Longer and more powerful defensive vocalizations will probably enhance the intimidation or frightening capability against predators with developed acoustic capabilities. Consequently, the larger the anuran, the higher will be its chances of survival.

If the size of the anuran is really directly related to the success of their acoustic defensive strategies, we may suggest a reason for why most of the small species do not use this defensive behavior. The distress calls of these species may be inefficient to most or all of their predators. Therefore, defensive vocalizations are being or have been eliminated throughout the evolution of the species; or, on the other hand, there may never have been any selective pressures for their appearance.

The analyzed calls of the species of the *Leptodactylus pentadactylus* group (*L. pentadactylus*, *L. savagei*, and *L. vastus*: present study; and *L. labyrinthicus*: Toledo *et al.*, 2005) have shorter distress calls than that expected by the regression analysis. This observation may be reflecting a phylogenetic bias that may have molded their calls. Another characteristic that may be related to phylogeny, considering the leptodactylids, is the presence of composed calls (with a high rate of calls/second) in some species of the *L. pentadactylus* and *L. fuscus* groups. Once more, these characteristics may be more related to a phylogenetic bias in the genus than to the size of the individuals.

Since the distress calls are emitted throughout the Anura clade, occurring from more basal species, such as *Leiopelma* spp. (Leiopelmatidae: Bell, 1978; Green, 1988) and voiceless (with regard to the emission of reproductive vocalizations) species, such as *Leiopelma* spp. and *Bokermannohyla izecksohni* (Hylidae: present study), up to the ranids, we can consider their emission as a plesiomorphic character for Anura. Even if we delve deeper into the amphibian phylogeny, looking at the basal and sister group of the anurans (Frost *et al.*, 2006), we can observe the same type of vocalization (in physical structure, social context, and form of emission) emitted by salamanders (e.g., Brodie Jr., 1978).

If the emission of distress calls is a plesiomorphic character in anurans, and size is a determinant factor for its presence, it seems that some groups have lost the capability of the emission of distress calls. This seems to be the case of the species of the genus *Scinax* (present study) or the members of the families Leiuperidae (present study), Myobatrachidae and Limnodynastidae (Williams *et al.*, 2000). These species are large enough to produce these calls but apparently, do not resort to this defensive behavior. Therefore, these species must rely on other defensive strategies.

Ultrasound in anurans was reported recently only for the advertisement calls of some Asiatic species (Feng *et al.*, 2002; 2006; Narins *et al.*, 2004). In the present study we clearly detected ultrasound harmonics in the distress calls of *Eleutherodactylus binotatus*. Its function, if there is one, remains unclear; it could be only a byproduct of the morphological structure of their vocal apparatus. On the other hand, ultrasound may be heard by many animals, including some of the anuran predators (see Toledo *et al.*, 2007), such as bats, carnivores, and rodents (Ryan, 1985; Pough *et al.*, 1999).

Therefore, the distress calls of this species may be related to its predators' auditory perception and/or interpretation.

Definitions and functions of the defensive vocalizations

Defensive vocalizations are emitted in different contexts and, therefore, several terminologies have been used in the past, such as: aggressive call, alarm call, distress call, distress scream, fear scream, fright call, fright cry, mercy cry, warning call, warning signal, etc... (e.g., Noble, 1931; Barrio, 1963; Formanowicz Jr. & Brodie Jr., 1979; Toledo *et al.*, 2005). By reviewing the literature, it is possible to find more than one terminology for the same context, and sometimes, erroneous uses of the different names [e.g., Lingnau *et al.* (2004) used the term distress call to describe the release call of *Dendropsophus werneri*]. Therefore, we suggest the use of only three terms: distress, warning, and alarm calls, based on the different functions of the calls, and we define them below.

1) *Distress call*

In natural conditions this call is emitted by anurans when seized by their predators (or when running from the predator), and may be emitted with the mouth open or closed (e.g., Hoff & Moss, 1974; Webber, 1978; Martins, 1990). The functions already observed for this call are: to frighten potential predators (e.g., Brodie Jr. & Formanowicz Jr., 1981; Hödl & Gollmann, 1986); to attract other animals, which can be conspecifics (in this case the call can be considered also an alarm call; Leary & Razafindratsita, 1998), other potential predators and/or pirates (Högstedt, 1983; Schuett & Gillingham, 1990), or other curious animals (such as humans; pers. obs.). These extra individuals may interfere in the predation event and enhance the frog's chances of escape.

2) *Warning call*

In natural conditions, the warning call is emitted before the subjugation by a potential predator. This call functions like a deimatic signal that warns the potential predator that the potential prey is dangerous in one or more ways; i.e., the anuran (prey)

may be toxic (e.g., Brodie Jr., 1978; Formanowicz & Brodie, 1979; Brodie & Formanowicz, 1981), or present other defensive strategies that may cause injuries to the predator, such as biting or puncturing with spines (e.g., Barrio, 1963; present study). This call is commonly emitted by frogs of the genus *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus* (Barrio, 1963; Cei, 1990; present study).

3) Alarm call

The alarm call is emitted basically in two situations: when a frog is surprised by a potential predator and runs away emitting the scream (e.g., Capranica, 1968; Tunner & Hödl, 1978); or when a frog is being preyed upon (Noble, 1931; Bogert, 1960; Leary & Razafindratsita, 1998; present study). The emission of this call seems to call attention, making the frogs in the audible range alert and/or silent (Noble, 1931; Bogert, 1960; Capranica, 1968; present study), or stimulates an attempt by nearby conspecifics (Leary & Razafindratsita, 1998) or even other anuran species (Smith, 1977) to help the caller. This type of vocalization is much more frequent in vertebrates with a high social structure, such as crocodylians (Staton, 1978), birds (Jurisevic & Snaderson, 1998), rodents (e.g., Blumstein, 1999; Blumstein *et al.*, 2004), and humans (Christensson *et al.*, 1995). However, some reports of alarm calls exist for anurans as well, both in natural (e.g., Capranica, 1968; Smith, 1977; Leary & Razafindratsita, 1998; present study) and in experimental conditions (e.g., Yerks, 1903; Bogert, 1960). These experiments demonstrated intrinsic answers (changes in the oxygen consumption) by individuals in response to conspecific distress calls (see Yerks, 1903; Bogert, 1960).

The emission of alarm calls during the escape behavior into the water, such as that observed for some *Lithobates* and *Pelophylax* species, may imply in another signal to the nearby frogs. That is, the nearby frogs may be stimulated by the splashing sound caused by the frightened frog jumping into the water. Therefore, the warning signal emitted by the vocalization in this circumstance may be strengthened by the splashing sound. On the other hand, the production of a call in this circumstance (when jumping into the water) may be a consequence of rapid lung deflation, thus allowing the frog to dive into the water (Yerks, 1903; 1905; Capranica, 1968; Tunner & Hödl, 1978).

Similarities in the defensive vocalizations

We reported differences between the distress calls of several anuran species, as observed before (e.g., Barrio, 1963; Hödl & Gollmann, 1986). However, these differences are not as large as those observed among advertisement calls; in fact heterospecific distress calls are quite similar in structure, the majority of them resembling a loud and high pitched scream. Similarities in the distress calls of different species are also observed among birds (see Högstedt, 1983).

If defensive calls in anurans do not diverge much from one another, if the anurans are able to recognize defensive vocalizations (of the same or different species), and if they react defensively, it is possible that the emission of defensive vocalizations will benefit all anurans in the vicinity. Thus, anuran defensive vocalizations may be evidence of a highly structured social community, which is still poorly studied. However, we believe that anuran defensive calls are primarily a selfish rather than an altruistic defense (see also Högstedt, 1983).

Effectiveness of the defensive vocalizations

Some authors reported successful escapes by frogs that make use of defensive vocalizations. Cases where the emission of anuran defensive calls made the predators abandon their prey occurred with mammals (Brodie Jr. & Formanowicz Jr., 1981) or birds (Lutz, 1973). In the other failed predation attempts, which included snakes, birds, and mammals as predators, the successful escapes involved the association of chemical defenses, other defensive behaviors, or the interaction of a third (or more) individuals in the event (Smith, 1977; Formanowicz Jr. & Brodie Jr., 1979; Brodie Jr. & Nussbaum, 1987; Leary & Razafindratsita, 1998).

When multiple defences are involved in a predation attempt, generally, it is hard to elicit which defense(s) definitely saved the prey. However, when snakes are the predators, and they seem to be the major anuran predators (Toledo *et al.*, 2007), the distress calls are unlikely to be efficient, because snakes hardly hear above 400 kHz (Young, 2003), which is lower than most of the minimum frequencies of anuran distress calls (see also Sazima, 1975; Duellmann & Trueb, 1994). Therefore, when facing

snakes and other deaf (for the distress call frequencies) predators, frogs must rely on other defensive strategies (such as toxic skin secretions, or defensive behaviors). However, as far as we know, there is no evidence that anurans are able to distinguish the different predators with regard to their hearing sensitiveness. Actually, they seem to be able to evaluate the risk of predation based on the size of the potential predator (Hinsche, 1928; Smith 1977). This and other questions raised in the present study remain unsolved and are the starting point for future research.

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APPENDIX I.—Species reported to emit distress calls, their sex if adults (when they were juveniles sex was undetermined), information provided, and stimuli used to provoke the emission. One asterisk (*) denotes literature not consulted and two asterisks (**) denotes species that can emit distress calls with the mouth closed.

Species	Sex / Stage	Information provided	Emission stimuli	Source
<u>Alytidae</u>				
<i>Alytes obstetricans</i>	Adult	Call description	Human handling	Heinzmann, 1970*
<i>Discoglossus pictus</i>	Adult	Call description	Human handling	Weber, 1974*
<i>Discoglossus sardus</i>	Adult	Call description	Human handling	Weber, 1974*
<u>Amphignathodontidae</u>				
<i>Gastrotheca helenae</i>	Female	Report of the presence of the call	Human handling	Duellmann & Trueb, 1994
<u>Batrachophryniidae</u>				
<i>Caudiverbera</i>	Juvenile / Male / Female	Report of the presence of the call; Call description	Human handling	Donoso-Barros, 1972; Veloso, 1977
<i>caudiverbera</i>	Female	Call description		
<u>Brachycephalidae</u>				
<i>Craugastor latrans</i>	Female	Report of the presence of the call	Human handling	Jameson, 1954
<i>Pelorus inoptatus</i>	Not provided	Report of the presence of the call	Human handling	Noble, 1931
<u>Bufonidae</u>				
<i>Anaxyrus terrestris</i>				
<i>Anaxyrus woodhousei</i>				
<i>Chaunus arenarum</i>	Female	Report of the presence of the call	Human handling Human handling Human handling, encounter with predator	Aronson, 1944* Aronson, 1944* Gallardo, 1958
<i>Chaunus granulosus</i>	Male	Call description	Human handling	Hödl & Gollmann, 1986
<i>Epidalea calamita</i> **	Male	Call description	Human handling	Weber, 1978
<i>Pseudepidalea viridis</i>	Male	Call description	Human handling	Weber, 1978
<i>Rhinella margaritifera</i>	Male	Call description	Human handling	Hödl & Gollmann, 1986
<u>Ceratophryidae</u>				
<i>Ceratophrys ornata</i>	Female	Call description		Barrio, 1963; Cei, 1990
<i>Lepidobatrachus llanensis</i>	Male	Call description		Barrio, 1963; Cei, 1990
<u>Dicroglossidae</u>				

<i>Hoplobatrachus tigrinus</i>	Adult	Report of the presence of the call	Natural encounter with predator	Brodie Jr. & Nussbaum, 1987
<u>Hemiphractidae</u>				
<i>Hemiphractus fasciatus</i>	Adult	Report of the presence of the call	Human handling	Myers, 1966
<u>Hyllidae</u>				
<i>Dendropsophus minutus</i>	Adult	Report of the presence of the call	Natural encounter with predator or human handling	Sazima, 1975
<i>Hyla arborea</i>				Schneider, 1967*
<i>Hyla arenicolor</i>	Male / Female	Call description		Dickerson, 1906*
<i>Hyla savignyi</i>	Adult	Report of the presence of the call	Human handling	Weber, 1978
<i>Hyla versicolor</i>	Adult	Percentage of emission of the call	Provoked encounter	Brodie Jr. & Formanowicz Jr., 1981
<i>Hypsiboas albomarginatus</i>	Adult	Report of the presence of the call	Natural encounter with predator or human handling	Sazima, 1975
<i>Hypsiboas boans</i>	Male	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Hypsiboas</i> sp.(<i>pulchellus</i>)	Male	Call description	Human handling	Antunes <i>et al.</i> , in press.
<i>Hypsiboas exastis</i>	Male	Call description	Human handling	Loebmann, <i>et al.</i> , unpubl. data
<i>Hypsiboas faber</i>	Juvenile	Call description	Natural encounter with predator or human handling	Sazima, 1975
<i>Hypsiboas faber</i> **	Male	Call description	Human handling	Martins & Haddad, 1988
<i>Hypsiboas geographicus</i>	Adult	Percentage of emission of the call	Human handling	Azevedo-Ramos, 1995; Lima <i>et al.</i> , 2006
<i>Hypsiboas lanciformis</i>	Male / Female	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Hypsiboas pulchellus</i>	Adult	Report of the presence of the call	Human handling	Gallardo, 1958
<i>Hypsiboas raniceps</i>	Male / Female	Call description, Frequency of	Human handling	Hödl & Gollmann, 1986

<i>Litoria adelaidensis</i>	Adult	emission	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria alboguttata</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria aurea</i>	Adult	Call description	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria aurea</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria australis</i>	Adult	Call description	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria caerulea</i>	Adult	Call description	Human handling	Lankes, 1928*; Tyler, 1976*; Williams <i>et al.</i> , 2000
<i>Litoria cultripes</i>	Adult	Call description	Human handling	Tyler, 1976*; Williams <i>et al.</i> , 2000
<i>Litoria ewingi</i>	Adult	Call description	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria genimaculata</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria longipes</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria moorei</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria novaeollandiae</i>	Adult	Call description	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria peroni</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria raniformis</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria rothi</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria rubella</i>	Adult	Report of the presence of the call	Human handling	Williams <i>et al.</i> , 2000
<i>Litoria splendida</i>	Adult	Call description	Human handling	Williams <i>et al.</i> , 2000
<i>Osteocephalus taurinus</i>	Adult	Report of the presence of the call	Human handling	Lima <i>et al.</i> , 2006
<i>Pseudis paradoxa</i>	Adult	Call description	Human handling	Bosch <i>et al.</i> , 1996
<i>Smilisca baudinii</i>	Adult	Report of the presence of the call	Human handling	Duellman & Trueb, 1966
<i>Trachycephalus mesophaeus</i>	Adult	Report of the presence of the call	Natural encounter with predator	Lutz, 1973
<i>Trachycephalus venulosus</i>	Not provided	Call description	Natural encounter with predator	Leary & Razafindratsita, 1998
<u>Leiopelmatidae</u>				
<i>Leiopelma archeyi</i>	Male / Female	Call description	Human handling	Stephenson & Stephenson, 1957*; Bell, 1978; Green, 1988
<i>Leiopelma hamiltoni</i>	Male / Female	Call description	Human handling	Bell, 1978; Green, 1988

<i>Leiopelema hochstetteri</i>	Male / Female	Call description	Human handling	Bell, 1978; Green, 1988
<u>Leptodactylidae</u>				
<i>Hydrolaetare schimidti</i>	Female	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Leptodactylus fuscus</i>	Male / Female	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Leptodactylus hylaedactylus</i>	Male	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Leptodactylus knudseni</i>	Not provided	Report of the presence of the call	Human handling	Lima <i>et al.</i> , 2006
<i>Leptodactylus labyrinthicus</i>	Female	Call description	Human handling	Toledo <i>et al.</i> , 2005
<i>Leptodactylus ocellatus</i>	Male / Female	Call description, Frequency of emission	Human handling	Hödl & Gollmann, 1986
<i>Leptodactylus pentadactylus</i>	Male / Female	Call description, Frequency of emission	Human handling	Villa, 1969; Hödl & Gollmann, 1986; Duellman & Trueb, 1994; Lima <i>et al.</i> , 2006
<u>Microhylidae</u>				
<i>Microhyla carolinensis</i>	Male / Female		Human handling	Anderson, 1954*
<u>Pelobatidae</u>				
<i>Pelobates fuscus</i>		Call description		Boulenger, 1897*
<u>Scaphiopodidae</u>				
<i>Scaphiopus holbrooki</i>	Not provided	Report of the presence of the call	Human handling	Noble, 1931
<i>Scaphiopus couchi</i>	Not provided	Report of the presence of the call	Natural encounter with predator	Noble, 1931
<u>Rhacophoridae</u>				
<i>Polypedates maculatus</i>	Female	Call description	Not informed	Kanamadi <i>et al.</i> , 1993
<u>Ranidae</u>				
<i>Lithobates areolatus</i>				Altig, 1972*
<i>Lithobates catesbeianus</i> **	Male / Female / Juvenile	Call description; Percentage of emission of the call	Human handling	Carr Jr., 1940*; Capranica, 1968; Hoff & Moss, 1974; Smith, 1977; Formanowicz

<i>Lithobates clamitans</i>	Not provided	Call description; Percentage of emission of the call	Human handling	Jr. & Brodie Jr., 1979 Yerkes, 1903*; Bogert, 1960; Formanowicz Jr. & Brodie Jr., 1979
<i>Lithobates grylio</i>	Female	Call description	Human handling	Bogert, 1960
<i>Lithobates palustris</i>	Not provided	Percentage of emission of the call	Human handling	Formanowicz Jr. & Brodie Jr., 1979
<i>Lithobates pipiens</i>	Adults / Juvenile	Call description	Natural encounter with predator and human handling	Noble, 1931; Bogert, 1960; Smith, 1977; Schuett & Gillingham, 1990
<i>Lithobates sylvaticus</i>	Not provided	Percentage of emission of the call	Human handling	Formanowicz Jr. & Brodie Jr., 1979
<i>Pelophylax ridibundus</i>	Male / Female	Call description	Human handling	Tunner & Hödl, 1978

APPENDIX II.—The 111 handled species tested for the emission of distress calls, sex or stage (when juvenile), number of individuals tested (Ni), number (Ne) and percentage of individuals that emitted distress calls.

Species	Sex / Stage	Ni (Ne; %)	Species	Sex / Stage	Ni (Ne; %)
<u>Atrombatidae</u>					
<i>Allobates alagoanus</i>	Male	4 (0; 0%)	<i>Hypsiboas leptolineatus</i>	Male	3 (0; 0%)
<i>Ameerega flavipicta</i>	Male	1 (0; 0%)	<i>Hypsiboas lucianae</i>	Male	3 (0; 0%)
<u>Brachycephalidae</u>					
<i>Eleutherodactylus binotatus</i>	Female	4 (0; 0%)	<i>Hypsiboas lundii</i>	Female	2 (1; 50%)
<i>Eleutherodactylus binotatus</i>	Male	6 (1; 16.67%)	<i>Hypsiboas lundii</i>	Juvenile	2 (1; 50%)
<i>Eleutherodactylus guentheri</i>	Male	6 (0; 0%)	<i>Hypsiboas lundii</i>	Male	8 (5; 62.5%)
<i>Eleutherodactylus juipoca</i>	Male	1 (0; 0%)	<i>Hypsiboas marginatus</i>	Male	5 (0; 0%)
<i>Eleutherodactylus parvus</i>	Female	1 (0; 0%)	<i>Hypsiboas pardalis</i>	Male	8 (3; 37.5%)
<i>Eleutherodactylus ramagii</i>	Juvenile	1 (0; 0%)	<i>Hypsiboas pombali</i>	Male	5 (0; 0%)
<u>Bufonidae</u>					
<i>Chaunus abei</i>	Male	1 (0; 0%)	<i>Hypsiboas prasinus</i>	Male	5 (0; 0%)
<i>Chaunus crucifer</i>	Female	1 (0; 0%)	<i>Hypsiboas pulchellus</i>	Male	5 (0; 0%)
<i>Chaunus crucifer</i>	Male	10 (0; 0%)	<i>Hypsiboas raniceps</i>	Female	2 (1; 50%)
<i>Chaunus ictericus</i>	Juvenile	6 (0; 0%)	<i>Hypsiboas raniceps</i>	Male	4 (1; 25%)
<i>Chaunus jimi</i>	Male	10 (0; 0%)	<i>Hypsiboas semilieatus</i>	Juvenile	10 (0; 0%)
<i>Chaunus ornatus</i>	Female	1 (0; 0%)	<i>Hypsiboas semilieatus</i>	Male	20 (0; 0%)
<i>Chaunus ornatus</i>	Male	1 (0; 0%)	<i>Itapotihyla langsdorffii</i>	Male	6 (0; 0%)
<i>Chaunus scheneideri</i>	Female	8 (0; 0%)	<i>Phrynomedusa marginata</i>	Female	1 (0; 0%)
<i>Chaunus scheneideri</i>	Male	5 (0; 0%)	<i>Phyllodytes melanomystax</i>	Male	2 (0; 0%)
<i>Dendrophryniscus brevipolicatus</i>	Female	1 (0; 0%)	<i>Phyllomedusa bahiana</i>	Male	9 (0; 0%)
<i>Dendrophryniscus brevipolicatus</i>	Male	5 (0; 0%)	<i>Phyllomedusa burmeisteri</i>	Male	3 (0; 0%)
<i>Melanophryniscus moreirae</i>	Male	2 (0; 0%)	<i>Phyllomedusa distincta</i>	Male	8 (0; 0%)
<u>Cycloramphidae</u>					
<i>Cycloramphus eleutherodactylus</i>	Male	2 (0; 0%)	<i>Phyllomedusa nordestina</i>	Male	10 (0; 0%)
<i>Cycloramphus sp. (aff.)</i>	Female	4 (1; 25%)	<i>Pseudis cardosoi</i>	Female	1 (0; 0%)
			<i>Pseudis cardosoi</i>	Male	2 (1; 50%)
			<i>Pseudis paradoxa</i>	Male	1 (1; 100%)
			<i>Scinax auratus</i>	Male	3 (0; 0%)

<i>bolitoglossus</i>)						
<i>Cycloramphus</i> sp. (aff. <i>bolitoglossus</i>)	Male	3 (1; 33.33%)	<i>Scinax fuscovarius</i>	Female	5 (0; 0%)	
<i>Odontophrynus cultripes</i>	Male	3 (0; 0%)	<i>Scinax fuscovarius</i>	Juvenile	2 (0; 0%)	
<i>Odontophrynus americanus</i>	Female	1 (0; 0%)	<i>Scinax fuscovarius</i>	Male	16 (0; 0%)	
<i>Proceratophrys appendiculata</i>	Juvenile	1 (0; 0%)	<i>Scinax hayii</i>	Male	5 (0; 0%)	
<i>Proceratophrys boiei</i>	Juvenile	1 (0; 0%)	<i>Scinax hiemalis</i>	Male	8 (0; 0%)	
<i>Proceratophrys boiei</i>	Male	3 (0; 0%)	<i>Scinax pachyrrus</i>	Male	3 (0; 0%)	
<i>Thoropa megalympanum</i>	Male	5 (0; 0%)	<i>Scinax perpusillus</i>	Male	2 (0; 0%)	
<i>Thoropa militaris</i>	Male	2 (0; 0%)	<i>Scinax similis</i>	Male	51 (0; 0%)	
<u>Centrolenidae</u>			<i>Sphaenorhynchus</i> sp. (aff. <i>surdus</i>)	Male	1 (0; 0%)	
<i>Hyalinobatrachium uranoscopum</i>	Male	14 (0; 0%)	<i>Sphaenorhynchus surdus</i>	Male	1 (0; 0%)	
<u>Ceratophryidae</u>			<i>Trachycephalus mesophaeus</i>	Male	4 (0; 0%)	
<i>Ceratophrys joazeirensis</i>	Female	1 (1; 100%)	<u>Hylodidae</u>			
<i>Ceratophrys joazeirensis</i>	Male	1 (1; 100%)	<i>Hylodes dactylocinus</i>	Male	6 (0; 0%)	
<u>Hylidae</u>			<i>Hylodes meridionalis</i>	Male	3 (0; 0%)	
<i>Aparasphaenodon brunoi</i>	Female	1 (0; 0%)	<u>Leiuperidae</u>			
<i>Aplastodiscus albosignatus</i>	Female	1 (1; 100%)	<i>Eupemphix nattereri</i>	Male	5 (0; 0%)	
<i>Aplastodiscus arildae</i>	Male	4 (1; 25%)	<i>Physalaemus cf. nanus</i>	Female	1 (0; 0%)	
<i>Aplastodiscus cochranae</i>	Male	4 (3; 75%)	<i>Physalaemus cf. nanus</i>	Male	1 (0; 0%)	
<i>Aplastodiscus leucopygius</i>	Male	3 (2; 66.67%)	<i>Physalaemus cuvieri</i>	Female	5 (0; 0%)	
<i>Aplastodiscus perviridis</i>	Female	1 (1; 100%)	<i>Physalaemus cuvieri</i>	Juvenile	2 (0; 0%)	
<i>Aplastodiscus perviridis</i>	Male	2 (1; 50%)	<i>Physalaemus cuvieri</i>	Male	12 (0; 0%)	
<i>Bokermannohyla alvarengai</i>	Male	1 (0; 0%)	<i>Physalaemus fuscomaculatus</i>	Male	2 (0; 0%)	
<i>Bokermannohyla circumdata</i>	Female	5 (3; 60%)	<i>Physalaemus nanus</i>	Female	2 (0; 0%)	
<i>Bokermannohyla circumdata</i>	Male	6 (1; 16.67%)	<i>Physalaemus nanus</i>	Male	5 (0; 0%)	
<i>Bokermannohyla hylax</i>	Male	3 (2; 66.67%)	<i>Physalaemus nanus</i>	Male	1 (0; 0%)	
<i>Bokermannohyla izecksohni</i>	Male	4 (2; 50%)	<i>Physalaemus olfersii</i>	Male	5 (0; 0%)	
<i>Bokermannohyla luctuosa</i>	Male	1 (1; 100%)	<i>Physalaemus</i> sp. (gr. <i>cuvieri</i>)	Male	5 (0; 0%)	
<i>Corythomantis greeningi</i>	Male	3 (0; 0%)	<i>Pseudopaludicola</i> cf. <i>saltica</i>	Male	4 (0; 0%)	
			<u>Leptodactylidae</u>			

<i>Dendropsophus branneri</i>	Female	3 (0; 0%)	<i>Leptodactylus chaquensis</i>	Juvenile	10 (1; 10%)
<i>Dendropsophus branneri</i>	Male	6 (0; 0%)	<i>Leptodactylus furnarius</i>	Male	2 (0; 0%)
<i>Dendropsophus elianae</i>	Male	2 (0; 0%)	<i>Leptodactylus fuscus</i>	Male	8 (2; 25%)
<i>Dendropsophus giesleri</i>	Male	1 (0; 0%)	<i>Leptodactylus gracilis</i>	Male	2 (0; 0%)
<i>Dendropsophus haddadi</i>	Male	5 (0; 0%)	<i>Leptodactylus mystaceus</i>	Female	2 (1; 50%)
<i>Dendropsophus microps</i>	Female	2 (0; 0%)	<i>Leptodactylus mystaceus</i>	Male	2 (0; 0%)
<i>Dendropsophus microps</i>	Male	10 (0; 0%)	<i>Leptodactylus mystacinus</i>	Female	2 (0; 0%)
<i>Dendropsophus minutus</i>	Female	24 (1; 4.17%)	<i>Leptodactylus mystacinus</i>	Juvenile	3 (0; 0%)
<i>Dendropsophus minutus</i>	Male	31 (0; 0%)	<i>Leptodactylus mystacinus</i>	Male	6 (1; 16.67%)
<i>Dendropsophus nanus</i>	Male	8 (0; 0%)	<i>Leptodactylus ocellatus</i>	Female	6 (0; 0%)
<i>Dendropsophus samborni</i>	Male	12 (0; 0%)	<i>Leptodactylus ocellatus</i>	Juvenile	12 (0; 0%)
<i>Dendropsophus wernerii</i>	Male	2 (0; 0%)	<i>Leptodactylus ocellatus</i>	Male	26 (0; 0%)
<i>Hypsiboas albomarginatus</i>	Male	8 (4; 50%)	<i>Leptodactylus pentadactylus</i>	Female	1 (1; 100%)
<i>Hypsiboas albopunctatus</i>	Female	6 (0; 0%)	<i>Leptodactylus savagei</i>	Male	1 (1; 100%)
<i>Hypsiboas albopunctatus</i>	Male	20 (1; 5%)	<i>Leptodactylus troglodytes</i>	Male	5 (3; 60%)
<i>Hypsiboas atlanticus</i>	Female	2 (0; 0%)	<i>Leptodactylus vastus</i>	Female	1 (1; 100%)
<i>Hypsiboas atlanticus</i>	Male	6 (0; 0%)	<u>Microhylidae</u>		
<i>Hypsiboas beckeri</i>	Male	10 (0; 0%)	<i>Chiasmocleis albopunctata</i>	Juvenile	2 (0; 0%)
<i>Hypsiboas bischoffi</i>	Female	11 (4; 36.36%)	<i>Chiasmocleis albopunctata</i>	Male	2 (0; 0%)
<i>Hypsiboas bischoffi</i>	Male	26 (7; 26.92%)	<i>Elachistocleis ovalis</i>	Male	3 (0; 0%)
<i>Hypsiboas caingua</i>	Male	5 (2; 40%)	<u>Pipidae</u>		
<i>Hypsiboas caipora</i>	Male	12 (1; 8.33%)	<i>Pipa pipa</i>	Male	1 (0; 0%)
<i>Hypsiboas crepitans</i>	Male	5 (2; 40%)	<i>Xenopus laevis</i>	Female	3 (0; 0%)
<i>Hypsiboas exasitis</i>	Male	1 (1; 100%)	<i>Xenopus laevis</i>	Male	7 (0; 0%)
<i>Hypsiboas faber</i>	Female	3 (2; 66.67%)	<u>Ranidae</u>		
<i>Hypsiboas faber</i>	Juvenile	3 (2; 66.67%)	<i>Lithobates catesbeianus</i>	Female	20 (0; 0%)
<i>Hypsiboas faber</i>	Male	23 (15; 65.22%)	<i>Lithobates catesbeianus</i>	Juvenile	20 (0; 0%)
<i>Hypsiboas latistriatus</i>	Female	1 (1; 100%)	<i>Lithobates catesbeianus</i>	Male	20 (5; 25%)

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CAPÍTULO 5

DEFESAS COMPORTAMENTAIS EM ANUROS: UMA REVISÃO

Luís Felipe Toledo, Ivan Sazima & Célio F. B. Haddad



Thanatos (a morte)

Deus grego da morte, filho de Nyx (a noite) e irmão de Hypnos (o sono), encarregado de conduzir as almas dos mortais. Assim surgiu o nome thanatose, o comportamento de fingir-se de morto.

CAPÍTULO 5

BEHAVIORAL DEFENSES OF ANURANS: AN OVERVIEW

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Abstract

For vertebrates, defensive behaviors have been reviewed for fishes, salamanders, reptiles, birds, and mammals, but not yet for anurans. Although several defensive strategies have been reported for anurans, with a few exceptions these reports are limited in scope and scattered in the literature. This may be due to the lack of a review on defensive strategies of the anurans, which could offer a basis for further studies and insights on basic mechanisms that underlie these strategies, and thus lead to theoretical assumptions of their efficacy and evolution. Here we review the present knowledge on defensive behavioral tactics employed by anurans, add new data on already reported behaviors, describe a few new behaviors, and speculate about their origins. A total of 28 defensive behaviors (some with a few sub-categories), plus an ecological category, are here recognized. The terminology already adopted is here organized and some neologies are proposed. Some of the behaviors here treated seem to have an independent origin, whereas others might have evolved after preexistent physiological and behavioral characteristics. The role of predators in the evolution of defensive behaviors is still scarcely touched upon and this overview adds data to exploit this and other evolutionary unsolved questions.

Introduction

The commonest defensive strategy of mobile animals is to flee as fast as possible from its potential predator. However, there is a wide array of defensive strategies that are alternatively used to cope with the risk posed by a predator. Anurans, in particular, display a wide range of behaviors between the remaining motionless and fleeing extremes (e.g., Dodd Jr., 1976; Williams et al., 2000; Toledo et al., 2005). Even when remaining motionless or when fleeing, anurans may employ different synergistic tactics to enhance their survival chances (e.g., Marchisin & Andrews, 1978), especially in a world in which almost every carnivorous organism may eat a frog (reviews in Toledo, 2005; Toledo et al., 2007a).

Different defensive strategies act in different phases of predation: localization, identification, approach, subjugation, ingestion, and digestion. Thus, primary (that do not depends on the presence of the predator) and secondary (that is elicited by the presence of the predator) defensive strategies may have evolved to hamper or stop a predation attempt in one or more of these phases (Edmunds, 1974). For example, a cryptic anuran may avoid detection, and a venomous anuran may avoid ingestion. As a consequence, the evolution of defensive strategies is directly related to the senses predators use to locate and handle with their prey (e.g., Greenbaum, 2004). In some cases, the predators may evolve strategies that overcome anuran defenses, and thus generating predator-prey arms races (e.g., Brodie III & Brodie Jr., 1999).

Gathering data on defensive strategies of anurans in the field is not a difficult task; nevertheless, few extensive studies have been published (e.g., Williams et al., 2000). Most studies rely on scattered data, available as short notes (e.g., Sazima, 1978; Toledo et al., 2005). The lack of papers focusing on defensive strategies of anurans may be due to the lack of reviews or overviews which would organize current knowledge, and which would lead to further discussion and provide a starting point for more broad studies.

Taxa-restricted reviews on animal defensive behaviors have been published on invertebrates, mostly insects (e.g., Evans & Schmidt, 1990; Eisner, 2005), although such reviews also are available for fishes (Randall, 2005; Zacone et al., 2007), reptiles (Greene, 1988), birds and mammals (Caro, 2005) as well. For amphibians, knowledge on defensive behaviors of salamanders and newts (order Caudata) are reviewed in the

extensive work of Edmund Brodie Jr. and colleagues (e.g., Brodie Jr., 1977; 1983; 1990; Brodie et al., 1984; Williams et al., 2000). However, no such a review is available for anurans.

Our aim with the present overview is not to draw from all the reports available on anuran defensive behaviors, but to provide an organized view of the diversity of defensive strategies among this vertebrate group. Thus, we collected what we regard as representative information on anuran behaviors for an overview that would encompass most, if not all, the defensive repertoire of post-metamorphic anurans. Besides reviewing the literature, we add new data based on naturalistic observations and experiments in the field and laboratory, and propose here some neologies that complement the terminology already in use.

Material and Methods

Major herpetological journals (e.g., *Amphibia-Reptilia*, *Copeia*, *Herpetologica*, *Herpetological Bulletin*, *Herpetological Journal*, *Herpetological Review*, and *Journal of Herpetology*) were searched for reports on anuran defensive behaviors (both natural and experimental conditions were considered for our review).

New data were obtained during several field trips from 1969 to 2007 in Brazil, mainly in the biomes of the Cerrado and Atlantic rainforest. Staged encounters in the field were made by approaching an individual frog and recording its reaction to close approach, handling, grasping suddenly, hitting it gently with sticks (on the head and dorsum), lightly pinching the head, arms, and legs with a blunt forceps, or by presenting the frog to a non-venomous snake (generally an adult *Liophis miliaris*). Neither of these injure the frogs, such techniques being regarded as effective to simulate predators' attacks, and thus to produce defensive responses in anurans (Brodie Jr., 1977; Brodie Jr. et al., 1998; Williams et al., 2000; Toledo et al., 2005).

Experiments with captive anurans were generally avoided (although a few data were obtained from less than one week captive frogs), since the more a frog remains captive, the more it may change its physiological traits (Navas & Gomes, 2001) and, thus, it may present both quantitative and qualitative changes in its defensive behaviors (Boice & Williams, 1971; pers. obs.).

The presence/absence of defensive behaviors is presented in tables, with some of them highlighting specific characteristics, such as display of other behaviors, habitat use, diet, and colors. All scientific names of amphibians follow Frost (2007). Defensive strategies related to colors will be dealt with elsewhere (Toledo & Haddad, in prep.).

Results

Defensive behaviors in anurans are here organized into 28 categories, plus one “ecological”, described below. The most commonly observed defensive behavior was fleeing, followed by remaining motionless, which together represented about 50 % of the records (Figure 1).

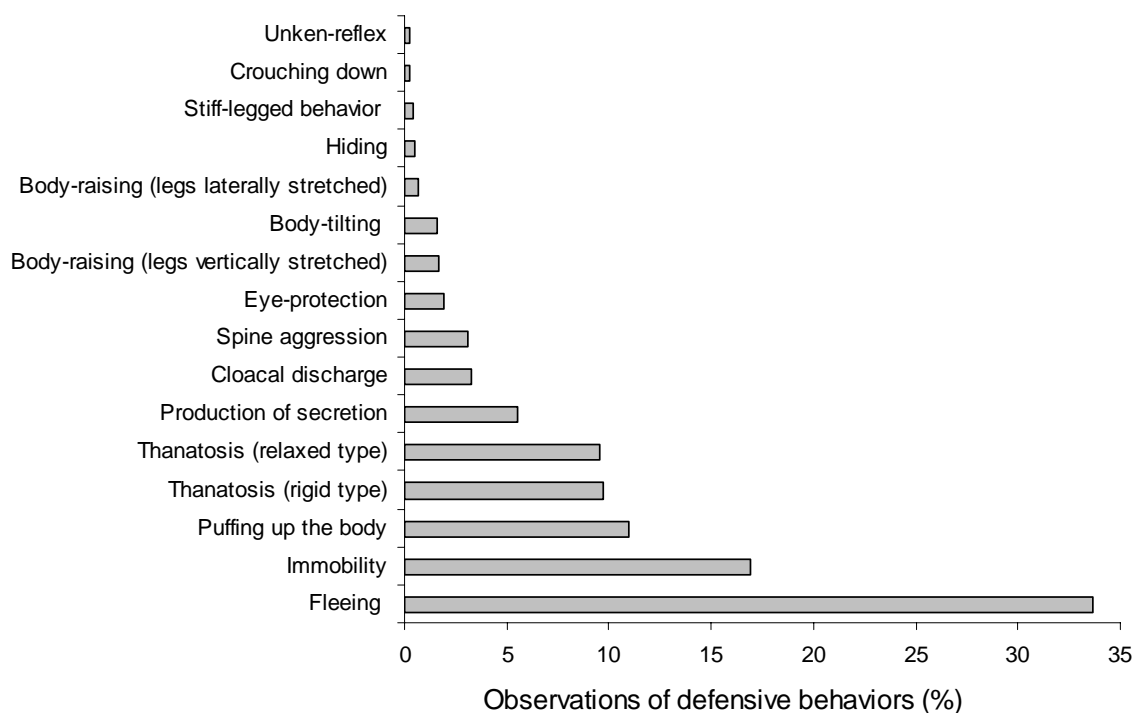


Figure 1. Percentage of records of selected defensive behaviors in the field.

1) *Immobility or Remaining Motionless*

Remaining motionless in the same posture the animal held before the approach of a threat (which, besides the observers, could occasionally be a predator or a larger animal passing nearby) is widespread among anurans. Individuals of all species observed in the field remained motionless as a first line of defense during our approach.

In two experiments (one adult male of *Bokermannohyla circumdata* and one adult male of *Dendropsophus elianeae*) that remained motionless when offered to a colubrid snake (*Liophis miliaris*) went unnoticed, and thus were not preyed by the snake.

Possible synergistic behaviors: motionless is the basis of most of the behaviors discussed below, including fleeing, which may precede or follow a motionless period. Besides these behaviors, coloration, morphology, and granular glands may enhance immobility benefits for the anurans (these aspects will be discussed elsewhere).

2) Crouching down

The frog holds itself in a lower than normal sitting posture, ranging from a slightly lowered position to a full crouch in which the chin touches the substrate. The eyes may remain closed and the forearms may be extended forward or flexed toward the body.

Possible synergistic behaviors: chin-tucking (see below) is almost always present and puffing up the body and skin secretions may co-occur with this behavior.

3) Thanatosis or Death Feigning

Thanatosis is displayed by several species and is found from juvenile to adult phases of both sexes (Table 1). This behavior can be subdivided in two types (“relaxed” and “rigid”) according to changes an observer is able to do in the postures adopted by the frogs.

a) *Thanatosis – relaxed type*

The frog remains motionless, even when touched, generally with its eyes open, but in some cases the eyes may be closed (Figure 2). The legs and arms are not kept in any specific position; they can be moved by the observer to any position and the frog will keep the position (Figure 3). This type was the most commonly recorded and occurs in several families (Table 1).

b) *Thanatosis – rigid type*

In this situation the frog remains motionless, generally with the eyes closed, but in few cases the eyes may remain open. The legs and arms are kept close to the body,

but if the observer tries to outstretch them, they are forced by the frog to the initial position, generally against the belly. Some individuals also flex the dorsum getting an arched shape (Figure 3). This type was recorded for several bufonids, cycloramphids, and hylids. However, it is typically observed in phyllomedusines, in species of *Hypsiboas* of the *pulchellus* group, and bufonids in the genera *Bufo* and *Chaunus* (Table 1).

There are species that may display the two types of thanatosis (see Table 1). Furthermore, there are a few species that may display an intermediate pattern: arms in the posture described for the relaxed type and legs in the posture described for the rigid type. This intermediate pattern was recorded for the bufonids *Melanophryniscus moreirae* and *Chaunus ictericus*.

Possible synergistic behaviors: thanatosis is a motionless defense that may be accompanied by odoriferous secretions (e.g., Sazima, 1974; our pers. obs.) and aposematic colorations in the ventral region (our pers. obs.) or of the tongue (Figure 3; see also tongue protrusion). An extreme situation is exhibited by *Leptopelis rufus* (Arthroleptidae) while in relaxed thanatosis. This frog may remain with its mouth opened during the thanatosis (Figure 3) and, from the mouth, release a strong smell which stinks like ammonia. This would increase even more the illusion of a dead frog (Schmitz et al., 1999).

Table 1. Frogs that display thanatosis. When the number of recorded individuals was available these are presented; when they were not, an “X” indicates the occurrence of the behavior. A dash indicates that there is no information about the type of thanatosis observed. See text for the explanation of the two types of thanatosis. Families, genera, and species are presented in alphabetical order.

Family / Species	Relaxed	Rigid	Reference
<u>Aromobatidae</u>			
<i>Allobates femoralis</i>	-	-	Vaz-Silva & Frota, 2004
<u>Brachycephalidae</u>			
<i>Eleutherodactylus juipoca</i>	1		Present study
<i>Eleutherodactylus binotatus</i>	1		Present study
<i>Eleutherodactylus guentheri</i>	4		Present study
<i>Eleutherodactylus parvus</i>	1		Present study
<u>Bufo</u>			
<i>Bufo ocellatus</i>		X	Kokubum, 2005
<i>Chaunus abei</i>	1		Present study
<i>Chaunus ictericus</i>		8	Present study
<i>Chaunus jimii</i>		5	Present study

<i>Chaunus marinus</i>		X	Vaz-Silva & Frota, 2004
<i>Chaunus ornatus</i>	2		Present study
<i>Chaunus rubescens</i>		2	Present study
<i>Chaunus schneideri</i>		X	Zamprogno et al. 1998; Present study
<i>Dendrophryniscus berthaltutzae</i>	1	1	Present study
<i>Dendrophryniscus brevipolicatus</i>	1		Present study
<i>Dendrophryniscus minutus</i>	-	-	Russel, 2002
<i>Melanophryniscus moreirae</i>		2	Present study
<i>Ollotis occidentalis</i>	-	-	Abbadié-Bisogno et al., 2001
<u>Centrolenidae</u>			
<i>Hyalinobatrachium uranoscopum</i>	2		Present study
<u>Cycloramphidae</u>			
<i>Odontophrynus carvalhoi</i>		1	Present study
<i>Proceratophrys boiei</i>	1	1	Present study
<i>Rhinoderma darwini</i>	-	-	Pough et al., 2001
<u>Dicroglossidae</u>			
<i>Hoplobatrachus tigerinus</i>	-	-	Brodie Jr. & Nussbaum, 1987
<u>Hylidae</u>			
<i>Aplastodiscus arildae</i>		X	Carneiro & Rocha, 2005
<i>Aplastodiscus cochranae</i>		2	Present study
<i>Aplastodiscus perviridis</i>	1	2	Present study
<i>Bokermannohyla circumdata</i>		12	Present study
<i>Bokermannohyla hylax</i>		2	Present study
<i>Dendropsophus elegans</i>	3		Present study
<i>Dendropsophus elianeae</i>	1		Present study
<i>Dendropsophus giesleri</i>	1		Present study
<i>Dendropsophus microps</i>	7	2	Present study
<i>Dendropsophus minutus</i>	6		Present study
<i>Dendropsophus werneri</i>	1		Present study
<i>Hypsiboas albopunctatus</i>	1	6	Sazima, 1972; Present study
<i>Hypsiboas beckeri</i>		10	Present study
<i>Hypsiboas bischoffi</i>	8	11	Present study
<i>Hypsiboas caingua</i>		1	Present study
<i>Hypsiboas faber</i>	2		Present study
<i>Hypsiboas guentheri</i>	2		Present study
<i>Hypsiboas latistriatus</i>		1	Present study
<i>Hypsiboas leptolineatus</i>		1	Present study
<i>Hypsiboas marginatus</i>		2	Present study
<i>Hypsiboas polytaenius</i>		3	Present study
<i>Hypsiboas pulchellus</i>		1	Present study
<i>Hypsiboas semilineatus</i>		2	Azevedo-Ramos, 1995; Present study
<i>Phrynomedusa marginata</i>		2	Present study
<i>Phyllomedusa azurea</i>		3	Present study
<i>Phyllomedusa bahiana</i>		5	Present study
<i>Phyllomedusa burmeisteri</i>		6	Present study
<i>Phyllomedusa centralis</i>		11	Bokermann, 1965; Present study
<i>Phyllomedusa distincta</i>		8	Present study
<i>Phyllomedusa centralis</i>		11	Present study

<i>Phyllomedusa nordestina</i>	9		Present study
<i>Phyllomedusa rohdei</i>	2		Sazima, 1972; 1974; Present study
<i>Phyllomedusa sauvagii</i>	1		Present study
<i>Phyllomedusa tetraploidea</i>	6		Present study
<i>Pseudacris regilla</i>	1		Brattstorm & Warren, 1955; Foster, 2007
<i>Scinax alterus</i>	1		Present study
<i>Scinax catharinae</i>	1		Present study
<i>Scinax fuscomarginatus</i>	15		Toledo, 2004b
<i>Scinax fuscovarius</i>	2	2	Sazima, 1972; Rodrigues & Rodrigues, 2007; Present study
<i>Scinax hayii</i>	1		Present study
<i>Scinax hiemalis</i>	4		Present study
<i>Scinax perpusillus</i>	1		Present study
<i>Xenohyla truncata</i>	-	-	Napoli, 2001
<u>Hyperoliidae</u>			
<i>Kassina fusca</i>	X		Rödel & Braun, 1999
<u>Leiuperidae</u>			
<i>Eupemphix nattereri</i>	3		Present study
<i>Physalaemus cuvieri</i>	5		Present study
<i>Physalaemus nanus</i>	4		Present study
<i>Pseudopaludicola mystacalis</i>	1		Present study
<i>Pseudopaludicola saltica</i>	2		Present study
<u>Leptodactylidae</u>			
<i>Leptodactylus cunicularius</i>	1		Present study
<i>Leptodactylus labyrinthicus</i>	X		Toledo et al., 2005
<i>Leptodactylus fuscus</i>	1		Present study
<i>Leptodactylus marambaiae</i>	-	-	Siqueira et al., 2006
<i>Leptodactylus mystacinus</i>	3		Present study
<i>Leptodactylus ocellatus</i>	3		Present study
<i>Leptodactylus plaumanni</i>	1		Present study
<u>Limnodynastidae</u>			
<i>Neobatrachus pictus</i>	-	-	Williams et al., 2000
<i>Neobatrachys sudeli</i>	-	-	Williams et al., 2000
<u>Microhylidae</u>			
<i>Elachistocleis cf. ovalis</i>	1		Toledo, 2004a
<u>Myobatrachidae</u>			
<i>Crinia georgiana</i>	X		Williams et al., 2000
<i>Crinia glauerti</i>	X		Williams et al., 2000
<i>Geocrinia laevis</i>	X		Williams et al., 2000
<i>Mixophyes fasciolatus</i>	X		Williams et al., 2000
<i>Mixophyes schevilli</i>	X		Williams et al., 2000
<i>Pseudophryne bibronii</i>	X		Williams et al., 2000
<i>Pseudophryne semimarmorata</i>	X		Williams et al., 2000
<u>Ranidae</u>			
<i>Clinotarsus curtipes</i>	-	-	Gramapurohit et al., 2001
<i>Lithobates pipiens</i>	-	-	Boice & Williams, 1971

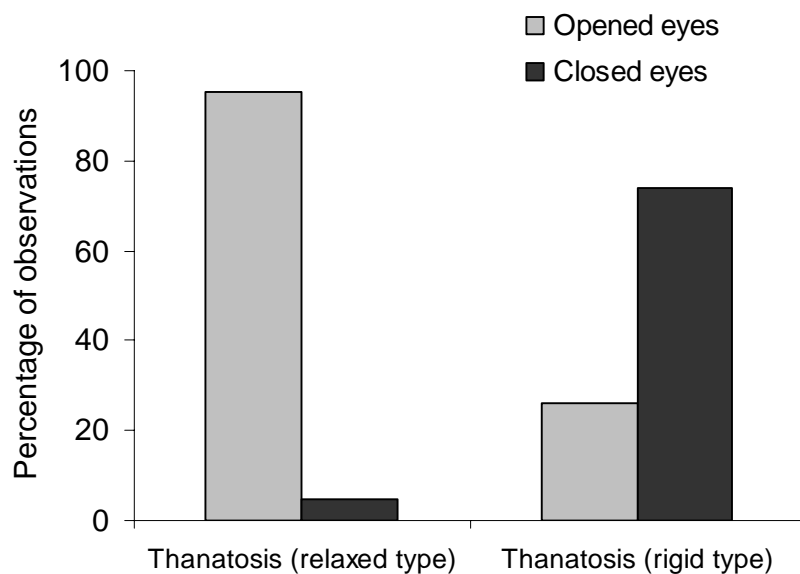


Figure 2. Percentage of open (gray bars) and closed eyes (black bars) during display of thanatosis of the relaxed and rigid types (n = 48 observations).



Figure 3. Thanatosis of the relaxed type in *Scinax fuscomarginatus* (A) and of the rigid type in *Phyllomedusa bahiana* (B). Tong protrusion in *Acanthixalus spinosus* (C) and *Leptopelis rufus* with its mouth opened for the secretion of ammonia-like smell (D), both during thanatosis of the relaxed type.

4) *Chin-tucking*

Chin-tucking is recorded for several species (Table 2) and is characterized by the chin pulled toward the pectoral region, flexing the head towards the belly. Eyes may be closed in some cases. Although probably widespread, reports on this behavior are scarce likely due to its preceding other, more conspicuous behaviors.

Possible synergistic behaviors: chin tucking may precede or be part of crouching, thanatosis (rigid type), phragmosis, and puffing up the body.

5) *Phragmosis*

Phragmosis is the use of the head to obstruct the access to the body of the frog. Thus, there must be a tunnel-like structure to be used to shelter the body of the frog. Species known to use phragmosis may use rock crevices, burrows, tree holes, or bromeliads as shelter (Table 3).

Possible synergistic behaviors: chin-tucking is almost always present and puffing up the body may be present in some cases. Presence of bony spines associated with noxious glands in the head may be related to phragmosis as well (see Jared et al., 2005).

Table 3. Frog species that display phragmosis and the substrate used for it. The inclusion of *Anothea spinosa* here is a suggestion (see discussion). Families, genera, and species are presented in alphabetical order.

Species	Substrate used	Source
<u>Bufonidae</u>		
<i>Chaunus granulatus</i>	Burrows in the ground	Present study
<i>Peltophryne empusa</i>	Burrows in the ground	Barbour, 1914
<u>Hylidae</u>		
<i>Anothea spinosa</i>	Holes in trees or bamboos	Present study
<i>Aparasphenodon bokermanni</i>	Bromeliads	Present study
<i>Aparasphenodon brunoi</i>	Bromeliads	Lutz & Lutz, 1939; Duellman & Klaas, 1964
<i>Corythomantis greeningi</i>	Rock crevices	Jared et al., 2005; Present study
<i>Smilisca fodiens</i>	Burrows in the ground	Firschein, 1951
<i>Triprion petasatus</i>	Holes in trees	Stuart, 1935; Duellman & Klaas, 1964
<i>Triprion spatulatus</i>	Holes in trees	Duellman & Klaas, 1964

Table 2. Chin-tucking, crouching, puffing up the body, hiding, cloacal discharge (liquid), spine-aggression (three types), and production of secretions (four types) in frogs. See text for further explanations. Families, genera, and species in alphabetical order.

Species	Chin-tucking	Crouching	Puffing up the body	Hiding	Cloacal-discharging	Spine-puncturing	Spine-scratching	Spine-traumatizing	Secretion (odor)	Secretion (adhesive)	Secretion (noxious)	Secretion (slippery)	Source
<u>Aromobatidae</u>													
<i>Allobates alagoanus</i>				X									Present study
<u>Bombinatoridae</u>													
<i>Bombina bombina</i>			X								X		Bajger, 1980
<u>Brevicipitidae</u>													
<i>Callulina krefftii</i>		X	X										Harper & Vonesh, in press
<u>Bufonidae</u>													
<i>Anaxyrus americanus</i>	X	X	X	X									Marchisin & Andrews, 1978
<i>Anaxyrus boreas</i>	X	X	X	X									Pearl & Hayes, 2002
<i>Anaxyrus quercicus</i>	X	X	X	X									Marchisin & Andrews, 1978
<i>Anaxyrus terrestris</i>	X	X	X	X									Marchisin & Andrews, 1978
<i>Bufo ocellatus</i>			X		X								Kokubum, 2005
<i>Chaunus ictericus</i>			X		X						X		Present study
<i>Chaunus ornatus</i>	X										X		Present study
<i>Chaunus schneideri</i>	X	X									X		Toledo & Jared, 1995
<i>Melanophryniscus moreirae</i>					X								Present study
<u>Cryptobatrachidae</u>													
<i>Stefania woodleyi</i>													
<u>Cycloramphidae</u>			X										Kok et al., 2007

<i>Cyclopramphus acangatam</i>				X					Present study
<i>Cyclopramphus eleutherodactylus</i>				X					Present study
<i>Eupsophus emiliopugini</i>		X							Formas & Poblete, 1996
<i>Macrogenioglottus aliptoi</i>		X		X					Present study
<i>Odontophrynus americanus</i>		X		X					Present study
<i>Proceratophrys boiei</i>		X							Present study
<i>Proceratophrys cururu</i>		X						X	Present study
<u>Dendrobatidae</u>									
<i>Oophaga pumilio</i>								X	Hagman, 2006
<u>Dicroglossidae</u>									
<i>Hoplobatrachus tigerinus</i>		X							Brodie Jr. & Nussabaum, 1987
<u>Hylidae</u>									
<i>Acris crepitans</i>		X							McCallum, 1999
<i>Acris gryllus</i>		X	X						Marchisin & Andrews, 1978
<i>Aplastodiscus arildae</i>		X	X	X				X	Present study
<i>Bokermannohyla alvarengai</i>					X				Present study
<i>Bokermannohyla circumdata</i>		X		X				X	Present study
<i>Bokermannohyla hylax</i>		X		X				X	Present study
<i>Bokermannohyla luctuosa</i>					X			X	Present study
<i>Hyla arenicolor</i>									Powell & Lieb, 2003
<i>Hyla chrysoceles</i>	X	X	X					X	Marchisin & Andrews, 1978
<i>Hyla cinerea</i>		X	X						Marchisin & Andrews, 1978
<i>Hyla femoralis</i>		X	X						Marchisin & Andrews, 1978
<i>Hypsiboas albomarginatus</i>								X	Present study
<i>Hypsiboas bischoffi</i>	X			X				X	Present study
<i>Hypsiboas faber</i>				X					Present study
<i>Hypsiboas pardalis</i>				X	X			X	Present study
<i>Hypsiboas prasinus</i>				X	X				Present study
<i>Hypsiboas raniceps</i>				X				X	Present study
<i>Litoria alboguttata</i>			X						Williams et al., 2000

<i>Litoria caerulea</i>									X	Williams et al., 2000
<i>Litoria ewingi</i>	X	X							X	Williams et al., 2000
<i>Litoria novaehollandiae</i>	X	X							X	Williams et al., 2000
<i>Phyllomedusa bahiana</i>	X									Present study
<i>Phyllomedusa burmeisteri</i>	X									Present study
<i>Pseudacris crucifer</i>		X							X	Marchisin & Andrews, 1978
<i>Pseudacris ocularis</i>		X							X	Marchisin & Andrews, 1978
<i>Scinax fuscomarginatus</i>									X	Toledo, 2004b
<i>Scinax fuscovarius</i>									X	Present study
<i>Scinax similis</i>									X	Present study
<i>Trachycephalus venulosus</i>		X							X	Manzanilla et al., 1998; Present study
<i>Xenohyla truncata</i>		X							X	Napoli, 2001
<u>Hyperoliidae</u>										
<i>Kassina kuvangensis</i>		X								Channing & Howell, 2003
<i>Kassina maculata</i>		X								Channing & Howell, 2003
<i>Kassina cochranae</i>		X								Channing & Howell, 2003
<i>Kassina lamottei</i>		X								Channing & Howell, 2003
<i>Phlyctimantis verrucosus</i>									X	Channing & Howell, 2003
<u>Leiopelmatidae</u>										
<i>Leiopelma archey</i>	X									Green, 1988
<i>Leiopelma hamiltoni</i>	X									Green, 1988
<i>Leiopelma hochstetteri</i>	X									Green, 1988
<u>Leiuperidae</u>										
<i>Physalaemus nattereri</i>		X							X	Rodrigues & Filho, 2004
<u>Leptodactylidae</u>										
<i>Leptodactylus fuscus</i>									X	Present study
<i>Leptodactylus labyrinthicus</i>		X						X	X	Toledo et al., 2005; present study
<i>Leptodactylus mystaceus</i>									X	Present study
<i>Leptodactylus mystacinus</i>									X	Carvalho Jr., 2005; Present study
<i>Leptodactylus ocellatus</i>								X	X	Present study

<i>Lithobates clamitans</i>	X	X	X	X	Marchisin & Andrews, 1978
<i>Lithobates palustris</i>	X	X	X	X	Marchisin & Andrews, 1978; Grant, 2001
<i>Lithobates pipiens</i>	X	X	X	X	Marchisin & Andrews, 1978
<i>Lithobates septentrionalis</i>					Grant, 2001
<i>Lithobates sylvaticus</i>		X			McCallum et al., 2003
<i>Rana muscosa</i>				X	Grant, 2001
Scaphiopodidae					
<i>Spea hammondi</i>				X	Waye & Shewchuk, 1995
<i>Spea intermontana</i>				X	Waye & Shewchuk, 1995
<i>Spea multiplicata</i>				X	Livo et al., 1997
<i>Scaphiopus holbrookii</i>		X		X	Marchisin & Andrews, 1978

6) Puffing up the body

Puffing up the body consists in filling the lungs with air, and thus enlarging the frog's size. This behavior may be performed on the ground or vegetation, floating in the water, or while seized by a predator. During the disinflation of the lungs, some bufonids may emit a noise produced by the expiration. In snakes a similar noise is considered a defensive strategy (Martins, 1996). For anurans there is no evidence that it would function as a defensive behavior.

Possible synergistic behaviors: puffing up the body may be accompanied by crouching, chin-tucking, thanatosis, phragmosis, body-raising, body-tilting, mouth-gaping, and eye protection (for these four latter behaviors, see below).

7) Body-raising

Two types ("legs vertically stretched" and "legs laterally stretched") of body-raising are here considered:

a) Body-raising (legs vertically stretched)

This behavior is described mostly for toxic species (Table 4). This body-raising type may be displayed in two forms: a) partial: the frog stretches the legs vertically and keeps its snout close to, or touching, the ground; or b) full: the frog stretches the legs and arms, thus lifting the belly and snout off the ground. In both postures the eyes may be closed and aposematic colors and eyespots-like glands (which were hidden in the normal posture) may be displayed (Figure 4).

b) Body-raising (legs laterally stretched)

In this type of body-raising, the frog stretches the legs keeping its snout close to, or touching, the ground, similarly to the partial body-raising; however, it also stretches the legs laterally in such way that in its maximum it extends the legs in front of its snout (Table 4; Figure 5).

Possible synergistic behaviors: body-raising of both types are closely related to puffing up the body (almost always present) and body-tilting (almost always present), presence of skin secretions (noxious or odoriferous). Eye-protection (most commonly among species that display body-raising of the first type), and mouth-gaping may co-

occur with body-raising (most commonly among species that display body-raising of the second type).



Figure 4. Body-raising of the “legs vertically stretched” type (partial) and eyespots-like glands in *Edalorhina perezii* (A) and *Eupemphix nattereri* (B); resting posture (C) and body-raising of the full “legs laterally stretched” type (D) in *Leptodactylus lineatus*; same behavior but partial in *L. bolivianus* (E) and *L. labyrinthicus* (F). *Leptodactylus lineatus* and *L. labyrinthicus* additionally display aposematic colorations (hidden in resting postures).

Table 4. Frog species that display body-raising (“legs vertically stretched” and “legs laterally stretched” types) and body-tilting. Presence/absence of aposematic (warning) coloration in the posterior region (post-femoral and groin), eyespots-like glands, and noxious skin secretions. See text for further explanations. Families, genera, and species in alphabetical order.

Species	Body-raising type	Aposematic coloration	Noxious skin secretion	Intensity of body-raising	Body tilting	Source
<u>Brachycephalidae</u>						
<i>Eleutherodactylus curtipes</i>	Legs vertical	No	No	NA	?	Duellman & Trueb, 1994
<u>Bufonidae</u>						
<i>Chaunus ornatus</i>	Legs vertical	No	Yes	Full	Yes	Toledo, 2004c
<i>Ollotis alvaria</i>	Legs vertical	No	Yes	Full	Yes	Hanson & Vial, 1956
<u>Ceratophryidae</u>						
<i>Atelognathus praebasalticus</i>	Legs vertical	No	?	Full	?	Cei, 1980
<u>Cycloramphidae</u>						
<i>Eupsophus emiliopugini</i>	Legs vertical	?	?	?	?	Formas & Poblete, 1996
<i>Macrogenioglottus alipioi</i>	Both	Yes	?	Full	Yes	Present study
<u>Dendrobatidae</u>						
<i>Ameerega flavopicta</i>	Legs vertical	Yes	Yes	Partial	No	Toledo et al., 2004
<u>Dicroglossidae</u>						
<i>Hoplobatrachus tigrinus</i>	Legs vertical	No	Yes	Partial	?	Brodie Jr. & Nussabaum, 1987
<u>Hylidae</u>						
<i>Aplastodiscus albosignatus</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus arildae</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus callipygius</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus cochranae</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus leucopygius</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus perviridis</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Hyla versicolor</i>	Legs vertical	Yes	Yes	Partial	Yes	Brodie Jr. & Formanowicz, 1981
<i>Hyloscirtus tapichalaca</i>	Legs lateral	?	?	NA	?	Kizirian et al., 2003
<i>Hypsiboas semilineatus</i>	Legs lateral	?	?	NA	?	Azevedo-Ramos, 1995
<i>Litoria alboguttata</i>	Legs vertical	Yes	Yes	Full	Yes	Williams et al., 2000

<i>Litoria aurea</i>	Legs vertical	Yes	Partial	Yes	Williams et al., 2000
<i>Litoria australis</i>	Legs vertical	No	Full	?	Williams et al., 2000
<i>Litoria caerulea</i>	Legs vertical	Yes	Partial	Yes	Williams et al., 2000
<i>Litoria cultripes</i>	Both	No	Partial	?	Williams et al., 2000
<i>Litoria novaehollandiae</i>	Legs vertical	No	Partial	?	Williams et al., 2000
<i>Xenohyla truncata</i>	Legs lateral	?	NA	?	Napoli, 2001
<u>Hyperoliidae</u>					
<i>Phlyctimantis keithae</i>	Legs vertical	Yes	?	?	Rödl & Ernst, 2001
<i>Phlyctimantis boulengeri</i>	Legs vertical	Yes	?	?	Rödl & Ernst, 2001
<u>Leiuperidae</u>					
<i>Edalorhina perezii*</i>	Legs vertical	No	Partial	Yes	Present study
<i>Eupemphix nattereri*</i>	Legs vertical	No	Partial	Yes	Sazima & Caramaschi, 1988; Lenzi-Mattos et al., 2005
<i>Physalaemus deimaticus*</i>	Legs vertical	No	Partial	Yes	Sazima & Caramaschi, 1988
<i>Physalaemus marmoratus</i>	Legs vertical	No	Partial	Yes	Present study
<i>Pleurodema brachyops*</i>	Legs vertical	Yes	Partial	?	Martins, 1989
<i>Pleurodema bufonina*</i>	Legs vertical	No	Partial	?	Cei, 1962
<i>Pleurodema thaul*</i>	Legs vertical	No	Partial	?	Cei & Espina, 1957
<u>Leptodactylidae</u>					
<i>Leptodactylus labyrinthicus</i>	Legs vertical	Yes	Full	Yes	Toledo et al., 2005
<i>Leptodactylus laticeps</i>	Legs vertical	Yes	Full	Yes	Cei, 1980; Heyer & Scott Jr., 2006
<i>Leptodactylus mystacinus</i>	Legs vertical	Yes	Full	Yes	Carvalho Jr., 2005
<i>Leptodactylus ocellatus</i>	Legs vertical	No	Partial	Yes	Present study
<u>Limnodynastidae</u>					
<i>Heleioporus eyrei</i>	Legs vertical	No	Full	?	Williams et al., 2000
<i>Limnodynastes dumerilii</i>	Legs vertical	No	Partial	?	Williams et al., 2000
<i>Limnodynastes convexiusculus</i>	Legs vertical	No	Partial	?	Williams et al., 2000
<i>Limnodynastes lignarius</i>	Legs vertical	No	Partial	?	Williams et al., 2000
<i>Limnodynastes tasmaniensis</i>	Legs vertical	No	Full	?	Williams et al., 2000
<i>Limnodynastes terraereginae</i>	Legs vertical	Yes	Partial	?	Williams et al., 2000

<i>Opisthodon spenceri</i>	Legs vertical	No	No	Partial	?	Williams et al., 2000
<u>Microhylidae</u>						
<i>Ctenophryne geayi</i>	Legs vertical	No	?	Partial	?	Menin & Rogrigues, 2007
<i>Elachistocleis erythrogaster</i>	Legs lateral	?	?	NA	?	Kwet & Solé, 2002
<i>Elachistocleis ovalis</i>	Both	Yes	No	Partial	?	Kokubum & Menin, 2002
<i>Phrynomantis microps</i>	Legs lateral	?	?	NA	?	Rödel & Braun, 1999
<i>Plethodontohyla tuberata</i>	Legs vertical	Yes	?	?	?	Nincheri & Andreone, 2002
<u>Myobatrachidae</u>						
<i>Pseudophryne bibronii</i>	Legs lateral	Yes	Yes	NA	?	Williams et al., 2000
<i>Pseudophryne semimarmorata</i>	Legs lateral	Yes	Yes	NA	?	Williams et al., 2000
<i>Uperoleia altissima</i>	Legs vertical	Yes	Yes	Partial	Yes	Williams et al., 2000
<i>Uperoleia aspera</i>	Legs vertical	Yes	Yes	Partial	?	Brodie Jr. et al., 1998
<i>Uperoleia borealis</i>	Legs vertical	Yes	Yes	Partial	?	Brodie Jr. et al., 1998
<i>Uperoleia laevigata</i>	Legs vertical	Yes	Yes	Partial	Yes	Torr, 1991
<i>Uperoleia lithomoda</i>	Legs vertical	Yes	Yes	Partial	Yes	Brodie Jr. et al., 1998
<i>Uperoleia littlejohni</i>	Legs vertical	Yes	Yes	Partial	Yes	Williams et al., 2000
<i>Uperoleia mjobergi</i>	Legs vertical	No	Yes	Full	?	Brodie Jr. et al., 1998
<i>Uperoleia talpa</i>	Legs vertical	No	Yes	Full	?	Brodie Jr. et al., 1998
<u>Scaphiropodidae</u>						
<i>Spea intermontana</i>	Legs vertical	No	?	Partial	Yes	Waye & Shewchuk, 1995

* Species with eyespots-like glands.

“NA” = Not applies.

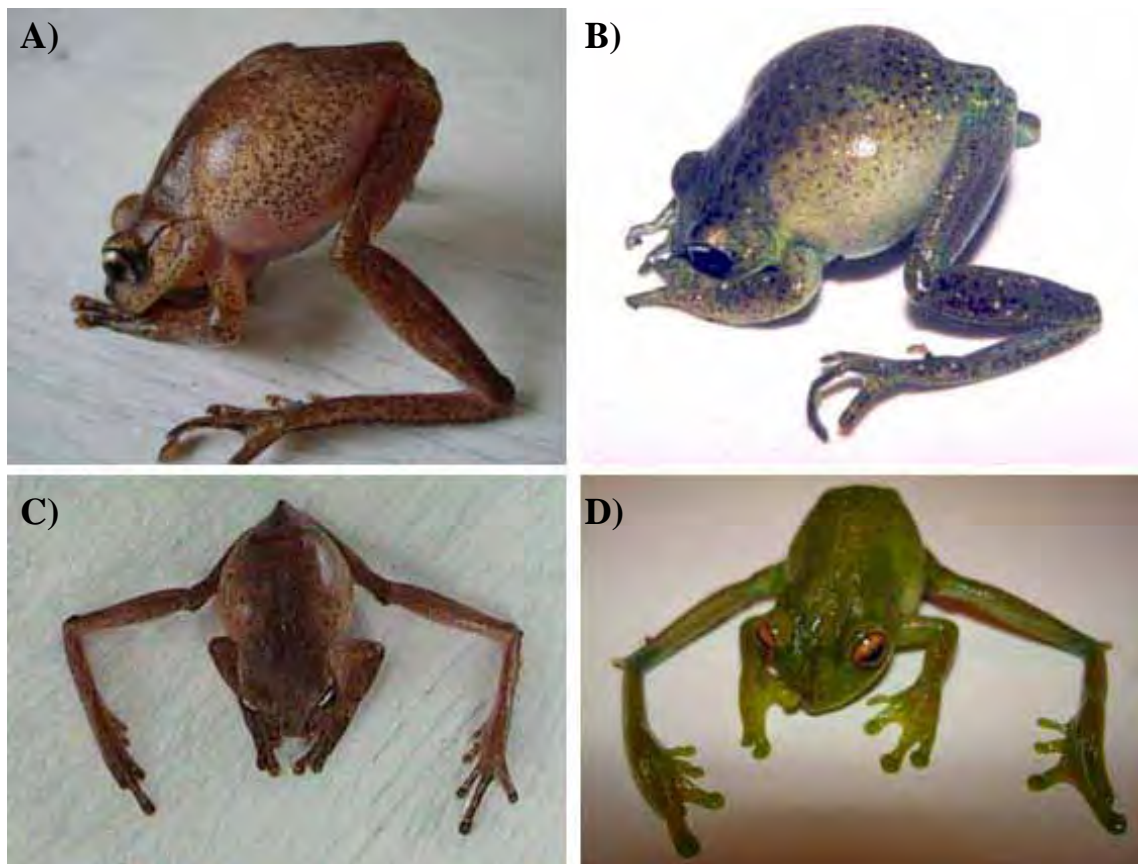


Figure 5. Body-raising of the “legs laterally stretched” type in *Aplastodiscus cochranae* (A) and *A. perviridis* (B) in lateral view, and *A. cochranae* (C) and *A. albosignatus* (D) in dorsal view.

8) Body-tilting

During the approach of a predator, where tactile contact with the prey may be the strongest stimulus for the display of defensive behavior, a body-raising frog may direct its dorsum towards the predator (Table 4).

Possible synergistic behaviors: body-tilting always involve body-raising (both types), and is strongly marked by the presence of puffing up the body, display of glands and aposematic coloration, and skin secretions (noxious, odoriferous, or slippery ones).

9) Stiff-legged behavior

Stiff-legged behavior, as coined by Sazima (1978), is a motionless behavior preceded by short leaps. After leaping one or a few times in an erratic fashion, the frog ends with its belly down and limbs stretched backwards (Figure 6). This defensive behavior is known for a few Neotropical species that dwell on the forest floor and have cryptic coloration of fallen brown or green leaves (Table 5).

Possible synergistic behaviors: stiff-legged behavior is highly related to cryptic (leaf-like) dorsal coloration. No other defensive behavior has been reported to co-occur with this peculiar behavior.

Table 5. Frog species that display stiff-legged behavior, their habitat, and general pattern of dorsal coloration. Families, genera, and species in alphabetical order.

Species	Habitat	Dorsal coloration pattern	Source
<u>Brachycephalidae</u>			
<i>Euparkerella cochranae</i>	Forest floor	Dead leaf	Present study
<u>Bufo</u>			
<i>Dendrophryniscus berthaltzuae</i>	Forest floor	Dead leaf	Present study
<i>Dendrophryniscus brevipollicatus</i>	Forest floor	Dead leaf	Bertoluci et al., 2007
<i>Dendrophryniscus leucomystax</i>	Forest floor	Dead leaf	Bertoluci et al., 2007
<u>Cycloramphidae</u>			
<i>Proceratophrys appendiculata</i>	Forest floor	Dead leaf	Sazima, 1978
<i>Proceratophrys boiei</i>	Forest floor	Dead leaf	Toledo & Zina, 2004
<i>Proceratophrys melanopogon</i>	Forest floor	Dead leaf	Present study
<i>Zachaenus parvulus</i>	Forest floor	Dead leaf	Rocha et al., 1998
<u>Leptodactylidae</u>			
<i>Paratelmatoobius poecilogaster</i>	Forest floor	Dead leaf	Present study
<i>Scythrophrys</i> sp.	Forest floor	Dead leaf	Garcia, 1999
<u>Microhylidae</u>			
<i>Ctenophryne geayi</i>	Forest floor	Dead leaf	Schlüter & Salas, 1991; Menin & Rodrigues, 2007
<i>Stereocyclops parkeri</i>	Forest floor	Dead leaf	Sazima, 1978

10) Eye-protection

While remaining motionless in the chin-tucking or other defensive postures, some frog species may cover the head, eyes and/or the tympanum with the forearms. Some species may arch slightly the body upwards while displaying the eye protection behavior. Some individuals close the eyes when in the arched posture (Table 6; Figure 7).

Possible synergistic behaviors: Puffing up the body and body-raising may come with eye-protection. Additionally, some species produce odoriferous secretions.

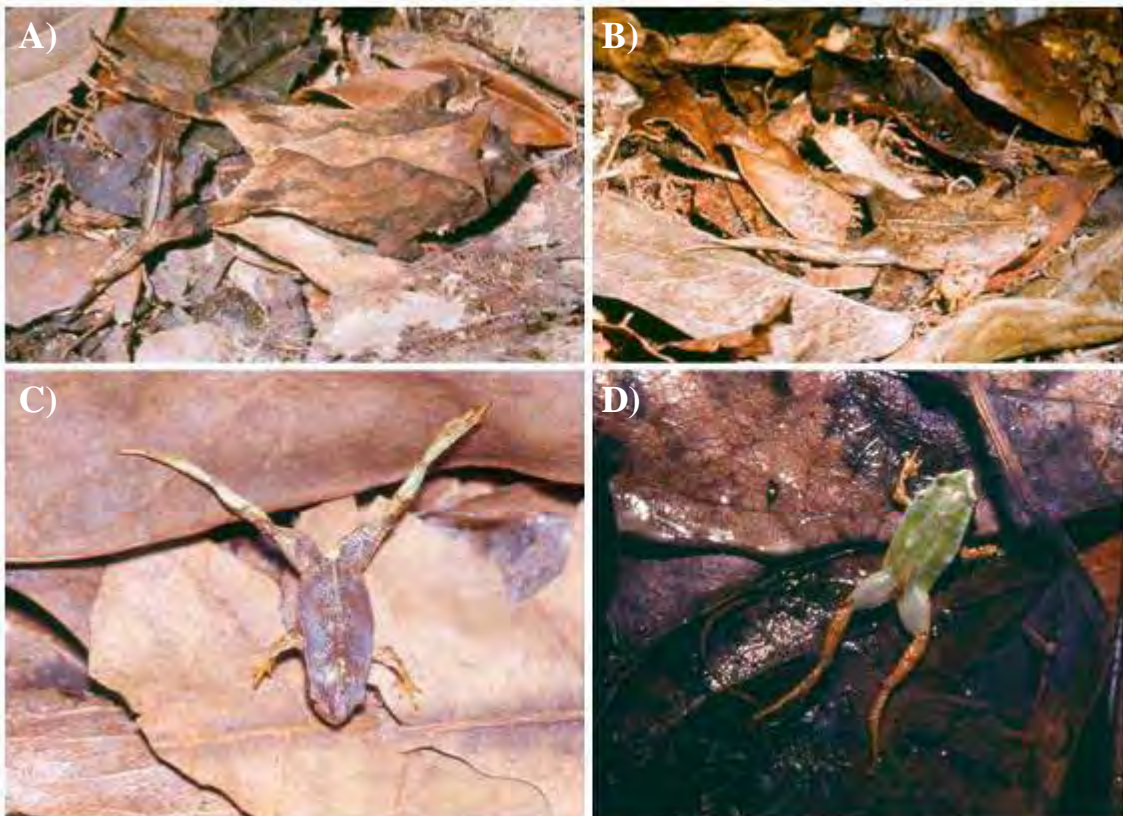


Figure 6. Stiff-legged behavior in *Proceratophrys appendiculata* (A), *Stereocyclops incrassatus* (B), a brown morph (C) and a green morph (D) *Scythrophrys* sp.

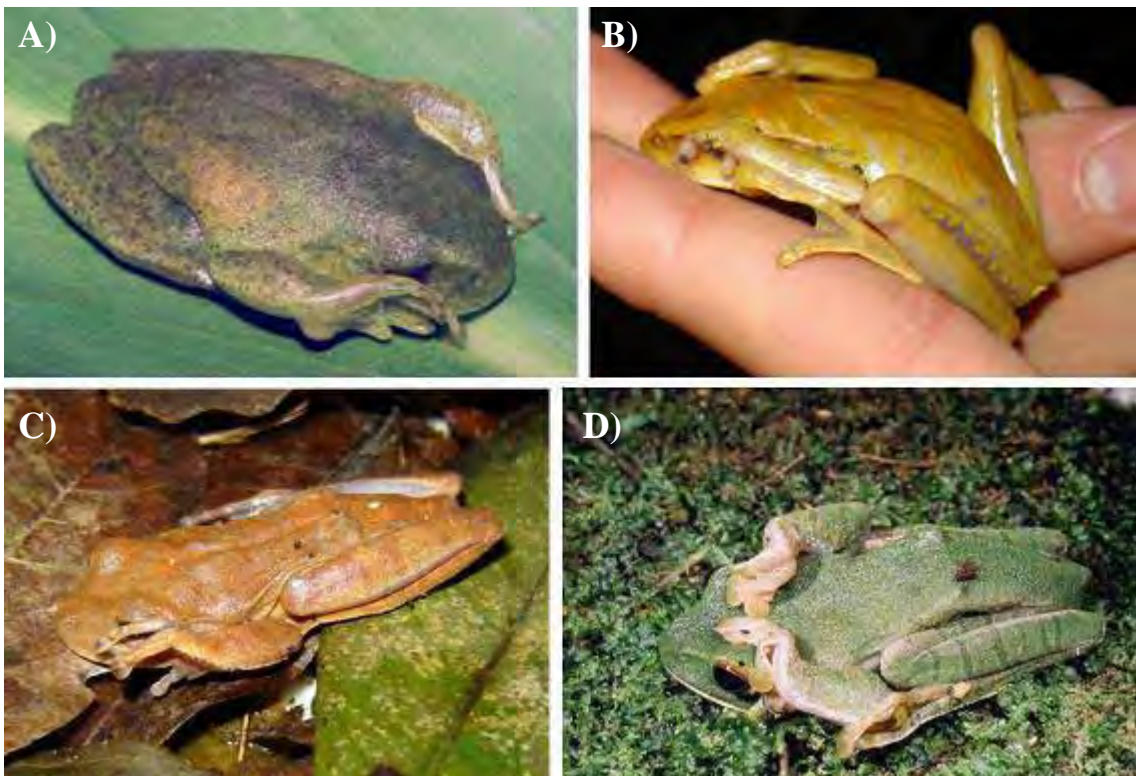


Figure 7. Eye-protection in *Aplastodiscus perviridis* (A), *Hypsiboas albopunctatus* (B), *Bokermannohyla luctuosa* (C), and *Boophis albilabris* (D).

Table 6. Frog species that protect the eye with hand, have aposematic (warning) coloration, and produce noxious secretions. Families, genera, and species in alphabetical order.

Species	Aposematic coloration	Noxious secretions*	Source
<u>Hylidae</u>			
<i>Acris crepitans</i>	No	?	McCallum, 1999
<i>Aplastodiscus albosignatus</i>	No	?	Present study
<i>Aplastodiscus cochranæ</i>	No	?	Present study
<i>Aplastodiscus leucopygius</i>	No	?	Present study
<i>Aplastodiscus perviridis</i>	No	?	Present study
<i>Bokermannohyla alvarengai</i>	No	?	Vrcibradic & van Sluys, 2000
<i>Bokermannohyla hylax</i>	No	?	Present study
<i>Hypsiboas albopunctatus</i>	No	No	Present study
<i>Hypsiboas calcaratus</i>	No	?	Angulo & Funk, 2006
<i>Hypsiboas fasciatus</i>	No	?	Angulo & Funk, 2006
<u>Mantellidae</u>			
<i>Boophis albilabris</i>	No	?	Andreone, 2002
<u>Limnodynastidae</u>			
<i>Heleioporus eyrei</i>	No	Yes	Williams et al., 2000
<i>Neobatrachus pictus</i>	No	Yes	Williams et al., 2000
<i>Neobatrachys sudeli</i>	No	Yes	Williams et al., 2000
<u>Racophoridae</u>			
<i>Nyctixalus pictus</i>	Yes	?	Das et al., 2004
<u>Ranidae</u>			
<i>Lithobates capito</i>	No	?	Means, 2004
<i>Lithobates sylvaticus</i>	No	?	McCallum et al., 2003
<i>Rana draytonii</i>	No	?	Wilkinson, 2006
<i>Rana temporaria</i>	No	?	Haberl & Wilkinson, 1997

11) Unken Reflex

This behavior is known for species of the genera *Bombina*, *Melanophryniscus*, *Pseudophryne*, and *Smilisca* (Table 7). “Unken” means *Bombina* in German, a genus widely known due to its peculiar defensive posture. Unken reflex involves withdrawing and lifting the four legs off the substrate, and arching the body showing contrasting aposematic colors on the belly, throat, and ventral surface of feet and hands (except for *Smilisca fodiens*). While displaying the unken reflex, the frog may close the eyes and produce noxious secretions.

This behavior shows individual variation in the presence/absence of it (Löhner, 1919) and in the extent it is displayed (Bajger, 1980). Young *Bombina* sp., which have no contrasting abdominal colors yet, are unable to display the unken reflex (Löhner,

1919). In adult *Bombina* spp. and *Melanophryniscus* spp., the behavior may vary from a partial unken reflex to a full one (*sensu* Bajger, 1980). In the full reflex the bright ventral color is clearly visible (Figure 8A) and the eyes are closed. In the partial reflex the limbs are off the ground, the bright ventral color is sometimes visible, and the eyes are open (Figure 8B). The species that were recorded displaying the full unken reflex also displayed the partial one. The opposite is not recorded (Bajger, 1980; present study).

Possible synergistic behaviors: unken reflex may be accompanied by noxious secretions, puffing up the body (Bajger, 1980), and ventral aposematic colors as a rule (except for *Smilisca fodiens*).

Table 7. Frog species that display the unken reflex. Families, genera, and species are presented in alphabetical order.

Species	Dorsal coloration	Ventral coloration	Unken reflex extent	Source
<u>Bombinatoridae</u>				
<i>Bombina bombina</i>	Cryptic Black	Aposematic Orange/red	Full	Bajger, 1980; Haberl & Wilkinson, 1997
<i>Bombina orientalis</i>	Cryptic Green	Aposematic Orange/red	Full	Bajger, 1980; Haberl & Wilkinson, 1997
<i>Bombina variegata</i>	Cryptic Black	Aposematic Yellow	Full	Haberl & Wilkinson, 1997
<u>Bufonidae</u>				
<i>Melanophryniscus cambaraensis</i>	Aposematic Green	Aposematic Red	Partial	Present study
<i>Melanophryniscus fulvoguttatus</i>	Aposematic Black/yellow	Aposematic Red/yellow	Partial	C. P. A. Prado, pers. comm.
<i>Melanophryniscus moreirae</i>	Cryptic Brown	Aposematic Red	Partial	Present study
<i>Melanophryniscus parnaciaensis</i>	Cryptic Brown	Aposematic Orange	Partial	D. Loebmann, pers. comm.
<i>Melanophryniscus stelzneri</i>	Aposematic Black/yellow	Aposematic Red/yellow	Full	Cei, 1980
<i>Melanophryniscus tumifrons</i>	Cryptic Brown	Aposematic Red	Full	Present study
<u>Hylidae</u>				
<i>Smilisca fodiens</i>	Cryptic Brown	White	Full	Firschein, 1951
<u>Myobatrachidae</u>				
<i>Pseudophryne semimarmorata</i>	Cryptic Gray/black	Aposematic Blue/orange/black	Partial	Williams et al., 2000

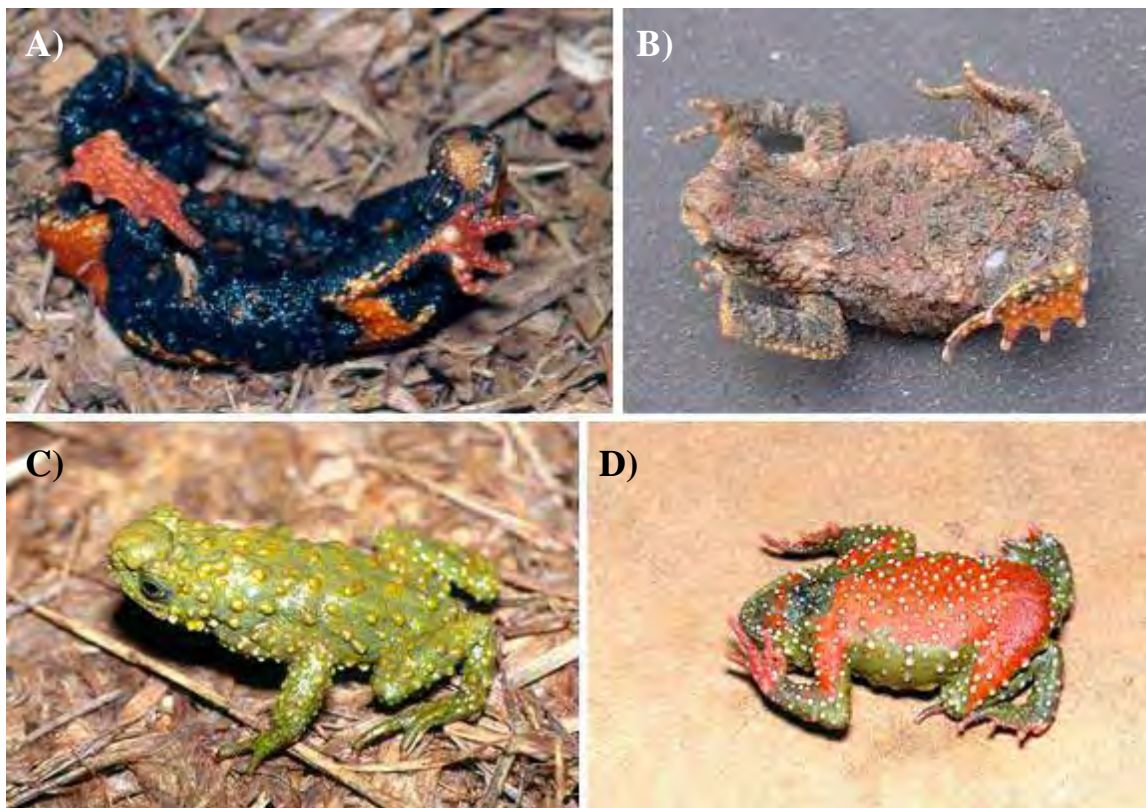


Figure 8. Full (A) and partial (B) unken reflex in *Melanophryniscus tumifrons* and *M. parnaciaensis*, respectively. Below, *M. cambaraensis* in an undisturbed posture (C) and turned with its belly up (D).

12) Legs-interweaving

This unusual behavior has been described only for the hyperoliid *Phlyctimantis keithae*. When disturbed the frog twists onto its back, throwing its limbs across the body and displaying aposematic or disruptive colors on the legs and belly. This behavior breaks the outline of the frog (Channing & Howell, 2003).

Possible synergistic behaviors: legs-interweaving is accompanied by disruptive or aposematic color patterns and possibly by the presence of noxious secretions.

13) Flipping onto the back

Some frogs when frightened may jump and end with the belly upwards (*Scinax hiemalis* and *Melanophryniscus cambaraensis*: present study), or they may just flip onto the back (*Pseudophryne bibronii* and *P. semimarmorata*: Williams et al., 2000), generally displaying aposematic (warning) colors.

Possible synergistic behaviors: a motionless behavior followed by thanatosis and eventual fleeing.

14) Hiding

Hiding implies movement to behind or under an object, such as a leaf fallen to the ground, dead or live vegetation, or to burrows or crevices.

15) Digging

Some individuals of a few species [*Leptodactylus mystaceus*, *Eupemphix nattereri*, *Odontophrynus americanus*, *Proceratophrys cururu*, *P. moratoi* (present study), *Gastrophryne carolinensis*, and *Scaphiopus holbrookii* (Marchisin & Andrews, 1978)] when disturbed or cornered bury themselves in the ground digging with their hindlimbs. All these species are fossorial (burrowing) for at least a period of the year.

16) Active escape or fleeing

Fleeing may be used by all species of anurans. Indeed, all individuals of species observed in the field tried to escape. This escape can be either quick and erratic, or less rapid but directed and vigorous. Besides fleeing in any direction, the frog may do so moving backward, climbing, walking, jumping into the water, entering into a burrow, or parachuting.

There is a particular case of fleeing, called “balling behavior” described for bufonid species of the genus *Oreophrynella*: *O. vasquezi*, *O. nigra*, and *O. quelchii*. The frogs adopt a crouched posture with chin tucking and fold their arms and legs under the body, and when they are on a sloping terrain, they would move downhill as a rolling stone (McDiarmid & Gorzula, 1989).

Possible synergistic behaviors: fleeing may be accompanied with liquid cloacal discharge, distress calls, and flash colors. Balling behavior may be accompanied by aposematic colorations.

17) Cloacal discharge

Cloacal discharge is generally produced when the frog is seized by or fleeing from a predator. The discharged material may be liquid or solid. Liquid cloacal discharge (extrusion of bladder contents) is the commonest behavior, occurring in many species (Table 4). Solid discharge or defecation (feces expelled with force from the

intestine) was reported for *Anaxyrus terrestris* only, while seized by a snake (Marchisin & Andrews, 1978).

Possible synergistic behaviors: cloacal discharge occurs during fleeing or fighting a predator. Besides this, it may co-occur with puffing up the body.

18) Charging

Threatened anurans may charge at the predator as an intimidating technique. This behavior was observed for *Leptodactylus ocellatus*, *Ceratophrys aurita*, and *C. joazeirensis* (present study).

Possible synergistic behaviors: while charging the frog may emit warning calls, display mouth-gaping and/or aposematic coloration, puff up the body, and display body-raising. If the frog gets close to the predator, charging may end in biting or head hitting.

19) Head hitting

Some leptodactylids (*Leptodactylus bolivianus*, *L. chaquensis*, *L. ocellatus*, and *L. podicipinus*) are known to hit predators with the head. In all recorded instances the frogs were females guarding foam nests or tadpoles (Vaira, 1997; Prado et al., 2000; present study).

Possible synergistic behaviors: charging generally precedes head hitting.

20) Biting

Biting as a defensive strategy is reported for 16 frog species, and we add here five species to this list: *Ceratophrys aurita*, *C. joazeirensis*, *Cycloramphus acangatan*, *C. eleutherodactylus*, and *Hemiphractus johnstonei* (Table 8; Figure 9).

Possible synergistic behaviors: Puffing up the body and body-raising are related to biting. Besides this, biting may be preceded or followed by mouth-gaping.

21) Mouth-gaping

Mouth-gaping is reported for three frog species, *Eupsophus emiliopugini* (Formas & Poblete, 1996), *Hemiphractus fasciatus* (Myers, 1966), and *Gastrotheca helenae* (Duellmann & Trueb, 1994). While handling or approaching some frogs in the field we also observed mouth-gaping displays in *Brachycephalus ephippium*, *B.*

hermogenesi, *Brachycephalus* sp. (aff. *vertebralis*), *Eleutherodactylus binotatus*, *E. cf. ramagii*, *Ceratophrys aurita*, *C. joazeirensis*, *Cycloramphus acangatan*, *C. boraceiensis*, *Hemiphractus johnstonei*, *Bokermannohyla izecksohni*, and *Megophrys* sp. (Table 8; Figure 10).

Some individuals of *Hemiphractus fasciatus* and *Eleutherodactylus binotatus* may arch (slightly or vigorously, respectively) the body backwards during the mouth-gaping displays (Myers, 1966; present study; Figure 10).

Possible synergistic behaviors: all species that display mouth-gaping also emit defensive vocalizations (except for *C. acangatan*, which was not tested for distress calls). Mouth-gaping display may precede charging, and be preceded or followed by biting.

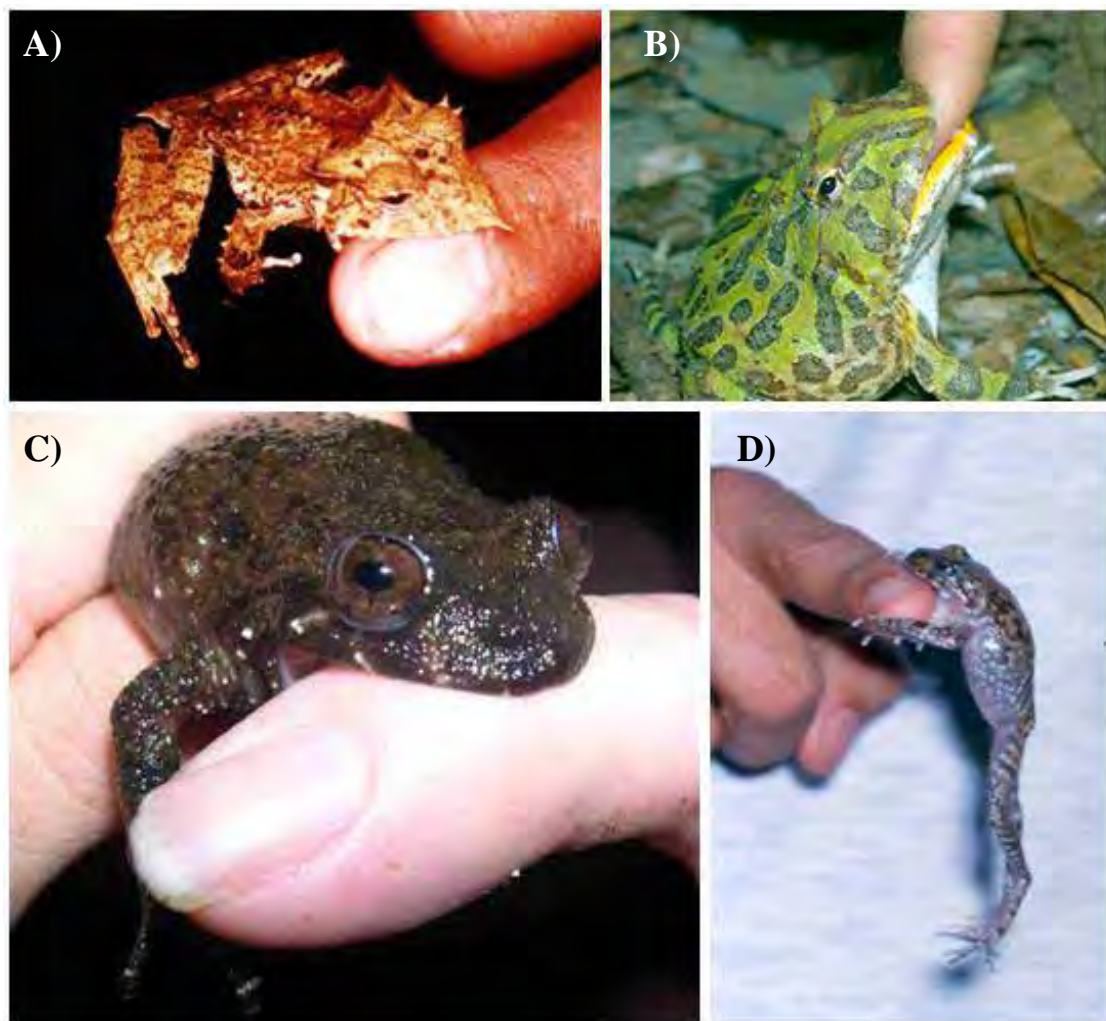


Figure 9. Frogs biting human fingers upon handling: A) *Hemiphractus johnstonei*, B) *Ceratophrys joazeirensis*, C) *Cycloramphus boraceiensis*, and D) *Cycloramphus eleutherodactylus*.

Table 8. Frog species that bite and mouth-gape defensively, presence/absence of parental care, batrachophagic habits and defensive vocalization. Families, genera, and species in alphabetical order.

Family / species	Parental care	Frog eating	Defensive vocalization	References
Centrolenidae				
<i>Hyalinobatrachium colymbiophyllum</i>	Yes	No	No	Drake & Ranvestel, 2005
Ceratobatrachidae				
<i>Ceratobatrachus guentheri</i>	?	?	?	Noble, 1931
Ceratophryidae				
<i>Ceratophrys aurita</i>	No	Yes	Yes	Present study
<i>Ceratophrys cranwelli</i>	No	Yes	?	Fabrezi & Emerson, 2003
<i>Ceratophrys joazeirensis</i>	No	Yes	Yes	Present study
<i>Ceratophrys ornata</i>	No	Yes	Yes	Donoso-Barros, 1972
<i>Lepidobatrachus</i> sp.	?	Yes	Yes	Fabrezi & Emerson, 2003
Leptodactylidae				
<i>Leptodactylus chaquensis</i>	Yes	Yes	?	Present study
<i>Leptodactylus ocellatus</i>	Yes	Yes	Yes	Vaz-Ferreira & Gehrau, 1974; 1975
<i>Leptodactylus pentadactylus</i>	Yes	Yes	Yes	Villa, 1969
Hemiphractidae				
<i>Hemiphractus fasciatus</i>	Yes	Yes	Yes	Myers, 1966
<i>Hemiphractus johnstonei</i>	Yes	Yes	?	M. Barbosa, pers. comm.
Cycloramphidae				
<i>Cycloramphus acangatam</i>	?	?	?	Present study
<i>Cycloramphus boraceiensis</i>	Yes	Yes	?	Hartmann et al., 2003; Present study
<i>Cycloramphus dubius</i>	Yes	?	?	Giaretta & Cardoso, 1995
<i>Cycloramphus eleutherodactylus</i>	Yes	?	?	Present study
Megophryidae				
<i>Brachyarsophrys carinensis</i>	?	?	?	Noble, 1931
<i>Megophrys</i> sp.	?	Yes	Yes	Present study
Pyxicephalidae				

BITING

<i>Aubria subsigillata</i>	?	Yes	?	Fabrezi & Emerson, 2003
<i>Pyxicephalus adspersus</i>	Yes	Yes	Yes	Cook et al., 2001; Fabrezi & Emerson, 2003
<i>Pyxicephalus edulis</i>	Yes	Yes	?	Loveridge, 1945
Amphignathodontidae				
<i>Gastrotheca helenae</i>	Yes	?	Yes	Duellmann & Trueb, 1994
Brachycephalidae				
<i>Brachycephalus ephippium</i>	No	No	No	Present study
<i>Brachycephalus hermogenesi</i>	No	No	No	Present study
<i>Brachycephalus</i> sp. (aff. <i>vertebralis</i>)	No	No	No	Present study
<i>Eleutherodactylus binotatus</i>	?	No	Yes	Present study
<i>Eleutherodactylus</i> cf. <i>ramagii</i>	?	No	?	D. Loebmann, pers. comm.
Ceratophryidae				
<i>Ceratophrys aurita</i>	No	Yes	Yes	Present study
<i>Ceratophrys joazeirensis</i>	No	Yes	Yes	Present study
Cryptobatrachidae				
<i>Stefania woodleyi</i>	?	?	Yes	Kok et al., 2007
Cycloramphidae				
<i>Cycloramphus acangatam</i>	?	?	?	Present study
<i>Eupsophus emiliopugini</i>	?	?	Yes	Formas & Poblete, 1996
Hemiphractidae				
<i>Hemiphractus johnstonei</i>	Yes	Yes	Yes	Present study
<i>Hemiphractus fasciatus</i>	Yes	Yes	Yes	Myers, 1966
Hyllidae				
<i>Bokermannohyla izecksohni</i>	No	No	Yes	I. Martins, pers. comm.
Megophryidae				
<i>Megophrys</i> sp.	?	Yes	Yes	Present study



Figure 10. Mouth-gaping by *Eleutherodactylus cf. ramagii* (A), *Brachycephalus* sp. (aff. *vertebralis*) (B), *Hemiphractus johnstonei* (C), *Eleutherodactylus binotatus* (D-E), *Bokermannohyla izecksohni* (F), *Ceratophrys aurita* (G), *Cyclorampus acangatan* (H), and *Megophrys* sp. (I). Note the contrasting yellow lower jaw of *C. aurita*, visible only while the mouth is open. In *C. aurita*, *H. johnstonei*, and *Megophrys* sp. note the sharp lower jaw teeth.

22) Tongue protrusion

Perret (1961) describe this behavior for *Acanthixalus spinosus*: the frog half-closes its eyes, keeps its limbs motionless close to the body, and protrudes its orange/yellow tongue (Figure 3).

Possible synergistic behaviors: This behavior may be exhibited while in relaxed thanatosis.

23) Fighting

During subjugation by a potential predator, a frog may fight. The most commonly observed movements while fighting were holding (frogs that have adhesive disks hold on nearby objects and try to pull itself out of the predator hands or mouth) and kicking (when the frog is grasped by the head it pushes the predator's face with the hind legs and kicks).

Possible synergistic behaviors: spine aggression, puffing up the body, production of secretions (odoriferous, noxious or adhesive), defensive vocalizations (distress or alarm calls), cloacal discharge, regurgitating, and biting.

24) Spine aggression

Use of spines in the prepollex, prehallux, and/or chest as a defense is recorded for several frog species (Table 2). However, not all species that present spines use them in defense. This is, for example, the case of species of the *Hypsiboas pulchellus* group, of which we tested several individuals of *Hypsiboas beckeri*, *H. bischoffi*, *H. caingua*, *H. guentheri*, *H. leptolineatus*, *H. polytaenius*, *H. prasinus*, and *H. pulchellus*, and species of the genus *Crossodactylus* (Hylodidae) as well. Species that use no their spines defensively are smaller than those that use their spines (ANOVA $F = 65.87$; $P < 0.001$; $N = 48$: Figure 11). We divided this aggression in three types:

- a) Spine-puncturing is the piercing of spines on the frog's prepollex in any reachable body part of a predator (e.g., skin, tympanum, eyes, and oral mucosa).
- b) Spine-scratching is the use of spines on the frog's prepollex or prehallux (as of *Xenopus* spp.) to scratch any reachable body part of a predator (e.g., skin, eyes, and oral mucosa).

- c) Spine-hurting is the use of spines on prepollex on a predator without penetrating the skin (or other body parts) as does spine-puncturing.

Possible synergistic behaviors: spine aggression may co-occur with defensive vocalizations, puffing up the body, fighting, cloacal discharge, and production of secretions (odoriferous, noxious, and slippery).

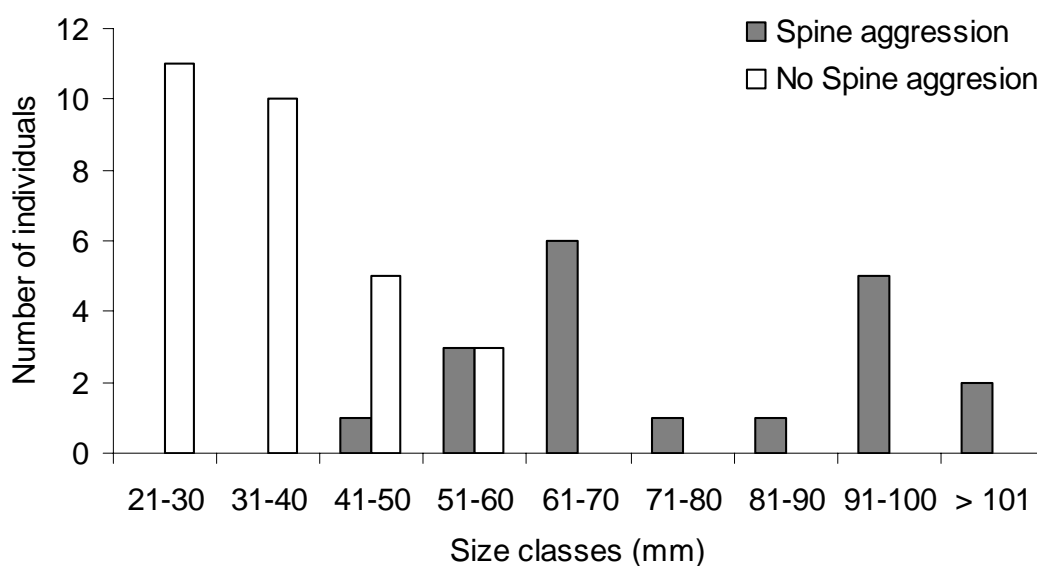


Figure 11. Size classes (mm) of individuals that use spine-aggression (puncturing) as a defensive behavior (gray bars) and those who do not use them (white bars), although spines on prepollex are present.

25) Phalanx-aggression

Some African arthroleptids (*Astylosternus* spp. and *Trichobatrachus robustus*) have openings in the distal skin of the fingers (Boulenger, 1902). These openings allow the protrusion of distal phalanges of the fingers, which are used to deeply scratch a would be predator (W. Böhme, unpubl. data).

26) Regurgitating

Two individuals of *Spea intermontana* (Scaphiropodidae) regurgitated stomach contents or bubbles while handled (Waye & Shewchuk, 1995).

Possible synergistic behaviors: odor production.

27) Defensive vocalization

Defensive high-pitched screams are almost universal (except for the aquatic pipids) and may be a basal character among anurans. Based on the context of emission three terminologies for defensive vocalizations have been proposed: i) distress calls (the most common, when the frogs are seized or when fleeing from predators), ii) warning calls (an intimidating scream directed towards a predator), and iii) alarm calls (a kind of help scream that may attract other animals to the predation scene). Further definitions, discussion, and a literature review are in Toledo & Haddad (in prep.).

Possible synergistic behaviors: defensive vocalizations may be coupled with fleeing, charging, body-raising, puffing up the body, mouth-gaping, fighting, spine aggression, and production of secretion. While screaming, *Litoria australis* jumps vertically and lands in the spot on the ground where it was previously resting (Behler & Behler, 2005).

28) Production of secretions

Four broad secretion types may be released by frogs while threatened. The secretion released by a given frog species may be of more than one type at the same time. For example, it is adhesive and noxious (e.g., *Trachycephalus venulosus*) or odoriferous and noxious (e.g., *Leptodactylus labyrinthicus*).

- a) Odoriferous: vary from malodorous to floral-like odors (see Smith et al., 2004).
- b) Adhesive: viscous secretions typically produced by *Trachycephalus* spp. and *Hyophryne histrio*.
- c) Noxious: toxic secretions produced by several frog species (e.g., Table 2). In an experimental trial we fed the snake *Liophis miliaris* with an adult male of *Trachycephalus mesophaeus* (Hylidae). When seized, the anuran remained motionless and was ingested. After ca. 5 minutes the snake regurgitated its prey unharmed and alive. We attribute this outcome to production of secretions noxious to the snake's digestive system (see also Sazima 1974).
- d) Slippery: lubricating secretions produced generally by aquatic or semi-aquatic species, such as pipids, ranids, and leptodactylids.

Possible synergistic behaviors: production of secretion may occur with several other defensive behaviors: immobility, thanatosis, phragmosis, crouching, puffing up the body, body-raising, body tilting, unken reflex, eye protection, biting, mouth-gaping, tongue protrusion, fighting, spine aggression, regurgitation, and defensive vocalizations.

29) Ecological defenses

a) *Anachoresis or Inaccessibility*

Frogs may live in places or spots difficult to reach for most predators. For example, some species spend their whole life cycle, including feeding, reproduction, resting, thermoregulation, and development of all life stages (eggs, tadpoles, adults) inside a bromeliad. This life style would difficult taking such a frog by several potential predators, and thus it may be considered as a defense associated to the ecology of the species. However, specialized predators are able to find and prey on frogs with such specialized ecological traits (Toledo et al., 2007a).

b) *Chorus vocalization*

Most of frogs call during their reproductive period. They usually call in chorus, which may disorientate predators. With a disturbance nearby, the frogs usually stop calling, but those that are far from the disturbance remain calling. Thus, a predator may keep changing the target without finding the frogs by acoustic cues. Furthermore, the entire chorus may quit calling in the presence of a predator, recognized as such by visual or acoustic cues (e.g., Tuttle et al., 1982), or by acoustic cues emitted by other nearby frogs (L. F. Toledo, unpubl. data).

c) *Group movements*

Several individuals of the same or different species may metamorphose at the same time. Consequently, they leave the aquatic environments synchronously. Froglets are very fragile and do not have much of the defensive strategies of the adults; thus, remaining in a large group may reduce individual chances of being preyed inasmuch as the predator is progressively sated (e.g., Arnold & Wassersug, 1978; DeVito, 2003). Not only juveniles group; aposematic species of *Brachycephalus* (Brachycephalidae) are found in high densities on the forest floor (Toledo et al., 2007a).

d) *Wide distribution*

Some frog species are widely distributed on the forest floor during the reproductive season. This strategy may reduce their predation chances as compared to species that aggregate for reproductive purposes (see also Toledo et al., 2007a for cases of non-aposematic brachycephalids).

Discussion

Function and effectiveness of some behaviors

Thanatosis and eye-protection may work similarly. Both would likely be effective against predators that do not feed on carrion (necrophagy) and against those which need movement cues to find and handle further their prey. Thanatosis also would work for those anurans that are able to produce noxious secretions in the mouth or digestive tract of predators (e.g., Sazima, 1974; present study).

Some frog species are known to flip onto their back to display aposematic (warning) colorations. Similarly, frogs that rely on thanatosis may also display aposematic colorations on the belly, when they are turned with their belly up by the predator.

It is suggested that the partial body-raising with vertically-stretched legs occurs during the day only, because it may involve visual signalization (Martins, 1989). However, we have seen this behavior during the night as well (for *Eupemphix nattereri* and *Physalaemus marmoratus*). Furthermore, we do not believe that this signalization will work only with daily visually orientated predators. Nocturnal, visual signaling is already described for frogs (e.g., Hartmann et al., 2005; Toledo et al., 2007b), and thus other potential predators (including frogs) may also be able to recognize visual signals during the night or in conditions of reduced luminosity, such as in subterranean retreat sites (Martins, 1989).

The body-raising with laterally-stretched legs results in losing the characteristic frog shape, and difficulty in subduing and ingesting the prey. However, information is still lacking about the effectiveness of this strategy.

Body-tilting may be effective in presenting to the predator the dorsal macroglands (*sensu* Toledo & Jared, 1995). In this case the first body parts that the

predator would bite are the glands, which would squeeze noxious secretions into the predator's mouth. These secretions may cause paralysis, irritation, or simply be distasteful, hampering or precluding the predation. Alternatively or non-exclusively, when performing body tilting a frog is showing its largest surface to the predator. This may act as an intimidating behavior, as the frog is actually larger when compared to the size initially perceived by the predator, or it may discourage the predator making the prey more difficult to seize.

Cloacal discharge during active fleeing may be effective in three ways: the cloacal contents may be distasteful for the predator (if the discharge hits the predator's mouth; most probably during seizing), it may startle an endothermic predator with the cold discharge, and/or it may get the frog lighter, and consequently faster to flee.

Regurgitating is recorded only once, in a quite well studied species (e.g., Morey & Reznick, 2000; Hall et al., 2002 and references therein). Therefore, care should be taken to consider this behavior as an actual defensive strategy. The recorded regurgitating behavior could be a consequence of stomach squeezing while handling the frogs.

Puffing up the body is suggested to enlarge the size of the frog upon seeing a predator (Stebbins & Cohen, 1995; Williams et al., 2000). It is also reported to be effective in causing flotation. An aquatic turtle (*Kinosternum* sp.) could not sink easily a *Chaunus marinus* with its lungs inflated; after struggling for a while, the turtle gave up and the frog escaped with traces of poison on its paratoid glands, which may have played an important role during the predatory/defensive interaction (Blair, 1947). Furthermore, synergistically with phragmosis, anurans may easily wedge themselves into crevices, bromeliad axils, or burrows (in trees and in the ground) by inflation (person. obs.). This is another example where the association between behaviors (in this case, phragmosis and puffing up the body) may amplify the effectiveness of several behaviors (see below). Another behavior that acts synergistically with puffing the body is the display of eye-like glands, some of which produce a distasteful and/or noxious secretion (e.g., Sazima & Caramaschi, 1986; Toledo & Jared, 1995).

Multiple behaviors benefits

Larger number of defensive strategies used together likely results in higher chances of a frog to escape from a predator. Moreover, when two or more defensive strategies are used together probably the net benefit is higher than the simple sum of effective, isolated behaviors. For example, the emission of warning calls by *Ceratophrys aurita* and *C. joazeirensis* is strengthened by the visual signal given by the contrasting colors of the bright yellow lips against the white mouth lining and the mottled green dorsal pattern. This double or multiple signalization may stop the action of those predators that are intimidated by the defensive scream, those that are intimidated by the aposematic coloration of the gaping display, and those predators that are only intimidated when multiple signals are emitted (however, this suggestion needs experimental data). Defensive vocalizations seem to be useless against some predators, such as snakes, probably the major anurans predators (Toledo et al., 2007a), which likely are unable to hear frogs' screams (Toledo & Haddad, in prep.). Thus, the use of multiple behaviors, such as mouth-gaping, likely are effective not only by the advantageous sum of the isolated behaviors, but because this strategy type enhances the probability of broadcasting a signal that can be recognized as defensive by the predator.

Evolution of defensive behaviors

Immobility in anurans and salamanders has been shown to be successful against several predator types, mainly birds and snakes (Brodie Jr., 1977; Marchisin & Andrews, 1978; present study). Besides the frog species reported here, two *Lithobates pipiens* individuals were offered to a snake and the one that remained crouched (and thus motionless) went undetected by the snake, which chased and preyed on the moving one (Marchisin & Andrews, 1978). Even while detected, remaining motionless rather than attempting to flee reduces the intensity of the predator attack (Brodie Jr., 1977). Thus, the risks of detection and lethal injuries may have been two pressures acting separately or in concert for the evolution of motionless defenses and the synergistic behaviors displayed while fleeing. Examples are flash-colors (Brodie Jr. & Formanowicz, 1981) and stiff-legged behavior (Sazima, 1978), which enhance the chances of misleading a predator after the prey was detected.

It is possible that the thanatosis of the rigid type has evolved from the relaxed type, due to the higher complexity of the first one: eyes generally closed, arms and legs

in fixed positions, and head ventrally flexed. Besides the differences in the complexity level between the two types, the relaxed thanatosis is widespread in the anuran clade whereas the rigid type seems to be taxa restrained, i.e., occurs in given phylogenetic groups, such as phyllomedusines and bufonids.

However, regardless the order of appearance of these behaviors, it is hard to attribute a higher defensive protection to any of the two types. Relaxed thanatosis seems more realistic “dead” posture since the frog may be put and remains in any posture. On the other hand, the rigid type likely protects vital areas, such as the belly (legs and arms close to it), eyes (kept closed), legs and arms (close to the body). Thus, rigid thanatosis is a behavior with more complex function, not only making a frog to resemble dead (see also Honma et al., 2006). Rigid thanatosis seems to occur mostly (if not only) among frog species that have a chance of outliving being swallowed, as they produce noxious secretions while in a predator’s gut. Some frogs are regurgitated alive after swallowed by snakes (*Dendrobates auratus*: Brodie Jr. & Tumbarello, 1978; *Phyllomedusa rohdei*: Sazima, 1975; *Trachycephalus mesophaeus*: present study). This ultimate strategy (as it acts on digestion, the latest phase of predation) may explain the co-occurrence of thanatosis and eye protection.

Some postures occur synergistically with poison glands (Sazima & Caramaschi, 1986; Toledo & Jared, 1995; Lenzi-Mattos et al., 2005). In some cases the glands may have evolved after the behavior. This seems to be the case of phragmosis in *Corythomantis greeningi* (Jared et al., 2005). Phragmosis also occurs in closely related species (*Aparasphenodon* spp.), and thus it seems to be a phylogenetically restrained behavior. However, species of *Aparasphenodon* have no spines and gland structures on the head as those found in *C. greeningi* (see Jared et al., 2005; C. Jared, person. com.). *Anothea spinosa* is an arboreal hylid that calls and reproduces in from tree holes or bamboo internodes containing water (Jungfer, 1996). It has the skull ornamented with sharp and dorsally pointed spines in the margins of frontoparietal, maxilla, nasal (including canthal ridge), and squamosal bones, and is a sister group of *Triprion* (Faivovich et al., 2005). We suggest that *A. spinosa* displays phragmosis and has noxious glands similar to those of *C. greeningi*. In *Chaunus granulatus* the origin of macroglands (*sensu* Toledo & Jared, 1995) on the head likely anteceded phragmotic behavior, since all *Chaunus* species present such glands. Indeed, in most other cases in

which the glands are directed toward the predator, especially while body-tilting (but also in chin-tucking, crouching, and body-raising), the origin of such behaviors may have occurred after the origin of dorsal macroglands.

Odoriferous secretions may act as a chemical warning, in which a specific odor is related to noxiousness and/or unpalatability (Smith et al., 2004). Furthermore, it is possible that it functions as a chemical camouflage and/or mimicry as well. Some frog species produce odors that resemble smashed plants (Smith et al., 2004; present study) that may mislead a predator, especially if the frog remains motionless and the predator would not have visual nor chemical cues to find the prey. In any case, chemical as well as acoustic defenses (e.g., vocalization) are signals especially useful to be emitted at night (Smith et al., 2004) or in subterranean retreat sites.

There is a suggestion that the full body-raising with vertically stretched legs have evolved before the partial body-raising (Brodie Jr. et al., 1998). Furthermore, it is suggested that the origin of aposematic colorations (involving noxious glands) preceded the origin of the partial body-raising (Brodie Jr. et al., 1998). The authors suggest three steps: 1) full body-raising with vertically stretched legs; 2) aposematic colorations; 3) partial body-raising with vertically stretched legs (Brodie Jr. et al., 1998).

Some authors (e.g., Harbel & Wilkinson, 1997; McCallum, 1999; Andreone, 2002) compared eye-protection with unken reflex. However, this seems to be inappropriate, as the unken reflex is likely an aposematic signal in most of the cases, whereas eye-protection seems to be, for example, a protective posture allowing a frog to be swallowed without much harm after regurgitation (see above).

Biting is strongly related to frog-eating diet and/or parental care. Frogs that eat large prey items have large heads and wide mouths (Emerson, 1985; Pough et al., 1998), and frogs that eat other vertebrates have a specialized cranial architecture with rigid and fused lower jaws, large maxillary teeth, hyperostosis of the cranium, and are, in most cases, ambushing predators (Lynch, 1971; Duellman & Lizana, 1994; Fabrezi & Emerson, 2003; Scott & Aquino, 2005). Thus, frog-eating habit likely is at the evolutionary origin of defensive biting (Scott and Aquino, 2005; present study).

In the cases of *Hyalinobatrachium colymbiphylum* (which do not feed on large or vertebrate prey), *Leptodactylus ocellatus*, and probably in the case of *Cycloramphus*

spp., biting occurs mainly or exclusively during parental care (Vaz-Ferreira & Gehrau, 1974; 1975; Cook et al., 2001; Hartmann et al., 2003; Drake & Ranvestel, 2005).

Mouth-gaping, on the other hand, calls the attention of the predator to a visual display that may intimidate the predator and thus hamper the predatory sequence. Mouth-gaping is intensified by the contrasting colors of the mouth lining, tongue, and/or the lower jaws in relation to body pattern (Figure 10 D), as reported by other authors (Myers, 1966; Duellmann & Trueb, 1994).

Mouth-gaping is likely related with emission of defensive vocalizations. Some frog species that are reported perform mouth-gaping also are known to emit defensive vocalizations induced by a predator approach or seizing. Furthermore, the emission of defensive vocalization is almost exclusively done with the mouth open (Toledo & Haddad, in prep.). Thus, it is possible that mouth-gaping has originated from animals that use to scream defensively, but lost this ability and maintained the behavior of opening of the mouth. This latter visual signal may be as effective as the emission of distress calls for a snake (which does not react to defensive vocalizations, Toledo & Haddad, in prep.), but less energetically costly.

Constraints in the origin of the defensive behaviors

Spines on toes and chest are generally used during aggressive interactions between males (e.g., Martins et al., 1998; Toledo et al., 2007b) and its presence is widespread among anurans (see Fabrezi, 2001). However, not all species use them as a defensive strategy (present study). Thus, spines apparently evolved initially for territorial interactions, as most of the species that have spines use them during intraspecific fights. However, there may be a size constraint involved, as only large species use them as a defensive weapon. Spines of small species may not be effective (hurting) against predators, and thus use of spine aggression had evolved among large species only.

Besides this, there are other relationships between size and presence of some defensive behaviors. For instance, small juveniles of *Bombina* spp. have no aposematic coloration and do not display unken reflex (Löhner, 1919); defensive vocalization is absent in small species (Toledo & Haddad, in prep.); spine aggression is present in large species only (present study); and larger frogs may be benefited simply by their size,

since size alone reduces the assemblage of predators that is able to handle large prey (review in Toledo et al., 2007a). Furthermore, it has been suggested that long-legged or very small species may lack defensive behaviors other than active fleeing (Williams et al., 2000; Behler & Behler, 2005). Thus, there seems to be upper and lower limits that shape the quantity and quality of defensive behaviors for size classes at individual ontogenetic level and at species level. In this context, it is noteworthy that recently-metamorphosed *Hypsiboas faber* utters defensive calls (Sazima, 1975).

Another factor that may have shaped presence/absence of some particular defensive behaviors is the microhabitat. For example, the stiff-legged behavior is reported only for species that live in the leaf litter and that have a dead-leaf dorsal color pattern, independently of the taxonomic group (Sazima, 1978; present study). Another example is that of species that inhabit streams (such as the hylodids *Hylodes* spp. and *Megaelasia* spp.) have no defensive strategies other than their camouflaging pattern against and their jumping into the fast-running water (pers. obs.).

There are several widespread behaviors that seem to have originated in the beginning of the diversification of the living anurans, such as defensive vocalizations, puffing up the body, immobility, and fleeing. On the other hand, there are some behaviors that seem to be exclusive to particular groups and/or species, such as the legs-interweave, balling behavior, and defecation. There are still others that likely are instances of convergence, such as unken reflex, phragmosis, and the stiff-legged behavior. The origin of defensive behaviors is difficult to assess, and frogs in different geographic regions likely were selected by different environmental conditions and predator pressures (although there surely are some “universal predators” such as snakes and birds). Studies that focus on geographic variation of defensive behaviors (e.g., Williams et al., 2000), reactions due to actual presence of predators (e.g., Brodie Jr. et al., 1978), and those testing the efficacy of defensive behaviors (e.g., Brodie Jr. & Tumbarello, 1978; Brodie Jr. & Formanowicz Jr., 1981; Brodie Jr. & Nussbaum, 1987), will ultimately help to elucidate several questions about evolution of defensive behaviors in anurans.

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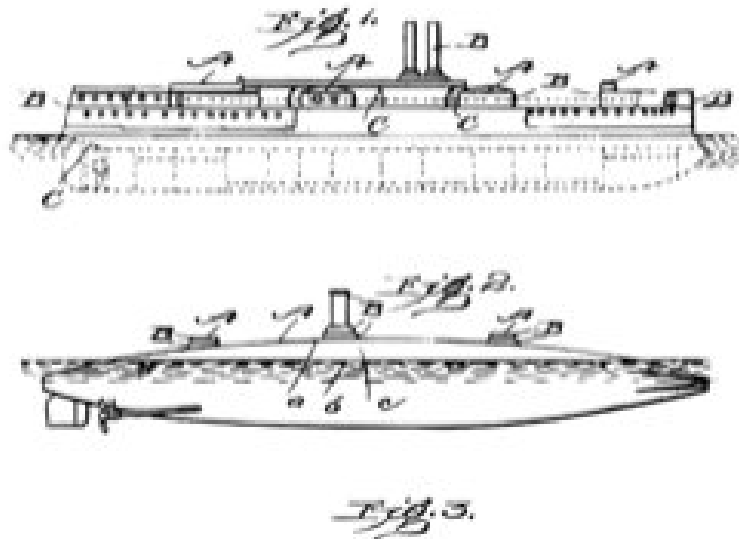
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CAPÍTULO 6

CORES E MIMETISMO COMO ESTRATÉGIAS DEFENSIVAS EM ANUROS

Luís Felipe Toledo & Célio F. B. Haddad



Gerald Handerson Thayer (1883 – 1939)

Pintor e naturalista que em um livro desenvolveu a teoria da camuflagem e aplicou-a na pintura de barcos durante a I Guerra Mundial (desenho acima). O termo camuflagem só veio a ser utilizado para animais após esta guerra.

CAPÍTULO 6

COLORS AND MIMICRY AS DEFENSIVE STRATEGIES OF ANURANS

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ABSTRACT

Some anurans may be bright colored and some others may be also completely camouflaged. These are two of the several uses of coloration in the defensive mechanisms that anurans may exhibit. For example, mimicry (Batesian, Müllerian, Arithmetic, or Browerian), polymorphism, and polyphenism are also possible to occur. These reports have been published widespread in the available literature and some possible functions of these colorations have not been mentioned. Therefore, we reviewed the literature and added new data to this subject. We classified the use of colors and mimicry into three major categories: mimicry, aposematism, and dissuasive coloration. Each one of these categories was subdivided into sub-categories. Mimicry was divided into the major sub-categories camouflage, homotypy, and non-deceitful homotypy (these groups were also sub-categorized). Aposematism was divided into coloration and deimatic behavior. Dissuasive coloration was divided into flash color, polymorphism, and polyphenism. Therefore, we grouped the use of colors and mimicry in post-metamorphic anurans into 11 main categories and sub-categories. Finally, we propose functions and forms of evolution of some colors and mimicry in post-metamorphic anurans.

INTRODUCTION

Anurans are remarkable by their color patterns, which may vary from totally dark, as *Cycloramphus boraceiensis* (Cycloramphidae), up to brightly blue, orange, red, yellow, and green in the same individual, as in *Agalychnis callidryas* (Hylidae). These two distinct situations may be related to two different types of primary defenses, which operate regardless of whether or not a predator is in the vicinity (Edmunds, 1974). Both situations help anurans to survive in nature: crypsis and aposematism, as generally understood. The first intends to avoid detection and the second have been selected or maintained to signalize that the individual is dangerous in one or several ways, from which being toxic is the most common (Edmunds, 1974). Besides these, there are several other defensive strategies involving colorations, such as the deimatic behavior, mimicry, or flash color (e.g., Martins, 1989; Sazima & Caramaschi, 1986; Symula, Schulte & Summers, 2001).

The presence of these and other defensive colorations and mimicry in anurans has been published for several species in a fragmented way and has never been reviewed. Herein, in order to organize the current knowledge and fundament future research, we reviewed this subject, added new data, and provided information about the evolution of the use of colors and mimicry in anurans, with special reference to Neotropical species.

MATERIALS AND METHODS

We reviewed the literature searching defensive strategies in anurans that are related with coloration. Both natural and experimental observations were considered. Additional data were obtained during several field expeditions in Brazil from 1972 up to 2007, mainly in the Cerrado and Atlantic Forest domains in the southeast.

All scientific names of amphibians follow Frost (2007) and the specific nomenclature for the categories of colorations was adapted from Pasteur (1982). The terms “dupe” and “selective agent” has been suggested to be preferentially used, other than ‘predator’, due to their broader significances (Pasteur, 1982; Starrett, 1993); i.e., not always the coloration of the anuran was selected or maintained to warn or avoid a

predator, many times the ‘signal receiver’ (Wickler, 1965) is other anuran or a large passing by individual. However, in the present paper, we choose to use ‘predator’ to designate every animal that may be a potential risk to the anurans (preys), because we are studying mimicry and color use in the light of defensive strategies. For the same reason, we will not deal with aggressive and reproductive mimics in this paper.

RESULTS

The use of colors can be divided into three major categories: mimicry, aposematism, and deceptive coloration (Table 1).

Table 1. Summary of the major categories and sub-categories of mimicry and use of colors as defensive strategies in post-metamorphic anurans.

Major	2 nd major	3 rd major	Sub-Categories
Mimicry	Camouflage	Eucrypsis	Visible color spectrum mimesis
			Non-visible color spectrum mimesis
		Mimesis	Cryptic mimesis
			Phaneric mimesis
			Self-mimesis
		Homotypy	Concrete homotypy
	Browerain mimicry		
	Abstract homotypy		Definable model
			Model not definable
	Nondeceitful homotypy	Müllerian mimicry	
Arithmetic mimicry			
Aposematism			Coloration
			Deimatic behavior
Deceptive coloration			Flash color
			Polymorphism
			Polyphenism

1) Mimicry

Mimicry is generally related to Batesian mimicry concept, in which a non-toxic (or otherwise dangerous, e.g., the species can be able to bite) species mimics of a dangerous model species (generally toxic). However, there are several types of mimicry, from which anurans may be included into 11 sub-categories (Table 1), divided into three major groups: camouflage, homotypy, and non-deceitful homotypy (see below).

1.1) Camouflage

Camouflage may be defined as the resemblance of an animal to part of the environment (Edmunds, 1974), specially in the views of the predator at the time and place in which the prey is most vulnerable to predation (Endler, 1978).

In post-metamorphic anurans, the camouflage may be at least optical, chemical (e.g., production of floral, leaf-like, and ammonia odors), or acoustical (may occur, for example, when the frogs stop calling in the presence of a predator: e.g., Tuttle, Taft & Ryan, 1982). Below we will give special reference to optical camouflage, which implies in avoidance of detection by possible predators.

1.1.1) *Eucrypsis*

Definition: homochromy (imitation of reflected light) acting alone. The model is undefined: it is the background.

a) Visible color spectrum mimesis

Many frogs are cryptic with the substrate they use, and there are a great variety of backgrounds and mimic frogs. Anurans may use as substrate rocks with lichens, tree trunks, leaves, forest litter, mossy and rocky fields, for example. For any of these substrates there are mimic frogs that live in (Fig. 1). The eucrypsis may be strengthened or weakened by the angle of vision of the predators; i.e., the anuran may be more cryptic from a lateral view, than from a dorsal view (Fig. 1F and 1E, respectively).

As more distant a predator watches the site occupied by an anuran, the higher may be the crypsis benefits. For example, it is easy to find a *Dendropsophus nanus* in its reproductive site when we are close to it. However, from a certain distance, the

colors and shape of this hylid gets mixed with the general view of the area. The size and colors of *D. nanus* are generally similar to part of the foliage, and it is hard to distinguish them from the yellowish leaves (Fig. 1K-1L).

b) Non-visible color spectrum mimesis

Humans may fall in a narrow perception of color crypsis due to our limited trichromatic color vision spectrum, based on our three color cones (blue, green, and red) and black and white rods. Although it is an advanced system of vision, the anuran predators may be able to perceive other wavebands, such as the infrared and ultraviolet spectra.

Studies have shown that several anuran species of different families may show a pronounced rise in reflectance in the infrared part of the spectrum (e.g., Schwalm, Starrett & McDiarmid, 1977; Emerson, Cooper & Ehleringer, 1990; Summers, Cronin & Kennedy, 2003). Therefore, some anurans may have evolved infrared reflectance in order to be cryptic to the foliage (background) and be not perceived by the predator (Emerson et al., 1990).

Many anuran predators, such as rodents, other amphibians, lizards, and mainly birds, are tetrachromatic color vision (including ultraviolet cones), and therefore may see in the ultraviolet wavelength (e.g., Honkavaara et al., 2002). This capability may be used to hunt and a specific protection may have evolved for that, but, as far as we know, it has never been reported.

1.1.2) *Mimesis*

Definition: homomorphy (imitation of morphology) and/or homokinemy (imitation of movements and postures) add to homochromy. The model is defined: it is an object.

a) *Cryptic mimesis*: when the model is a dominant element of the mimic's environment, such as green or brown leaves, sticks, rocks, lichens, and mosses. Many examples may be cited, but to pick up some we may refer to species of the genera *Proceratophrys* and *Scythrophrys* that resemble fallen leaves (Fig. 1I and 1J, respectively), and some species of *Theloderma* and *Bokermannohyla* that resemble mosses and lichens, respectively (Fig. 1B).

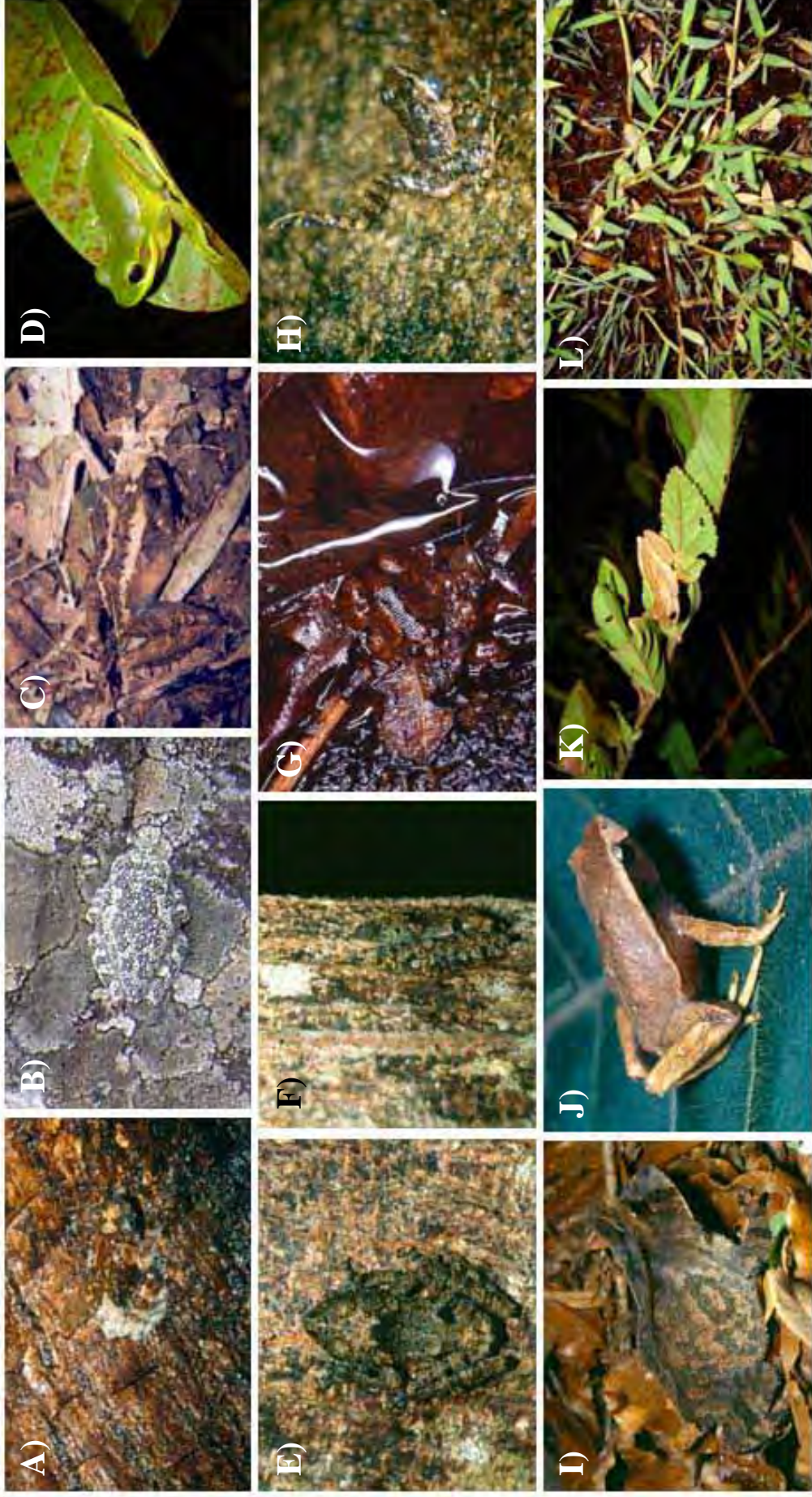


Figure 1. Different situations of cryptic mimicry in anurans: *Dendropsophus acreanus* (Hylidae) on a tree trunk (A), *Bokermannohyla alvarengai* (Hylidae) on a rock with lichens (B), *Eleutherodactylus guentheri* (Brachycephalidae) on the litter (C), green morph of *Hypsiboas prasinus* (Hylidae) perched on a leaf (D), dorsal and lateral views of *Theloderma horridum* (Rhacophoridae) on a tree (E-F, respectively), *Lankanectes corrugatus* (Nyctibatrachidae) in a lotic water body (G), *Hylodes asper* (Hylodidae) on a wet rock (H), *Proceratophrys boiei* (Cycloramphidae) on the litter (I), *Scythrophrys sawayae* (Leptodactylidae) on a dead leaf (J), an adult male of *Dendropsophus nanus* (Hylidae) of practically the same size and shape of the leaves (K) and its reproductive site (L).

The phyllomedusines of the genus *Phasmahyla* when walking sway slightly as if caught by the movement of the wind (= homokinemy). Indeed, the generic name *Phasmahyla* was coined in allusion to the similarity of the moving style with the walking-sticks of the order Phasmatodea (Cruz, 1990).

b) *Phaneric mimesis*: when the model is an isolated and conspicuous inanimate element of the mimic's environment, such as animal droppings and rocks (when there are few rocks in the environment). As examples we may cite some *Theloderma* spp. and *Dendropsophus marmoratus*, which resemble bird droppings and many species of the genera *Chaunus* and *Bufo* that resembles stones on the floor.

c) *Self-mimesis*: some animals when disturbed cease to move, mimicking its own death. This behavior is known as thanatosis, death feigning, or playing possum and will be reviewed elsewhere (L. F. Toledo, I. Sazima & C. F. B. Haddad, unpubl. data).

1.1.3) Factors of camouflage enhancement

Both eucrypsis and mimesis imply in camouflage, which could be strengthened by: a) countershading, b) disruptive coloration, c) shadow camouflage, d) wetting, and e) integumentary structures.

a) *Countershading*

Countershading occurs when the pigmentation of the anuran is darker dorsally and lighter ventrally. This transition may be gradual or abrupt, which could involve different camouflage strategies (see Thayer, 1896; Ruxton, Speed & Kelly, 2004).

Two main functions have been attributed to countershading: I) it is believed to have the effect of reducing conspicuous shadows cast on the ventral region of an animal's body. In essence the distribution of light on objects that are lit from above will cause unequal reflection of light on a solid body of uniform color. Such shadows could provide predators with visual cues to a prey's shape and projection. Countershading therefore, reduces the ease of detection of prey by potential predators by counterbalancing the effects of shadowing. This effect occurs mainly in animals that

have a gradual transition of coloration (Thayer, 1896) and should be properly named “self-shadow concealment” (Ruxton et al., 2004); and II) the countershading coloration would work through background matching; i.e., when seen from the top, the dorsum (if cryptic colored) blends into the background below, which could be water bodies (when the anuran is swimming or floating) and from dry to flooded grounds (when the anuran is in the floor or perched in the vegetation). When seen from below, the lighter ventral area blends into the sun or moonlight (see Ruxton et al., 2004). This second explanation occurs generally with an abrupt transition of colors and seems to be the adequate for the anurans.

Countershading could result from other selective pressures than predation avoidance. For example, the dorsal surface needs to be protected against the damaging properties of UV light and/or abrasion (Kiltie, 1988; Braude et al., 2001), and the ventral side does not need to be pigmented as pigmentation may be costly (Ruxton et al., 2004). Therefore, the occurrence of countershading may result from multiple factors.

This system is so widespread among aquatic and terrestrial fauna that several authors have stated that it perhaps is the most universal feature of animal coloration (see Ruxton et al., 2004 and references therein). Equally, it is present in several anuran species and might work for terrestrial predators, for example, which may be in the ground when the anuran is perched in a tree branch. In aquatic species, such as the pipids (e.g., *Pipa* spp. and *Xenopus* spp.), the system may work as described for fishes.

b) *Disruptive coloration*

Disruptive coloration is a color pattern that breaks the appearance of body form. Several species of anurans have dorsal lines and/or blotches that may be considered constitutive of the disruptive coloration, breaking the general outline of the body. Some species may enhance their camouflage by having high contrast lines in the edges of colored patterns (see Osorio and Srinivasan, 1991). Besides this, several species present lateral lines that cross the eyes breaking the rounded shape of them (Fig. 1J). These are the most common forms of disruptive colorations in anurans.

A possible variation is the presence of aposematic coloration (see below for the explanation of aposematism) simultaneously with disruptive coloration, depending on

the predator and/or lightness of the night. This may occur because the colorful stripes and/or blotches of an aposematic anuran may turn into a disruptive pattern when seen by a color-blind predator, or by a color vision predator that is hunting in dark nights. (see Brattstrom, 1955; Brodie Jr. & Tumbarello, 1978).

Recently, it has been suggested and/or demonstrated that disruptive coloration is advantageous compared to the simple eucrypsis (see Cuthill et al., 2005; Endler, 2006, and references therein).

c) *Shadow camouflage*

The anurans may rest in areas combined with spots of sunlight and shadows, difficulting the recognition of the animals on the substrate. If part of the anuran is exposed to sunlight and other part is in the shadow, this light game may enhance the disruptive pattern of the anuran (e.g., Osorio & Srinivasan, 1991).

d) *Wetting*

Some individuals may remain in lotic water bodies, covered by a passing by film of water or with water drops. This situation may enhance the crypsis of the animals against terrestrial predators, specially creating reflected shining spots on the dorsum, which match with the shining spots of the water or substrate, e.g., rocks (Fig. 1G-1H).

e) *Integumentary structures*

Some integumentary structures seem to be associated with disruptive outlines and thereby aid in concealment. Such structures include small, irregular ridges, supraciliary processes (e.g., species of *Proceratophrys* and *Ceratophrys*), scalloped folds on the outer edges of limbs (e.g., *Cruziohyla craspedopus*), and calcars (e.g., several *Hypsiboas* spp.). Dorsal glands may also enhance crypsis promoting resemblance with lichens (e.g., *Bokermannohyla alvarengai*, *Itapotihyla langsdorffi*, and *Scinax nebulosus*) or mosses (e.g., *Theloderma corticale* and other Vietnamese mossy frogs) (Fig. 1).

2) Homotypy (assimilation to another type)

When the model elicits a reaction in the predator, the mimetic imitation elicits the same reaction.

2.1) Concrete homotypy (actual model)

The model is definite or an existing species (or cluster of similar species).

a) *Batesian mimicry*

The conception of Batesian mimicry (Bates, 1862) involves the success of a specific coloration against the experience of the predators; i.e., predators learn to avoid unpalatable species, which are identified by their aposematic coloration (which does not always mean bright colors: e.g., Pasteur, 1982; Wüster et al., 2004), odor, sound, or other signal. Then, a mimic could obtain protection by resembling the unpalatable or less palatable model. For anurans there are few cases described where some palatable frogs may be the mimics of some poison frogs (Table 2).

Table 2. Occurrence of Batesian and Müllerian mimicry in anurans, and distribution overlap between species.

Mimic	Model	Mimetism type	Sympatric species	Source
<u>Aromobatidae</u>	<u>Dendrobatidae</u>			
<i>Allobates zaparo</i>	<i>Ameerega bilinguis</i>	Batesian	Yes	Darst & Cummings, 2006
<i>Allobates zaparo</i>	<i>Ameerega parvula</i>	Batesian	Yes	Darst & Cummings, 2006
<u>Brachycephalidae</u>	<u>Dendrobatidae</u>			
<i>Eleutherodactylus gaigeae</i>	<i>Phyllobates lugubris</i>	Batesian	Yes	Myers & Daly, 1983
<i>Eleutherodactylus gaigeae</i>	<i>Phyllobates aurotaenia</i>	Batesian	Yes	Myers & Daly, 1983
<u>Leptodactylidae</u>	<u>Aromobatidae</u>			
<i>Leptodactylus lineatus</i> **	<i>Allobates femoralis</i> **	Batesian	Yes	Nelson & Miller, 1971
<u>Dendrobatidae</u>	<u>Dendrobatidae</u>			
<i>Ranitomeya imitator</i>	<i>Ranitomeya fantasticus</i>	Müllerian	Yes	Symula et al., 2001
<i>Ranitomeya imitator</i>	<i>Ranitomeya variabilis</i>	Müllerian	Yes	Symula et al., 2001
<i>Ranitomeya imitator</i>	<i>Ranitomeya ventrimaculata</i>	Müllerian	Yes	Symula et al., 2001
<u>Mantellidae</u>	<u>Mantellidae</u>			
<i>Mantella laevigata</i> *	<i>Mantella manery</i> *	Müllerian	Yes	Schaefer et al., 2002
<i>Mantella baroni</i> *	<i>Mantella madagascariensis</i> *	Müllerian	Yes	Schaefer et al., 2002
<i>Mantella pulchra</i> *	<i>Mantella cowanii</i> *	Müllerian	Yes	Andreone, 1992
<u>Dendrobatidae</u>	<u>Dendrobatidae</u>			
<i>Phyllobates aurotaenia</i> *	<i>Phyllobates lugubris</i> *	Müllerian	No	Present study

*In these cases the definition between the mimic and model is not possible.

**Further studies are needed in this case: see text.

Batesian mimicry involves the predator ability of learning, but in some cases innate knowledge. Several predators, such as invertebrates in general, are not well-endowed in terms of sight and memory as are mammals, and therefore, they may not have been the promoters of selective pressures for the evolution and persistence of Batesian mimicry (see also Pasteur, 1982).

A Batesian mimic do not necessarily needs to be identical to its model. Some times, it may exhibit intermediate resemblances between two (or more) models. By this way, the mimic may escape from some predators that avoid one model and from some predators that avoid the other model. This dual mimicry system has been proposed to coral snake mimics (Pough, 1988) and may be present in anurans.

An intriguing situation is the case of the Batesian mimetism proposed to the complex *Leptodactylus lineatus* and *Allobates femoralis*. This complex would actually represent a case of Müllerian mimicry, instead of a Batesian mimicry as proposed initially (Nelson & Miller, 1971), as *L. lineatus* seems to be a noxious species as well. When handling and fixing individuals of *L. lineatus*, they exude a great amount of milky secretions, probably noxious (C. F. B. Haddad, person. obs.). However, some tests made with *A. femoralis* indicated that this species is not toxic (see Grant et al., 2006 and references therein). If *A. femoralis* is not toxic and *L. lineatus* is, so it is again a case of Batesian mimicry, where *L. lineatus* is the model. If both species are discovered to do not contain toxic proprieties, so it would be a case of Arithmetic mimetism. Therefore, the relationship of this complex remains unsolved and further research is needed.

b) *Browerian mimicry*

When individuals within a species differ in palatability to the predators, more palatable individuals (mimics) will be benefited by those less palatable (models). The models can be of the same or from different sex from the mimic. Although never reported, this sort of mimicry may be present at least in aromobatids, bufonids, dendrobatids, mantellids, and myobatrachids. Individuals of the same noxious species of these families (cited above) acquire the alkaloids used in their noxious secretions from dietary arthropods (e.g., Daly, 1998; Saporito et al., 2004; Clark et al., 2005; and references therein). Therefore, if for any reason a group of individuals within a species

do not feed on arthropods that carry the alkaloids, feed on them but in a lower rate/proportion, or do not sequester those components, they will not be so poison (as if) as the others (e.g., Daly et al., 1994; 1997a; 1997b; Caldwell, 1996).

Indeed, there are reports that demonstrate spatial (geographical) and temporal (seasonal) variation in the alkaloid profiles of poison frogs (Saporito et al., 2006) that can support the Browerian mimicry theory for anurans.

1.2.2. Abstract homotypy (virtual model)

When the model is not an actual species, the homotypy is abstract.

a) *Definable model*

Occurs when the model looks like a general type of organism, part or indirect vestiges of another organism, but it is not identifiable at the species level. For example, the deimatic eyespots present on the back of leiuperids, which could resemble eyes of snakes (Sazima & Caramaschi, 1986) but not of a specific species of snake. Other example are frogs that rest on leaves and look like bird droppings (e.g., *Dendropsophus marmoratus* and *Theioderma* spp.). Besides this, the presence of calcars in many species of rainforest tree frogs, and their absence in other anurans, provoke the speculation that they might serve as points of runoff of water, mimicking drip tips of leaves (Duellman & Trueb, 1994, p. 371).

b) *Model not definable*

Occurs when the model is not identifiable at all, but a frightening or cryptic form is conjured up. This seems to be the case of the legs interweaves behavior described elsewhere (see Channing & Howell, 2003).

1.3. Nondeceitful homotypy

This category was created (Pasteur, 1982) for the inclusion, basically, of the Müllerian mimicry (Müller, 1878; 1879) and Arithmetic mimicry (van Someren & Jackson, 1959). In both cases there is no deceit of the predator, because both the model and the mimic are unpalatable, dangerous in other way (Müllerian mimicry), or palatable (Arithmetic mimicry).

This could be a result of convergence of two or more species to a similar color pattern. However, sometimes it is hard to distinguish a real nondeceitful homotypy from a possible phylogenetic influence. I.e., close related species, such as two species of *Dendrobates* may resemble one to another due to a simplesiomorphy (sharing of an ancestral character) and not by a coloration convergence (sinapomorphy). Although, either being a convergence or a simplesiomorphy, the resemblance would benefit the two (or more) species.

a) *Müllerian mimicry*

Müllerian mimicry will work in the way that one species will be benefited by the danger of the other; they would be under lower predation rates than they would be if they looked differently. To our knowledge there are only few cases of Müllerian mimicry in anurans (Table 2).

However, other possible mimicry relationships may be suggested based on the current reports. We could joint two mimicry pairs of *Mantella* (*M. baroni/madagascariensis* and *M. pulchra/cowanii*) into a larger group of mimicry species as all individuals are sympatric and exhibit homochromy and homomorphy. Furthermore, from the evidence of Batesian mimicry among *Eleutherodactylus gaigeae* of both models *Phyllobates aurotaenia* and *P. lugubris* we may suggest another Müllerian mimicry system. This system would be composed by *P. aurotaenia* and *P. lugubris*. These two species are not sympatric, however, chronosympatry (the presence of the model and mimic in the same time and place) is not a rule for the existence of mimicry (Rothschild, 1963; 1981); for example, their past distributions could have been overlapped (see also Myers and Daly, 1983) and/or the present distribution of the selective agents (predators) may overlap the distribution of both species (including the Batesian mimic *E. gaigeae*).

Furthermore, it is possible to exist another Müllerian mimicry system not based on coloration, but still a visual mimetism. For example, if two different coloration species, or different morphs of the same species, present the same toxic substances they could be chemical mimics. Therefore, based on other characters than coloration visual cues, such as body shape and brightness, they could be a part of a Müllerian mimicry

ring (see also Turner & Speed, 2001). This would explain in part the several cases of polymorphisms among aposematic species (see below).

b) *Arithmetic mimicry*

Sympatric edible and alike species share the burden of predation in proportion to their relative frequencies. I.e., as higher is the abundance of a determined morph in the predator foraging area lower are the chances of an individual prey to be preyed. In this case, predator learning (ontogenetic or inherited) is irrelevant. To our knowledge, arithmetic mimicry has never been reported for the anurans; however, it may be a very widespread phenomenon involving several sympatric (or even syntopic) alike (for example in homochromy, homomorphy, and homokinemy at the same time) species. As examples of pairs (or more) of species there are those of the syntopic *Leptodactylus furnarius* and *L. joly*; *Dendroposphus nanus*, *D. sanborni*, and *D. minutus*; *Porceratophrys appendiculata*, *P. boiei*, and *P. melanopogon*; and several species of *Eleutherodactylus*.

Furthermore, two different species in coloration (for example), but similar in size (for example), may also be arithmetic mimics. These two edible species, which share a predator foraging area, may be equally nutritive; therefore, provided that the predator can perceive that they are being jointly nutritive, they will be nutritional arithmetic mimics, benefited by the saturating theory (see Turner & Speed, 2001).

2) **Aposematism**

Aposematic coloration has also been referred as sematic, conspicuous, or warning coloration. Aposematism is the presence of contrasting and conspicuous coloration that is generally related to the presence of skin toxins in the individuals (Edmunds, 1974; Sttebins & Cohen, 1995). Furthermore, it may also signalize that the anuran is dangerous or unpleasant in other way. For example, aposematic anurans may bite, exhibit spine aggression, and/or emit loud defensive screams. Aposematism may occur as general coloration or as deimatic behavior.

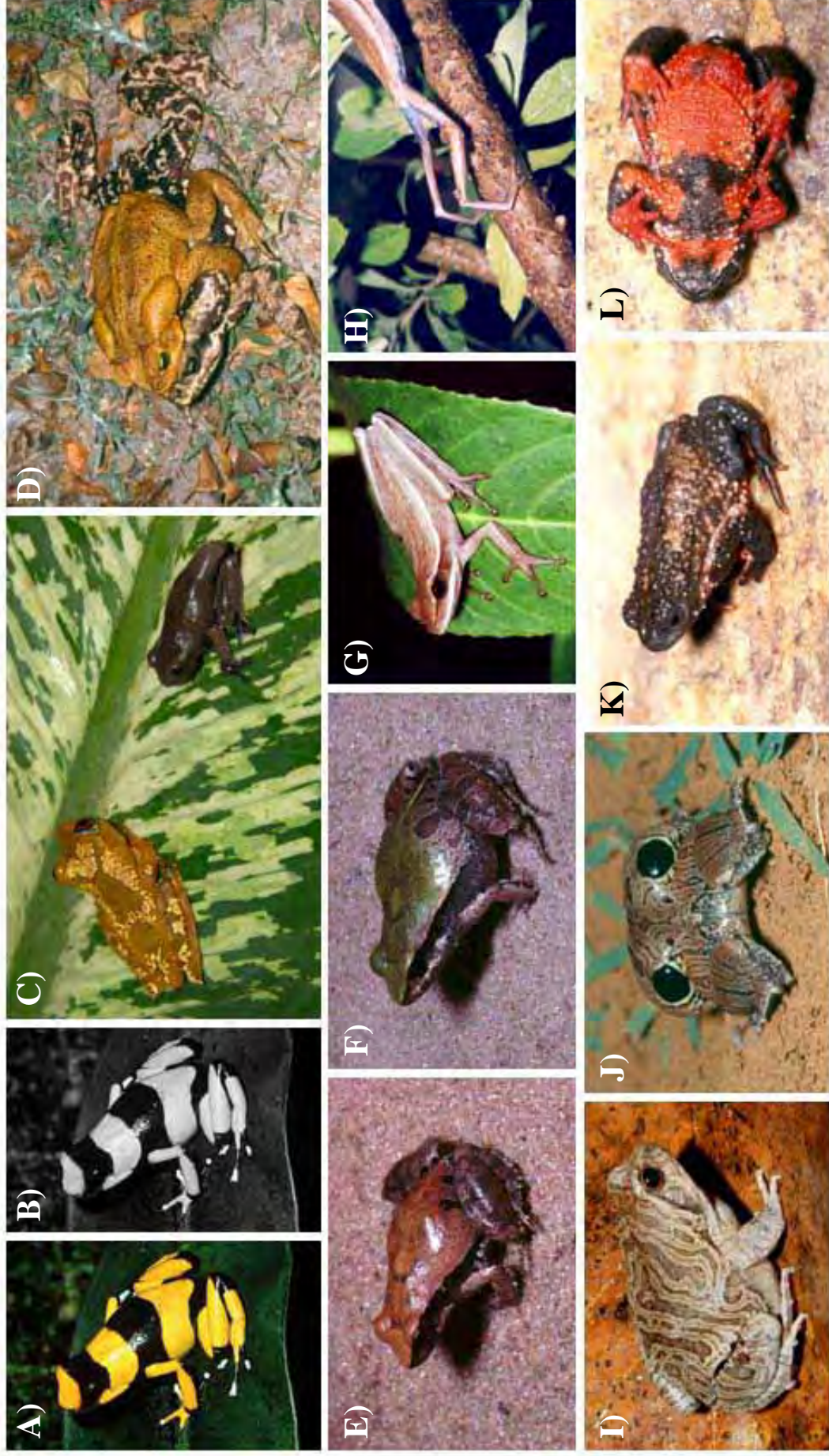


Figure 2. An aposematic *Oophaga lehmanni* (Dendrobatidae) (A) may have disruptive coloration at dark nights or when searched by a color-blind predator (B). An adult and a juvenile of *Hypsiboas semilineatus* (Hylidae) (C), an amplexant pair of *Chaunus ictericus* (Bufonidae) (D), and two morphs of *Physalaemus cuvieri* (Leiuperidae) (E-F) are examples of polyphenism. Flash color exhibited by *Hypsiboas polytaeniatus* (Hylidae) (G-H), deimatic behavior of *Eupemphix nattereri* (Leiuperidae) (I-J), and thanatosis of *Melanophryniscus moreirae* (Bufonidae) (K-L).

a) *Coloration*

Aposematic coloration is generally bright red, orange, yellow, and/or blue combined with a dark (generally black) contrasting background. Most commonly, this aposematic coloration may be widespread over the entire body, such as in species of *Allobates* (Aromobatidae), *Ameerega* and *Dendrobates* (Dendrobatidae), *Mantella* (Mantellidae), *Atelopus* (Bufonidae), and *Brachycephalus* (Brachycephalidae).

b) *Deimatic behavior*

Many times, the aposematic coloration may be confined in parts that are usually concealed when the frog is in the resting posture [e.g., some leiupeids (*Eupemphix nattereri* and *Physalaemus* spp.), hylids (*Phyllomedusa* spp.), bufonids (*Melanophryniscus* spp.), and leptodactylids (*Leptodactylus* of the *pentadactylus* group)]. In this case, the bright coloration is generally present on the back of the thighs, underside of the body, limbs, feet and hands, and are displayed by specific posturing such as the unken reflex or body raising.

For example, in some leiupeids (e.g., *Eupemphix nattereri*, *Physalaemus deimaticus*, and *Pleurodema brachyops*) when the individuals lift their hindparts, they exhibit a pair of black eyespots (Fig. 2I-2J). In species of *Ceratophrys* and *Hemiphractus* the aposematic coloration may be present on the lips or on the tongue, respectively, which are displayed when the individuals do the mouth-gapping display or while emitting defensive screams. In *Phyllomedusa* spp. the bright contrasting coloration may be displayed intentionally (e.g., during foot flagging) or when the individuals walk on the branches of trees. The foot signaling made by *Atelopus zeteki*, besides being an intraspecific communication, may be a visual display, including aposematic colorations (bright yellow contrasting with black stripes), for potential predators (Lindquist and Hetherington, 1996). In *Ameerega flavopicta* there seems to be a relation between parental care and body raising (Toledo et al., 2004). Several species have the belly (or other underside parts) conspicuously colored (e.g., *Paratelmatobius* spp., *Leptodactylus pustulatus*, or *Melanophryniscus* spp.). When facing a predator they might not present any specific behavior to display these colorations. However, they may display thanatosis (a widespread behavior in frogs) and during the handling by the predator, the anurans may be turned upside down and thus would display the aposematic coloration (Fig. 2K-2L). Species of *Oreophrynella*, after the ‘balling

behavior' while fleeing, may stop with the belly up, exposing the bright contrasting ventral coloration (see McDiarmid & Gorzula, 1989).

3) Deceptive coloration

3.1) Flash color

A fleeing anuran may escape from predators by the display of a flash of aposematic color(s), generally followed by staying motionless. This coloration is only visible when the anuran is moving, and concealed during resting posture (Fig. 2G-2H). Flash color is widespread among the anurans, occurring in several species and families.

The flash color behavior may function to disorientate and confuse an attacking predator (Edmunds, 1974), and/or warn predators of the presence of toxins (Dickerson, 1906). These two distinct functions, and implied predator responses, are contradictory and may vary between individuals or species of predator. I.e., some predators may be warned, and some may get confused. In the former case (warning), the behavior should be classified as a subcategory of deimatic behavior. In the second case (confusion), the predator may lose the anuran: the flash behavior may precede the motionless behavior, creating a prey search image that quickly disappears (Edmunds, 1974; Sttebins & Cohen, 1995). Besides this, the flash color behavior may halt the predator attack for an instant and thus giving extra time for the frog to escape (Caro, 2005).

3.2) Polymorphism

Polymorphism in anurans is characterized by the presence of fixed chromatic phenotypes within or between populations. The individuals seem to be unable to change their color, so there must be a genetic control involved. The polymorphism may benefit the anuran in the way that one or more of the phenotypes are not included in the predator's search image. Several species are known to present different chromatic morphotypes, and this polymorphism may occur in three ways:

a) *Between individuals independent of the sex and life stage*

Two morphotypes: for example, some adult individuals of *Physalaemus cuvieri* (Leiuperidae) and *Paratelmatobius* spp. (Leptodactylidae) are green and others are brown (Fig. 2E-2F). Other type of color dimorphism is exhibited by individuals of *Leptodactylus fuscus* (Leptodactylidae), which may or may not have a dorso-vertebral white line.

More than two morphotypes: several species of the cryptic genus *Eleutherodactylus* (Brachycephalidae) exhibit many different color morphotypes (Hoffman & Blouin, 2000). Besides this, even in aposematic species it is possible to observe this sort of polymorphism; for example, in *Anomaloglossus beebei* (Aromobatidae) there are five color morphotypes (Bourne, 2001) and in *Oophaga pumilio* (Dendrobatidae) there are at least 15 color morphotypes (e.g., Summers et al., 2003; Siddiqi et al., 2004). Multiple aposematic phenotypes are also observed in the other dendrobatids (Roberts et al., 2006) and African mantellids (e.g., Daly et al., 1996). Multiple aposematic phenotypes may sum the benefits acquired from the aposematism and the predator search image benefit (see above).

b) *Between life stages: juveniles different from adults.*

For example, this is the case of *Hypsiboas semilientus*, *H. lundii*, *H. pardalis*, and *H. raniceps* (Hylidae), in which the juveniles have a totally different coloration from adults, independently of the sex (Fig. 2C).

c) *Between sexes: males different from females.*

As a examples we may cite the case of *Chaunus ictericus* (Bufonidae), where males are light yellowish and females are black and white (Fig. 2D); *Leptopelis vermiculatus* (Arthroleptidae), where males are green and females are brown; and most contrasting is the *Ollotis periglenes* (Bufonidae), where males are brightly orange and females are black, red and yellow.

3.3) Polyphenism

Polyphenism is the ability of generating different phenotypes, by color-changing in this case, in the same individual. Polyphenism may be a better term to describe this phenomenon than polymorphism, which generally connotes a stronger genetic element for each particular appearance (Hanlon, Forsythe & Joneschild, 1999).

Many anurans may change their dorsal coloration by the rearrangement of the chromatophores. There is a continuous gradient in the timing for color changing in anurans: the change may occurs instantaneously, may take few minutes, hours, days, or weeks to occur.

Some species may change their color very quickly. We placed one individual of *Bokermannohyla circumdata* (Hylidae) in a dark place (inside a tight of tree) and let

other individual exposed to the laboratory light. After 15 minutes they were completely different from the initial coloration: dark reddish-brownish. The first individual (that was kept in the dark) was much darker, almost black, and the second individual (the exposed one) was almost white. A similar polyphenism was described for *Bokermannohyla alvarengai*, but in this case the color change was studied in the light of physiological adjustments for temperature and water loss control (Tattersall, Eterovick & Andrade, 2006).

The dorsal coloration of males of *Scinax fuscomarginatus* (Hylidae) is yellowish during the night (at reproductive activity) and grayish or brownish during the day. This may be related to the specific site they use: during the night they remain perched in yellowish grass vegetation (Toledo & Haddad, 2005) and during the day they may be found in dark sites, such as tree holes, under tights of trees, and in the middle of clumps of grass. Conversely, this color change may be due to testosterone amount during reproductive activity (calling), as the yellowish males also have an odor distinct from that they have during the resting daytime period. Additionally, individuals killed while still yellowish, left a yellow tinge in the preservative liquid (formalin, alcohol). The same phenomenon we recorded for *Scinax fuscovarius* and *S. hayii*. Furthermore, some phyllomedusines may change from purplish at night activity to greenish during resting at daytime. This polyphenism was observed in *Phasmahyla cochranae*, *P. guttata*, and *P. jandaia*. Occasionally this phenomena can be observed in *Phyllomedusa azurea*, *P. megacephala*, and *P. rohdei* (pictures in Eterovick & Sazima, 2004).

We observed a seasonal polyphenism for *Hypsiboas prasinus* (Hylidae), in which the higher presence of green individuals occurred mainly in the hot and rainy season of the year, and the higher presence of brown individuals occurred in the dry and cold season of the year. This pattern matches with the frequency of green and brown leaves of the semideciduous forests where this species dwells (Morellato et al., 1989): the peak of leaf fall precedes the peak of brown morphs and the peak of leaf flushing precedes the peak of green morphs (Figure 3). Seasonal color changing has been also observed for *Pseudacris regilla* (Hylidae) and it has been considered a response to divergent selection for crypsis in a heterogeneous, seasonally variable environment (Wente & Phillips, 2003). This is likely to be an explanation for the polymorphism in *H. prasinus* as well.

Polyphenism may be advantageous over the polymorphism, because the anuran may select the substrate and than adjust its color pattern. The polymorphic anurans may

find adequate substrates to fit their general coloration, which does not mean it is hard to find, but the polyphenic species may have a wider range of substrate that they can use.

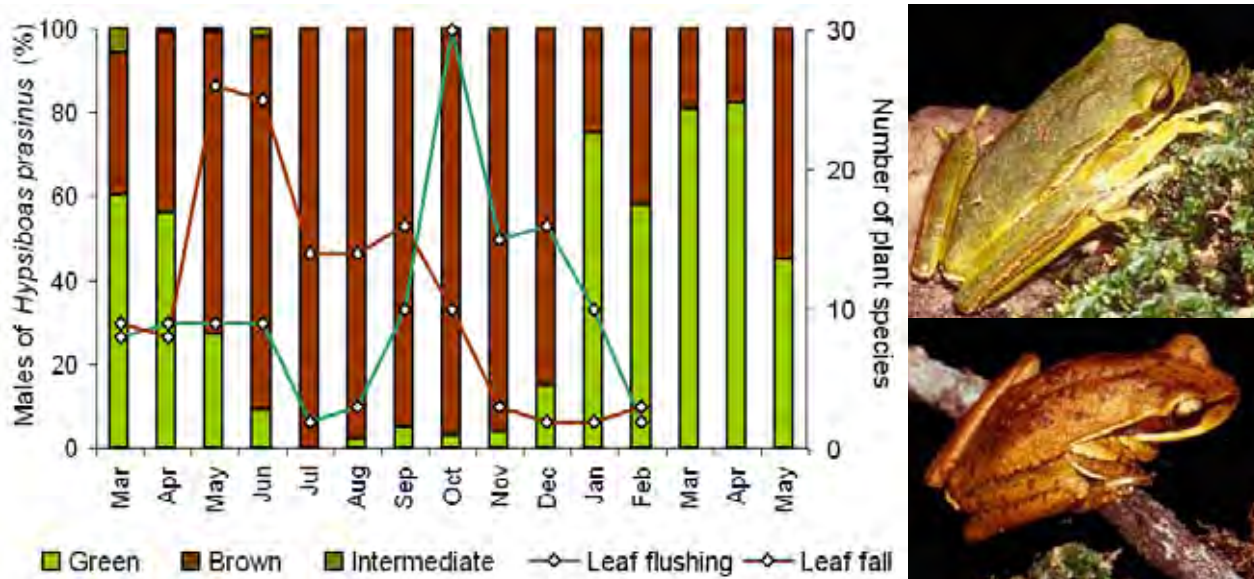


Figure 3. Seasonal variation (from March 1988 to May 1989) in the dorsal coloration of reproductive males of *Hypsiboas prasinus* (Hylidae), and number of plants that exhibited leaf fall (brown lines) and leaf flushing (green lines), in Serra do Japi, municipality of Jundiá, state of São Paulo, Brazil. Brown bars represent brown morphs (upper picture), green bars represent green morphs (lower picture), and olive bars represent intermediate (olive) coloration morphs. Plant fenology data were obtained from Morellato et al. (1989).

DISCUSSION

Evolution of color in anurans

As we observed above the anuran coloration may provide protection against predators by providing concealment (e.g., camouflage, homotypy, and arithmetic mimicry), by alerting the predator about a possible hidden danger or distasteful characteristic (aposematism), or by deceiving the predators (deceptive coloration). Camouflage may have been selected by the predation pressures, by the predatory behavior (such as feeding strategies), or both. Aposematism should have evolved after the acquisition of any dangerous or distasteful defensive strategy (see below). In the case of anurans these strategies can be biting, spine aggression, defensive screams, unpalatability (in terms of bad taste), or, most commonly, noxious secretions. Therefore, we would not expect to find an aposematic harmless anuran, except for those

involved in mimicry (mainly Batesian and Browerian) rings. However, we still do not have studied all the defensive strategies of all aposematic anurans to corroborate this hypothesis and as far as we know, every aposematic anuran (except mimics) has harmful defenses, such as poison (e.g., some species of Mantellidae, Dendrobatidae, and Brachycephalidae), or aggressive defenses (e.g., some species of Ceratophryidae and Leptodactylidae) (L. F. Toledo, I. Sazima & C. F. B. Haddad, unpubl. data). All deceptive coloration types are directly related with the predator search image (see above). Therefore, the pressures who promoted them are strictly related to the predator's vision and cerebral capability. Therefore, these three functions of the defensive colorations (mimicry, aposematism, and deceptive coloration) may have been selected differently across the evolution of anurans (see Table 3).

In Table 3 we included a possible reproductive selection factor that could be involved in the evolution of bright coloration (aposematic and deceptive). Although we do not have any data that corroborates this suggestion, it is possible that exists selection of males by females based on their bright colorations. This should be more evident in polymorphic species, where polymorphism occurs between sexes, and where males are aposematic, or at least present more contrasting colorations, and females are cryptic or less contrasting colorations (e.g., in the bufonids *Chaunus ictericus* and *Ollotis periglenes*).

Table 3. Main characteristics, benefits acquired, and constraints involved in the evolution of defensive coloration of anurans.

Function of the defensive coloration	Main characteristics	Benefits acquired	Constraints involved
Camouflage	Background matching	Predatory behavior Predation avoidance	Predator search image
Aposematism	Background contrasting	Predator avoidance Reproductive success?	Presence of harmful defenses*
Deceptive color	Body color contrasting	Predation avoidance Reproductive success?	Predator search image

*Except in the cases of Browerian and Batesian mimicry (see text).

Several factors are involved in the evolution of aposematism, such as unpalatability, honest signals, relative predator-prey abundance-dependence, and kin selection (review in Mallet & Joron, 1999). In anurans the aposematism have evolved multiple times (e.g., Summers & Clough, 2001; Santos, Coloma & Cannatella, 2003;

Vences et al., 2003). However, some of these authors have based their results in hypothesis of evolutionary relationships that have been recently modified or complemented (Frost et al., 2006; Grant et al., 2006). Therefore, a new overview of these evolutionary approaches on defense is needed, because their assumptions may be modified. For example, Summers and Clough (2001) did their study based on the monophyletic assumption for the old family Dendrobatidae, and in the monophyletic assumption of the former clade of toxic aposematic dendrobatids. However, this hypothetic monophyly was rejected (Santos et al., 2003; Vences et al., 2003) and the former dendrobatid family has been divided into two sister ones (Dendrobatidae and Aromobatidae) and the toxic species are divided into several mono and paraphyletic genera (e.g., *Adelphobates*, *Allobates*, *Ameerega*, *Dendrobates*, *Epipedobates*, *Hyloxalus*, *Myniobates*, and *Oophaga*) in the two families (Grant et al., 2006).

Although there might have some changes in the phyllogenetic inferences, it is still possible that the aposematic coloration has evolved in tandem with toxicity in anurans of the Bufonidae, Dendrobatidae, Aromobatidae, and Mantellidae families, as proposed before (e.g., Summers & Clough, 2001; Clark et al., 2005). “If differences among species in dietary preferences or predatory capabilities are heritable, then natural selection could act to favor brighter coloration in species that consistently have preferences for or access to prey with more or more potent toxins” (Summers & Clough, 2001). Speculations apart, the most evident fact is that the anuran aposematism has evolved by means of multiple convergent radiations, within the class, its families, and/or its genera (e.g., Santos et al., 2003; Vences et al., 2003; Chiari et al., 2004; Clark et al., 2005).

Future steps

This article sums information on the relationships of predation and defensive mechanisms of post-metamorphic anurans. From now we recommend at least four lines of research: I) focused studies on specific defensive strategies against predators and reports of predators-prey interactions; II) complementation of these recent reviews; III) broader and meta-analysis of the predator-prey interactions; and IV) going further on the understanding of the evolution (including phylogenetic approaches) of defensive strategies and their relation with the present and past predators. By now, these reviews organize our knowledge generating, at least, a universal standardization of the

nomenclature of the anuran defensive strategies, functions, effectiveness, and some predator-prey relationships.

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CONSIDERAÇÕES FINAIS

As desovas dos anuros são apresadas por diversos grupos animais, tanto na água, como fora desta, tanto em ninhos de espuma, quanto fora destes. Todavia, parece haver uma taxa de predação diferencial entre as diferentes estratégias de deposição de ovos nos anuros. Isto poderia indicar uma pressão seletiva que pode estar atuando (ou ter atuado) na evolução dos modos reprodutivos na ordem.

Anuros pós-metamórficos são apresados por diversos grupos animais, desde pequenos invertebrados a grandes vertebrados. Aranhas e baratas d'água (entre os invertebrados) e serpentes (entre os vertebrados) são seus principais predadores atuais.

A captura de anuros por seus predadores não é aleatória. Existe uma seleção em função do tamanho da presa em relação ao tamanho do predador, sendo que táticas de predação, como presença de veneno (nos predadores) e ataque em grupo, podem influenciar nesta relação.

Três tipos de vocalizações defensivas são reconhecidos: grito de agonia, grito de alarme e grito de alerta. Destes, o grito de agonia parece ser o mais difundido e deve ser um caráter ancestral para a ordem Anura.

Existem correlações entre o tamanho dos anuros e as características físicas dos seus gritos. Essas correlações podem estar relacionadas à eficácia das vocalizações contra predadores.

Foram encontradas influências ambientais e filogenéticas na presença/ausência das estratégias defensivas.

A predação foi (e deve estar sendo) um forte agente seletivo na evolução das formas e comportamentos dos anuros atuais, moldando incríveis adaptações e padrões de coloração, tornando este, um grupo único e fascinante.