



Universidade de Brasília  
Instituto de Ciências Biológicas  
Programa de Pós-Graduação em  
Zoologia

**Estratégias de defesa, sequências de extinção e adaptações locais em lagartos: O caso das ilhas artificiais da represa de Serra da Mesa, Norte de Goiás, Brasil**

Rogério Benevides de Miranda

Brasília - DF  
Agosto de 2021



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Tese de Doutorado apresentada ao Programa de Pós-Graduação *stricto sensu* em Zoologia da Universidade de Brasília como parte dos requisitos para obtenção do título de Doutor em Zoologia.

Autor: Rogério Benevides de Miranda

Orientador: Professor Dr. Reuber Albuquerque Brandão

Brasília - DF  
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**TERMO DE APROVAÇÃO**

ROGÉRIO BENEVIDES DE MIRANDA

**Estratégias de defesa, sequências de extinção e adaptações locais em lagartos: O caso das ilhas artificiais da represa de Serra da Mesa, Norte de Goiás, Brasil**

Tese de doutorado apresentada em 26 de agosto de 2021, junto ao Programa de Pós-Graduação em Zoologia do Instituto de Ciências Biológicas da Universidade de Brasília, sob orientação do Prof. Reuber Albuquerque Brandão, com o apoio financeiro da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), como parte dos requisitos para obtenção do título de Doutor em Zoologia.

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“A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra  
    Que vai de graça pro presídio  
        E para debaixo do plástico  
    Que vai de graça pro subemprego  
        E pros hospitais psiquiátricos  
A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra  
    Que fez e faz história  
        Segurando esse país no braço  
    O cabra aqui não se sente revoltado  
Porque o revólver já está engatilhado  
    E o vingador é lento  
        Mas muito bem intencionado  
            E esse país  
Vai deixando todo mundo preto  
    E o cabelo esticado  
        Mas mesmo assim  
    Ainda guardo o direito  
        De algum antepassado da cor  
Brigar por justiça e por respeito  
    De algum antepassado da cor  
Brigar bravamente por respeito  
    De algum antepassado da cor  
Brigar por justiça e por respeito  
    De algum antepassado da cor  
        Brigar, brigar, brigar  
A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra  
A carne mais barata do mercado é a carne negra”  
Seu Jorge/Marcelo Yuca/Ulisses Cappelletti, 1998  
    #vidaspretasimportam  
        #blacklivesmatter

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Começo meus agradecimentos pela família. Sou imensamente grato aos meus pais, José e Regina, por todo investimento feito em mim. Meu pai sempre disse que o melhor investimento é a Educação (faço questão de escrever em letra maiúscula) e por isso, mesmo com muita dificuldade, ele sempre se esforçou para que eu tivesse acesso à escolas privadas. Infelizmente, nosso país não oferece boa Educação gratuita, a não ser no nível superior. Foi graças ao sacrifício dos meus pais que pude transformar o meu privilégio em conhecimento. Privilégio porque sei que para um homem da minha cor e classe social, não é fácil alcançar o terceiro diploma de Universidade Federal e com fluência em uma segunda língua. Para que eu pudesse aprender a língua inglesa, a qual hoje me permite ambicionar algo fora do Brasil, meu pai vendeu seu carro e me deu o dinheiro para que eu pudesse me aventurar do outro lado do mundo, na Austrália. Meu orientador, a quem hoje considero um amigo, um dia me disse que no Brasil é impossível ter uma carreira acadêmica sem suporte financeiro familiar. Acho que ninguém discorda disso! Some-se a tudo isso a aflição dos pais ao verem o filho se dedicar, conquistar diplomas e, ainda assim, não ter qualquer perspectiva de sucesso profissional. Com toda certeza é muito complicado ser pai de cientista no Brasil! Mais complicado ainda é ser casado com um. Minha esposa, Ana Carolina, merece todas as honrarias. Além de me aturar, ela compra meu “barulho”. Um caso raro de parceria para vida! Viver a vida cigana ao lado de uma pessoa que vai em busca da oportunidade seja aonde for, é, com toda certeza, bastante desgastante. Juntos partimos do Rio de Janeiro para Brasília, de lá para uma experiência internacional em Washington/DC, durante meu doutorado sanduíche, e agora novamente no Rio de Janeiro. Tudo isso em menos de quatro anos! Te amo, Kakau! Um agradecimento especial aos meus estagiários caninos, Casquinha e Larica, pelo apoio emocional e companhia nas longas horas em frente ao computador. Obrigado ao meu amigo João Queiroz, por me acolher em sua casa em meu primeiro mês em Brasília. À minha irmã Roberta, cunhado Ricardo, e sobrinho Rayco, além de todos amigos e amigas que sempre me acompanharam e me incentivaram na minha busca pelas minhas metas, meu muito obrigado, de coração!

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No Brasil, apenas 0,2% da população possui doutorado, segundo levantamento de 2019. Apenas 11,4% dos pesquisadores de pós-doutorado são pretos (sendo que 56% da população se declara preta, dados do IBGE), de acordo com pesquisa de 2020. Num país onde TODOS OS GOVERNOS se recusam a investir em Educação, pois população sem escolaridade é mais fácil de manipular. Num país onde negligenciam e perseguem o Ensino Superior e a Ciência. Até teve governo que disse que seríamos o “país dos doutores”, mas esqueceu que nós precisamos de emprego depois de terminar o doutorado! Num país onde os números mostrados no início deste parágrafo evidenciam o quão difícil é para um preto atingir posições de liderança. Num país em que para nós o acesso se torna mais difícil devido ao racismo estrutural presente em todos os níveis sociais. Num país onde temos um racista/negacionista como inquilino do Palácio do Planalto. Apesar disso tudo, eu cheguei até aqui! E não é “dotô”, pronome de tratamento, é DOUTOR, com todos os méritos, com diploma, e sem banalização! Não me acho melhor do que ninguém, mas superei as adversidades do sistema.

O sistema é F@#! Mas eu sou mais!

## RESUMO

O Reservatório da Serra da Mesa começou a ser formado em meados dos anos 1990. Desde 1996, nosso grupo desenvolve estudos nas ilhas do reservatório da Serra da Mesa e a continuidade de tais estudos agregará mais informações à cerca do impacto deste tipo de empreendimento sobre a fauna do Cerrado. Elucidar como estratégias de defesa e ecologia afetam a permanência de determinadas espécies em detrimento de outras, além de compreender se adaptações locais ocorreram sob influência das mudanças ambientais é imprescindível para o planejamento de estratégias de conservação em situações de perda de hábitat e isolamento de populações. Foram compiladas estratégias de defesa de lagartos neotropicais presentes na literatura científica, executando-se também um mapeamento de caráter para compreensão dos processos evolutivos por trás desses comportamentos. Foi também avaliado o impacto da fragmentação do hábitat na riqueza e abundância da comunidade de lagartos afetada pela construção da barragem de Serra da Mesa. Por fim, verificou-se possível correlação relevante entre a genética de *Gymnodactylus amarali* (Sauria, Phyllodactylidae) e fatores ambientais, além de divergências genéticas entre populações deste lagarto que vivem em ilhas e populações oriundas do continente. A busca na literatura retornou 70 publicações deste século, 55 do século passado e três publicações do século XIX. A escassez de dados sobre a história natural de lagartos neotropicais afeta o nosso entendimento sobre a evolução das estratégias anti-predação destes animais, limitando estudos futuros. O mapeamento filogenético de caracteres forneceu informações valiosas a respeito da evolução das estratégias de defesa desses lagartos. O processo de enchimento do reservatório impôs uma perda severa de diversidade de hábitat. Houve um acentuado declínio na riqueza de espécies de maior porte e mais conspícuas, resultado da predominância de aves predadoras diurnas e com orientação visual. Como consequência, um processo de seleção direcional favoreceu lagartos mais raros, com menor porte e crípticos, nas ilhas. A análise discriminante (DAPC) detectou a presença de uma linhagem genética distinta de *G. amarali* em Serra da Mesa, com diferenciação das populações próximas do continente. Além disso, a análise de redundância apontou adaptação genética local dos lagartos, correlacionada à temperatura e precipitação, sugerindo uma adaptação ao clima de cada localidade. Além da seleção direcional, a adaptação local ao clima e a divergência genética da população de *G. amarali* de Serra da Mesa são consequências da influência humana trazida pela construção da represa. Embora não haja dados

suficientes anteriores à construção da barragem, estudos recentes na região apresentam resultados que suportam essa hipótese.

**Palavras-chave:** Comportamento; defesa; extinção; fragmentação; Brasil Central; reservatório.



## ABSTRACT

The Serra da Mesa dam reservoir started its flooding in the middle of the 1990s. Since 1996, our research group studies the artificial islands of the Serra da Mesa dam lake, and the continuity of these studies will aggregate more information about the impact of this kind of enterprise on the Cerrado fauna. Clarify how defense strategies and ecology affect the success of certain species to the detriment of others, and the comprehension of possible local adaptations under influence of environmental changes, might be essential for planning conservation strategies where habitat loss and populations isolation occur. I compiled information on defense strategies of Neotropical lizards found in the scientific literature and a character mapping aiming at understanding the evolutionary processes behind these behaviors. I detected a possible relevant correlation between the genetics of *Gymnodactylus amarali* (Sauria, Phyllodactylidae) and environmental factors, besides genetic divergences among island and mainland populations of this lizard. Lastly, I assessed the impact of habitat fragmentation in the richness and abundance of the lizard community affected by the Serra da Mesa dam building. The survey returned 70 publications from this century, 55 from the last, and three from the XIXth century. The lack of information about the natural history of Neotropical lizards affects our understanding about the evolution of anti-predatory strategies among these animals, limiting further studies. The reservoir flooding process caused severe loss of habitat diversity. There was a sharp decline in richness of larger and more conspicuous species due to a predominance of diurnal and visually oriented predator birds. Therefore, directional selection favored rarer, smaller, and cryptic lizards on the islands. The phylogenetic mapping of characters provided valuable information about the evolution of defensive strategies in these lizards. The DAPC detected the presence of a distinct genetic lineage of *G. amarali* in Serra da Mesa, which is differentiated from nearby mainland populations. The RDA pointed out local genetic adaptations correlated with temperature and precipitation, suggesting that lizards are adapting to the climate at each site. Besides the directional selection, the local adaptation to the climate and the genetic divergence of the *G. amarali* population from Serra da Mesa, are consequences of the human influence brought by the dam construction, as well. Although enough data prior to the dam construction are lacking, recent studies in the region present results that support such hypothesis.

**Keywords:** Behavior; defense; extinction; fragmentation; Central Brazil; reservoir.

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## INTRODUÇÃO GERAL

Squamata é a Ordem mais rica de Répteis, com 11.341 espécies e 2.224 subespécies, de acordo com o “The Reptile Database” (Uetz et al. 2017), sendo dividida em três subordens: Amphisbaenia, Serpentes e Lacertilia. Os primeiros Squamata datam do final do Triássico ou início do Jurássico (Estes 1983; Evans 2003), colonizaram todos os continentes durante sua diversificação (Pianka & Vitt 2003) e atualmente apresentam excepcional diversidade de nichos ecológicos (Pianka et al. 2017; Pelegrin et al. 2021). Tais características tornam Squamata interessante para estudos evolutivos e ecológicos (Vitt & Pianka 2005).

Lagartos possuem destaque nas interações tróficas, sendo considerados um componente relevante para inúmeros processos ecossistêmicos, especialmente em ilhas tropicais (Ríos-López et al. 2015). Como se alimentam principalmente de invertebrados, disponibilizam parte da biomassa presente nesses organismos para predadores que não se alimentam de invertebrados, criando um importante elo no fluxo de energia dos ecossistemas (Pianka & Vitt 2003). Como presas, são utilizados por uma ampla diversidade de predadores (Greene 1988; Zug 1993; Poulin et al. 2001). Tal fato os levou a desenvolver, ao longo da sua história evolutiva, uma pletera de estratégias anti-predação, as quais permitiriam maiores chances de sobrevivência frente à variedade de predadores (Martins 1996).

Observações de populações insulares influenciaram a percepção de Darwin (1859) e Wallace (1892) acerca de mudanças populacionais e evolução biológica. Devido ao tamanho reduzido (quando comparado ao dos continentes) e isolamento geográfico, as ilhas são consideradas laboratórios naturais para estudos evolutivos em espaços de tempo relativamente curtos (Jordan & Snell 2008). Nas ilhas, podem-se avaliar tanto processos que afetam a fisiologia de espécies (Velo-Antón et al. 2012) e expansões demográficas de populações (Carnaval & Bates 2007), quanto a estrutura de comunidades (Hasegawa et al. 2009). Por esta razão, estudos de fauna e flora insulares são considerados chaves para compreensão de diversos fenômenos biológicos relevantes para compreensão do processo evolutivo em diferentes escalas (Barton & Mallet 1996). Mais recentemente, as ilhas também ganharam destaque na formulação de ideias e conceitos relativos à conservação de diversidade biológica (Nogales et al. 2003; Howald et al. 2007; Grant & Grant 2014; Whittaker et al. 2017), por conta das relações entre espécies e área (MacArthur & Wilson 1967).

O Reservatório da Serra da Mesa começou a ser formado em meados dos anos 1990. O lago possui aproximadamente 300 ilhas, que variam entre 0,5 e 1000 ha (Lins 2013), cobertas por vegetação de Cerrado senso estrito (Eiten 1994; Ribeiro & Walter 1998). Desde 1996, nosso grupo desenvolve estudos nas ilhas do reservatório da Serra da Mesa. A continuidade de tais estudos irá agregar mais informações ao conjunto de conhecimento sobre o impacto deste tipo de empreendimento sobre a fauna do Cerrado, permitindo conhecer mais profundamente os fenômenos observados nessas ilhas em diferentes populações animais. Os estudos desenvolvidos por nosso grupo (Brandão 2002; Brandão & Araújo 2008; Amorim 2012; Santoro 2012; Lins 2013; Amorim et al. 2017) focam principalmente nos efeitos da formação das ilhas sobre a estrutura ecológica das comunidades herpetofaunísticas, na dinâmica das extinções registradas nas ilhas e na ecologia evolutiva dos organismos que ainda permanecem nas ilhas.

Amorim et al. (2017) compararam a dieta e a morfologia da lagartixa *Gymnodactylus amarali* em ilhas e margens do reservatório e detectaram que os indivíduos nas ilhas apresentaram maior amplitude de nicho alimentar e aumento da cabeça, registrando a ocorrência de evolução rápida no deslocamento de caracteres. O estudo demonstra que populações isoladas em ilhas formadas pela intervenção humana podem responder rapidamente ao isolamento e apresentar mudanças em sua morfologia, ecologia e, possivelmente, frequência alélica. Além disso, processos iniciais de extinção afetaram principalmente as espécies mais conspícuas a predadores visualmente orientados (Brandão 2002), que dependiam basicamente da fuga para escapar de predadores. As espécies que permaneceram nas ilhas, até o momento, são as de menor porte e mais crípticas, que também apresentam mecanismos de defesa mais elaborados (e.g. Brandão & Mota 2005).

Este estudo investiga a hipótese de que o empreendimento da Hidrelétrica de Serra da Mesa, através do enchimento de seu reservatório e posterior fragmentação do habitat, estaria causando impactos na comunidade de lagartos local. Para este fim, o estudo das estratégias de defesa dos lagartos pode ajudar na compreensão dos eventos de extinção observados ao longo dos anos nas ilhas de Serra da Mesa. Além disso, se por um lado *G. amarali* foi capaz de persistir e se adaptar a este ambiente fragmentado, por outro lado, um grande número de espécies foi perdido. Portanto, se faz necessário elucidar se *G. amarali* estaria se beneficiando de adaptações locais sob influência das mudanças ambientais. Elucidar como um empreendimento da magnitude da represa de Serra da Mesa impacta a biodiversidade local é imprescindível para o planejamento de estratégias de conservação em situações de perda de hábitat e isolamento de populações. Dessa

forma, com intuito de compreender mais profundamente como a comunidade de lagartos vem sendo afetada por tais eventos ao longo desses anos, este estudo estrutura-se da seguinte maneira:

Capítulo 1 – Neste capítulo faço uma compilação das estratégias de defesa de lagartos neotropicais presentes na literatura científica. Além desta reunião de dados sobre estratégias, executo um mapeamento de estados de caráter baseada na filogenia gerada por Tonini et al. (2016). Essa análise visa à compreensão dos processos evolutivos por trás dos comportamentos. Esse capítulo foi submetido para publicação e seguiu as normas de formatação do periódico “Ethology, Ecology & Evolution”, com fator de impacto 1.321 (2021).

Capítulo 2 – Aqui busco avaliar o impacto da fragmentação do habitat na riqueza e abundância da comunidade de lagartos afetada pela construção da barragem de Serra da Mesa. Este capítulo será submetido para publicação no periódico South American Journal of Herpetology, FI = 1.55 (2021).

Capítulo 3 – O último capítulo tem por objetivo identificar se existe correlação relevante entre a genética de *Gymnodactylus amarali* e fatores ambientais, além de divergências genéticas entre populações deste lagarto que vivem em ilhas e populações oriundas do continente. Este capítulo será submetido para publicação e seguiu as normas de formatação do periódico “Perspectives in Ecology and Conservation”, FI = 4.677 (2021).

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## CAPÍTULO 1

### **ESCAPING FROM PREDATORS: A REVIEW OF NEOTROPICAL LIZARDS DEFENSE STRATEGIES**

#### ABSTRACT

Lizards are commonly preyed on by a great variety of predators, including vertebrates and invertebrates. Therefore, it is expected that lizards have developed a wide range of anti-predation strategies, increasing their chances of successful survival during agonistic events with predators. Defense against predation is a phenomenon that involves up to five stages that can be grouped within two sets of behavioral strategies, commonly named primary and secondary strategies. The primary defenses include strategies that affect predator detection or interest and encompass immobility, mimicry, aposematism, and cryptic coloration. Secondary defenses occur after predator detection and attack, including strategies that aim to prevent or interrupt the lizard manipulation by a predator. These defenses include strategies as frightening (e.g., scratching or biting the predator), tail lashing, flouncing vigorously the body, cloacal discharge, agony vocalizations, and tail autotomy. We found a total of 203 scientific publications, including peer-reviewed journals, short communications, notes, and books. A compilation of 22 defense strategies was assembled, with 23% corresponding to passive defenses and 77%, consequently, to active defenses. Lizard species deal with a broad diversity of predators, but the number of field experiments and studies about the predation of lizards remains scarce. We reviewed the defense strategies presented by Neotropical lizards, using a phylogenetic approach in order to

understand and clarify the evolutionary process behind these strategies. Thanatosis, crypsis, and tail autotomy are symplesiomorphic for lizards, whereas venom and emetic substances are autapomorphic, and aposematism seems to be rare. Our character mapping provides valuable information about the evolution of defensive strategies in Neotropical lizards, combining natural history and phylogenetics. Trivial observations about any animal behavior might be important, and we strongly recommend that ethological observations describe the event in all possible details. We also present a novel case of defense strategy for Neotropical lizards.

**Keywords:** behavior; defense; lizards; phylogenetic reconstruction; predation.

## **Introduction**

Lizards are relevant food web components in many of the environments where they occur (Spiller & Schoener 1994; Schoener et al. 2002; Piovia-Scott et al. 2011). Considering their diversity in the Neotropics, expressed through the diversity of body sizes, feeding strategies, habitat use, and demographic dynamics, lizards are involved in several ecological interactions with their preys and predators (Smith 1981; Losos et al. 1993; Hödar et al. 1996; Barros et al. 2010). Independently of playing prey or predator roles, the loss of lizard species might cause substantial changes in the food web structure (see Chase 1998; Schoener et al. 2002; Zipkin et al. 2020).

Lizards are preyed on by a variety of predators (Galdino et al. 2006; Samia et al. 2015), such as snakes, birds, mammals, and arthropods (Jehle et al. 1996; Poulin et al. 2000; Downes 2002; Reardon et al. 2012; Zipkin et al. 2020), and a single lizard species can be preyed on by predators belonging to several taxa (Schall & Pianka 1980; Reardon et al. 2012; Watson et al. 2012).

Several snakes (Greene 1988; Martins 1993, 1996), some lizards (including cannibalism; Siqueira & Rocha 2008), mammals (as Felids, Canids, Procyonids, and Mustelids), and birds (as eagles, falcons, owls, several passerine species) regularly prey on lizards (Greene 1988; Jehle et al. 1996; Martins 1996; Poulin et al. 2000; Downes 2002; Reardon et al. 2012). Invertebrate carnivores, especially arachnids and insects, also feed on lizards, mainly on small-bodied species or juveniles (Pianka & Vitt 2003).

This wide diversity of predators, presenting their particular set of foraging strategies (Greene 1988; Jehle et al. 1996; Martins 1996; Poulin et al. 2000; Downes 2002; Reardon et al. 2012), elicits the development of a broad diversity of anti-predation strategies along the lizards evolutive history, enabling them to have a greater escape success when facing a predator (Rocha 1993; Abrams 2000; Sherbrooke 2008). Even fossorial lizards, thought to be less exposed to predators, deal with strong predatory pressure (Martins 1996).

Although predation could be defined as the act of one organism ingesting tissues of another (previously alive) organism (Abrams 2000; Arim & Marquet 2004), predation is a complex ecological interaction, presenting at least five stages grouped in two phases (Endler 1986). These stages describe how predators locate, subjugate, and ingest their prey (Endler 1986; Mappes et al. 2005). While predators develop different hunting strategies for each predatory stage, prey develops correspondent anti-predatory defenses, creating a complex and extraordinary “arms race” in nature (Dawkins & Krebs 1979; Abrams 2000; Mappes et al. 2005).

The first predatory phase involves strategies related to the detection, identification, and interest towards the prey, whereas capture and ingestion are part of the second phase (Endler 1986). To oppose to the first phase strategies performed by predators, lizards invest in defense strategies that make their recognition difficult or inhibit the interest of potential predators,

preventing detection, identification, or interest (Martins 1996). Many of these defense strategies are not energy demanding (e.g., camouflage, immobility, polymorphic coloration, mimicry, aposematism, disruptive coloration, or resting at out of sight shelters, as burrows or high perches), leading some authors to call them “passive defense strategies” (Greene 1988; Martins 1996; Sweet 2016).

The second predatory phase begins when the predator becomes interested and engages in capturing the prey. At this point, strategies are often energy demanding to lizards (as to the other preys) and known as “active defense strategies.” When detected and chased, lizards may try to escape, surprise or hurt the predator (Martins 1996; Blázquez et al. 1997; Cooper et al. 2009, 2014).

When predators are getting closer, lizards usually flee running to shelters like rock crevices, burrows, holes on dead logs or trees, or climbing vertical surfaces (tree trunks or rocky walls; Schall & Pianka 1980; Martins 1996). Running away from predators may seem like a commonplace defense strategy, but some species are capable of running over the water. This remarkable ability was reported for some *Anolis* lizards, young iguanas (Hsieh & Lauder 2004), and the tropidurid *Uranoscodon superciliosus* (Pianka & Vitt 2003). This strategy is even more extraordinary in the Corytophanidae genus *Basiliscus*, whose species uniquely mastered the ability of running across the water surface using only the hind limbs as a source of thrust and lift (Aerts et al. 2003; Hsieh 2003; Hsieh & Lauder 2004). Sometimes lizards could dive into nearby water bodies (Mesquita et al. 2006; Carvalho et al. 2012), like the common iguana (*Iguana iguana*), which has metabolic adaptations for diving (Moberly 1968) and to spend some time at the bottom of rivers and lakes. Semi-aquatic species like the teiids *Crocodylus lacertinus* and *Dracaena guianensis* also use water as escape route (Mesquita et al. 2006).

When cornered, lizards can assume aggressive postures and intimidation displays (e.g., raising the body, mouth opening to show the oral mucosa with aposematic coloration, hissing, and body flattening). Some species, like *Coleodactylus brachystoma*, can use their tail to resemble scorpions (Brandão & Motta 2005) or other noxious invertebrates. Aggressive displays intend to confuse the predator about prey location, to show the predator that the prey is already aware that detection happened and therefore successful capture will be unlikely, or to direct strike to a less vital part of the body (see Kircher & Johnson 2017).

When captured, the prey attempt to prevent or interrupt handling and submission. Lizards may try to hurt the predator (by scratching, biting, or lashing with the tail), vigorously thrash the body, release cloacal discharge, emit anti-predatory vocalizations, and autotomize the tail (Greene 1988; Martins 1996; Galdino et al. 2006). Other strategies involve the release of emetic substances produced by glands in their skin, which can cause nausea and vomiting (Greene 1988).

The most common defense presented by seized lizards is biting the predator. This strategy is very efficient, especially in venomous (e.g., helodermatids; Greene 1988; Martins 1996), or big but not venomous species (e.g., teiids; Haddad et al. 2008; Herrel et al. 2009; Almeida et al. 2015). The tough and slippery skin that hinders manipulation, and the ability of some sphaerodactilids that can lose their skin when grasped (Pianka & Vitt 2003), are also examples of active defenses found in some Neotropical lizards.

The most studied defense strategy is caudal autotomy (e.g., Daniels 1983; Arnold 1984; Bellairs & Bryant 1985; Greene 1988; Martín & López 2003), presumably because of its adaptive significance, as it is very likely that tail autotomy represents the ancestral condition for Lepidosauria (Leblanc et al. 2018).

Although several lizard species deal with a broad diversity of predators, each one showing particular hunting strategies related to their different capacity of detection and capture (Greene 1988), the number of field experiments and studies about predation of lizards remain scarce (Pianka & Vitt 2003). Herein, we compiled information regarding the defensive behavior presented by Neotropical lizards, assessing whether the presence of these strategies might be explained by phylogeny and, therefore, help us to understand and clarify the evolutive processes behind these behaviors. We also present a novel case of defense strategy for Neotropical lizards.

### ***Confusing the predator***

Both aposematism and mimicry are based on signals (Kikuchi & Pfennig 2013). Aposematic signals (distinctive color, smell, or behavior) are strategies to manipulate predators by sending a message that the prey is unprofitable (Mappes et al. 2005). These signals are more efficient when they are easily detected and memorized, facilitating avoidance learning (Ruxton et al. 2004; Mappes et al. 2005). H. W. Bates (1862) realized that birds avoided palatable butterflies which showed similar appearance to the toxic ones. The model was more abundant than non-toxic butterflies and, this way, more frequently found by the birds, making bad experiences on such colored butterflies (model) more frequent than positive experiences with similar colored butterflies (mimic). This experience educated predators about a pattern that should be avoided. This system is called Batesian mimicry. The other best-known kind of mimicry related to predator-prey relationship was described by F. Müller (1879), and is called Müllerian mimicry. In this system, many species converge on the same warning signal, which is also an effective way of educating predators about their unpalatability (Kikuchi & Pfennig 2013).

### *Aposematism*

Showing to the predator obvious visual signals is a valuable evolutionary strategy, which has independently evolved in many taxa, such as Lepidoptera, Coleoptera, Hemiptera, Anura, and Teleostei (see Tseng et al. 2014). Aposematic organisms present, together with conspicuous colors, some kind of risk, noxious or toxic taste that function as a defense against predators (Cott 1940; Edmunds 1974; Gamberale & Tullberg 1996).

### *Mimicry*

Mimicry is another strategy used by lizards for survival and considered very important in the studies focusing the evolution of ecological relationships (Bates 1862; Brandão & Motta 2005). Some mimicry systems were described for lizards, being those involving mimicry of venomous invertebrates better known (Pianka & Vitt 2003). There are reports of lizards mimicking centipedes, scorpions, and beetles (Figs. 3B, 3C, 3D, and 3F; Huey & Pianka 1977; Autumn & Han 1989; Vitt 1992; Brandão & Motta 2005) and involves both passive patterns and active postures. Folding the tail over the body is another manner to deceive predators, as they mistake the curly tail with the metasoma of scorpions. This strategy is documented for *Coleodactylus brachystoma* (Brandão & Motta 2005) and *Gonatodes humeralis* (Costa et al. 2009).

### *Cryptic coloration*

The defense strategies considered most successful are those that avoid capture. Cryptic coloration or camouflage is an adaptation against visual detection of predators, as preys become indistinguishable from the background, or are not evident in the environment (Merilaita 1999; Schaefer & Stobbe 2006; Moreno-Rueda et al. 2019; Moreno-Rueda 2020). Experiments have shown that smaller color differences between animal and background offer less chance of being



detected by predators (see Moreno-Rueda 2020). Crypsis is reached through several mechanisms, such as substrate matching, countershading, and disruptive coloration (Endler 1988; Merilaita 1999). Countershading is a color gradient, from dark on the dorsal region of the animal to a lighter coloration on the ventral region, and functions as a mechanism that reduces recognition by preventing three-dimensional image formation, hence its detection by predators (Ruxton et al., 2004a). This animal coloration effect is considered a fundamental principle and is present in a wide variety of taxa (Ruxton et al., 2004b). The color pattern that prevents prey image formation in the brain of predators is known as disruptive coloration. This effect is more efficient when some of its elements match the background while others differ strongly from it, resulting in confused image formation (Cott 1940; Schaefer & Stobbe 2006).

Aiming to achieve a more effective anti-predation outcome, multiple camouflage strategies might be exploited simultaneously (Hall et al. 2017). Camouflage encompasses the benefits of having a color pattern that merges with the background and from resembling irrelevant objects, which is called masquerade (Hall et al. 2017). Thus, while camouflage prevents detection, masquerading works by ensuring that organisms are not identified as a prey or predator after detection occurred (Skelhorn et al. 2011; Hall et al. 2017). An unreported case of masquerading is the darker coloration exhibited by *Norops meridionalis* in recently burned areas. The species is found in savanna habitats, usually close to soil or perched at low grasses and shrubs. These lizards commonly use armadillo holes as a shelter during the fire and present a dark color when emerging from these holes after the fire. The lizard skin becomes dark, and it is not just covered in soot from the fire. The dark color helps them to be camouflaged in the burned vegetation, while the yellowish longitudinal dorsal stripe makes them masquerade as partially burned leaves of grasses and some Cerrado trees, as *Kilmeyera* spp., which releases their leaves

after the fire. These leaves often keep the main nervure yellowish. The function of the opaque coloration of the tail and the head showed by the individuals in the recently burned areas remains unknown and is not related to skin shedding (Fig. 1).

#### *Color polymorphism and ontogenetic polymorphism*

Polymorphism is the simultaneous occurrence of more than one phenotype within a population and it is reported for all living organisms (Schoener & Schoener 1976; Bond & Kamil 2002; Zatz 2002). Since predators are usually more experienced with the more common morphotype, they tend to learn how to recognize and, consequently, consume the most abundant or the most evident morphotypes, whereas the color pattern less common or more cryptic tend to be less predated (Endler 1988; Zatz 2002). Ontogenetic polymorphism is reported for juveniles whose color pattern is different from adults (Rand & Andrews 1975). *Diploglossus lessonae* presents similar coloration to the noxious millipede *Rhinocricus albidolimbatus* when juvenile (Vitt 1992), whereas juvenile *Anolis cuvieri* presents different colors from adults, thus preventing intraspecific predation, once larger adults are active predators of smaller *A. cuvieri* (Rand & Andrews 1975).

#### *Using the tail*

When lizards sheds the tail, their social status is lowered, since the total size is a fundamental determinant of social status (Fox et al. 1990). However, survival is far more crucial than social status and the tail is a very relevant asset for the endurance of lizards. Tail presents several functions and shapes in lizards, being useful as predator distraction, for physical defense, in sexual display, for animal balance, fat storage, body stabilization on different surfaces, as support for climbing and aiding the escape from predators (Vitt et al. 1977). When handled by a predator, lizards can easily shed their tail through some type of neural or hormonal control

(Bateman & Fleming 2009). Regardless of losing an important part of the body and dealing with a range of limitations related to the absence of it, the tail will regenerate after some time (Fox et al. 1990).

### *Tail autotomy*

Caudal autotomy is a common response in lizards against predation attempts (Bateman & Fleming 2009). The term autotomy refers to voluntary loss of some body part, normally as an anti-predation behavior (Bateman & Fleming 2009). The capacity of shedding the tail is strongly affected by the phylogenetic history of lizards (Zani 1996), reflecting the fact that this behavior is considered an evolutionary adaptation within anti-predation strategies (Vitt & Ballinger 1982). Extant lizards present two types of tail autotomy: intravertebral autotomy is possible because the caudal vertebrae have pre-fracture planes where the tail breaks, whereas intervertebral autotomy occurs between adjacent caudal vertebrae (Leblanc et al. 2018).

As aforementioned, tails have some type of neural or hormonal control and store energy from fat. An energy-rich tail may function as a more attractive part to be attacked by predators (Clause & Capaldi 2006). The neural mechanism combined with fat supply allows the autotomized tail to remain moving during some time through anaerobic respiration (Pianka & Vitt 2003). Whilst the tail draws predator attention, the lizard escapes (Congdon et al. 1974). Energy is extremely valuable in nature and waste is not favored. Thus, some lizard species (e.g., species belonging to the *Eumeces* genus) return to the site where their tail was autotomized and eat it if the predator had not done it yet (Pianka & Vitt 2003). Some small varanids are known as collectors and feed on tails shed by gekkonids (Pianka 1969).

Despite caudal regeneration being a relatively rapid event, tail absence implies various losses to the animal (Pianka & Vitt 2003). Although caudal autotomy allows the escape, the cost

of losing the tail is high. The animal will have to deal with fitness decrease, even temporally, in exchange for survival. A tailless lizard loses an important mechanism of defense (Daniels 1983), suffers running speed decrease (Smyth 1974), energy loss (Pianka & Vitt 2003), has social status debasement (Fox et al. 1990), and compromises its balance when perched (Baird & Girard 1852).

### *Tail luring*

Several lizard species present tail displays, although these tail movements draw attention from predators (Mori 1990). Despite the risks, deflecting the strike to a non-vital body part enables a more successful prey escape (Clause & Capaldi 2006; Sousa et al. 2016). Some authors suggest that brilliant and colorful tails act as decoy for visual oriented predators (Wilkinson 2003; Watson et al. 2012; Fresnillo et al. 2015; Sousa et al. 2016). In order to attract interest from snakes, juveniles from the skink genus *Eumeces* hide their body under the leaf litter while whip the exposed tail (Cooper & Vitt 1985).

## ***Integumentary Adaptations***

### *Skin Shedding*

Integumentary adaptations presented by some lizards enable them to release their skin, distracting the predators and increasing escape success (Bauer et al. 1993). Thus, this is an analogous behavior to caudal autotomy. Skin shedding is allowed by the structure of the dermis, characterized by the discontinuity of collagen fibers inside the stratum compactum of the dermis and the presence of preformed areas of weakness (see Bauer et al. 1993). When the skin is lost, the lizard presents only a thin layer of stratum compactum and this layer will be the physiologic barrier against desiccation, infections, and solar radiation (Bauer et al. 1989, 1993). Despite external layer regeneration, scales structure will not be identical to the original skin (Bauer et al.

1993). The capacity of skin loss is an escape strategy observed in some species of geckos, skinks, and sphaerodactilids (Bauer et al. 1989; 1992; 1993), such as *Chatogekko amazonicus* and *Gonatodes hasemani* (Pianka & Vitt 2003), and it has evolved at least eight times in gekkonids (Bauer & Russel 1992).

### *Cornification*

The skin of lizards might have other antipredatory characteristics. Scale cornification provides tough and slippery skin, molding a compact structure that protects the animal against aggressors and makes grab and handling more difficult (Pianka & Vitt 2003). Furthermore, some species possess thorns that prevent capture, like lizards of the *Phrynosoma* genus. Manipulate and swallow thorny lizards might be a painful experience and, sometimes, predators even die (Pianka & Vitt 2003).

### *Thanatosis*

‘Thanatosis’ means death, in Greek, and derives from the word ‘Thanatos’, the Greek god of death (Toledo et al. 2010). Thanatosis, or death feigning, is mostly triggered by extremely dangerous and threatening situations, also by strong tactile stimuli, such as a predator grasp (Rogers & Simpson 2014). Thanatosis is slightly different from shrinking, which is another, but similar, defense strategy, triggered by the same situations. Shrinking is described as a behavior where the animal remains motionless and bends the limbs close to the body, protecting the ventral region, and sometimes keeps the eyes open (Toledo et al. 2010). When facing danger, the animal in thanatosis pretends to be dead, exposing aposematic colors in some cases (Bordignon et al. 2018), tongue protrusion and odoriferous secretions may occur (Toledo et al. 2010).

### ***Antipredatory vocalizations***

Vocal communication is a largely widespread mechanism among vertebrates for information transference (Phongkangsananan et al. 2014). These signals are useful to indicate food availability, mate attraction, territorial demarcation, and to warn about the presence of predators (see Phongkangsananan et al. 2014 and references therein). Lizards are also capable of acoustic communication and, although most species can produce only hisses, some of them present actual vocalizations (Marcellini 1974; Labra et al. 2013). Other than reptile vocalizations being known in a variety of taxa, knowledge about bioacoustics within this group is considered very poor (Phongkangsananan et al. 2014). Lizards vocalize as response to threat, mainly when grasped by a predator, and some species show vocalizations for social interactions (e.g., mate attraction). Gekkonids are the main study object in this area as, among lizards, only they possess larynx specializations for vocalization and well-developed auditory sensibility (see Labra et al. 2013). Vocalizations are phylogenetically and geographically widespread within gekkonids, with approximately 2000 species belonging to at least 20 different genera (Phongkangsananan et al. 2014).

### ***Aggressive displays***

Lizards have a variety of aggressive displays. When a predator is detected nearby, some geckos show deimatic behaviors in order to intimidate the aggressor. Limb extension and retraction, pushups, back-arching, tail waving, head-bobbing, and erect posture are some behaviors reported (Marcellini 1977). *Anolis cristatellus* was observed flexing the legs, extending and contracting the dewlap (i.e., dewlapping; see Leal & Rodríguez-Robles 1997; Leal 1999) when facing potential predators. Some animals fill their lungs with air and puff the body to look bigger and scarier, case of some teiids and varanids, and sometimes hisses and whistles are

also emitted (Pianka & Vitt 2003; Barros et al. 2010). Open the mouth exposing internal mucosa and tongue, which sometimes have dark coloration, like reported for the polychrotid *Polychrus acutirostris*, might increase the intimidation effectivity (Vitt & Lacher 1981; Abramjan et al. 2015).

### ***Emetic substances***

Several species from the *Phrynosoma* genus present the uncommon behavior of squirting blood from their ocular-sinus, such as *Phrynosoma asio*, *P. cornutum*, *P. coronatum*, *P. orbiculare*, *P. solare*, and *P. taurus* (see Sherbrooke & Middendorf 2001; Hodges 2004). Previous studies pointed out that this unique anti-predator strategy is specific against canids and possibly other mammalian predators (Sherbrooke & Middendorf 2001). Another singular characteristic of this behavior is the volume of blood loss, which may reach up to 53% of the total blood volume of a *P. cornutum* individual in a single squirt (Leaché & McGuire 2006).

### ***Locomotor escape***

When aggressiveness is not enough to drive away the predator, flight is the best escape strategy. Some morphological adaptations increase escape success in several species. Bipedalism in lizards seems to be an accidental outcome in response to selection for increased maneuverability, where the forward acceleration combined with a rearward shift in the body center of mass lifts the body of the lizard during the run (Aerts et al. 2003; Clemente 2014). Bipedal running is observed especially in lizards associated with sandy, rocky, and open environments (see Rocha-Barbosa et al. 2008), such as teiids (*Salvator* spp. and *Ameiva ameiva*), and tropidurids (*Tropidurus* spp.; Lema 1983; Rocha-Barbosa et al. 2008; Clemente 2014). Iguanas may jump from their perches and sprint (Pianka & Vitt 2003) or, in case of water bodies available in the area, they dive and swim (Carvalho et al. 2012). Swimming away from predators

is also observed in semi-aquatic lizards, such as *Crocodilurus* spp., *Dracaena* spp., and the gymnophthalmids *Neusticurus* spp. and *Potamites* spp. (Vitt & Ávila-Pires 1998; Vitt et al. 1998; Mesquita et al. 2006; Bauer & Jackman 2008).

Besides riverine and semi-aquatic species, three terricolous species from open Cerrado areas and another two from the Amazon region were reported using diving as opportunist escape strategy. In a mangrove area in Pará, Brazil, a *G. humeralis* individual was seen running through a partially submerged tree trunk and submerging into the water to escape from observers (Fernandes et al. 2009). *Tropidurus torquatus*, *T. oreadicus*, and *Copeoglossum nigropunctatum* were observed thermoregulating and dove into the nearby water body as observers approached (Carvalho et al. 2012). Another case was recently reported with *Plica plica*. During a nocturnal search in a “Várzea” forest site, researchers spotted a *P. plica* specimen that dove from a trunk into the water (Maciel et al. 2021).

### ***Most observed behaviors***

As well as thanatosis, body thrashing, cloacal discharge, running, scratching, and bite are behaviors showed by all studied species, adding little information to relationships. Some species use more frequently certain strategies than others, depending on the defense repertoire of each animal, environment, and predators. Scratching is a very common behavior among lizards as well, and seems to be more efficient in larger saxicolous and terricolous lizards compared to geckos and smaller species.



## **Material and Methods**

### ***Data searching***

We searched databases specialized in scientific literature, mainly Google Scholar, Scopus, and Web of Science. The online survey occurred during June 2017 and complementary searches happened through June until September 2021. We completed the survey with books, such as field guides, academic books, and others, in order to achieve a survey as deep as possible. We found 203 scientific publications in total (Table 1), the oldest published in 1852 and the most recent from 2021, including peer-reviewed journals, short communications, notes, and books. The first reference consulted was Pianka & Vitt (2003). After the reading, some keywords were used to begin the online search. The terms used in the search were “lizard” combined with “predator escape” (e.g., “lizard” and “predator escape”), “anti-predator mechanisms”, “anti-predator adaptations”, “tail autotomy”, “tail display”, “tail luring”, “mimicry”, “crypsis”, “camouflage”, “thanatosis”, “death feigning”, “skin loss”, “aggressive displays”, “vocalizations”, “acoustic signaling”, “emetic substances”, “venom”, “color polymorphism”, “diving”. The results were filtered to select only publications about lizards from the Neotropical region, and studies which were considered relevant (e.g., tail display related to sexual interactions was disregarded), independently of the year the study was published. Grey literature was also disregarded (e.g., dissertations and thesis). Google Scholar was the main source of data, followed by Scopus. The current species name and distribution were checked using The Reptile Database (Uetz et al. 2017). Out of the 203 total references, only 128 were used herein (Fig. 1).

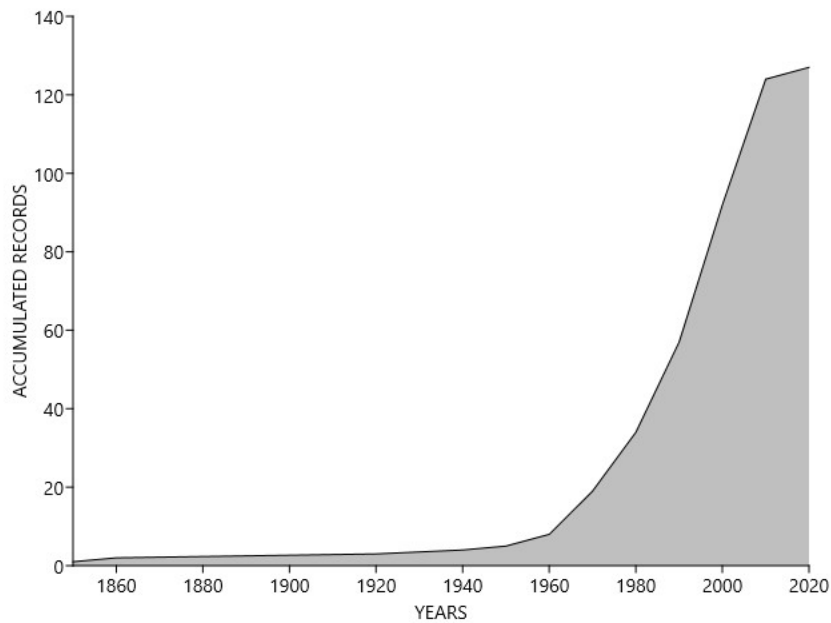


Figure 1. Accumulative records of used studies focusing on defense strategies displayed by Neotropical lizards along the time.

### ***Character Mapping***

Each strategy found was coded for mapping as a character state with two possible states: zero (0) for not observed, and one (1) for observed. We chose each character state and defense strategy supported by literature and by our empirical experience. Character mapping was accomplished using the R package ‘phytools’ (Revell 2012). The function ‘make.simmap’ was used to detect how many times the character transitioned along the tree branches. The transition model was set to Equal Rates, and we run 100 simulations. The phylogeny used for this reconstruction was obtained from Tonini et al. (2016), and trimmed to retain only the Neotropical species, except for the taxon *Sphenodon punctatus*, which was sustained as outgroup (supplemental material).

## Results

The bibliographic survey returned information regarding escape strategies for 83 Neotropical lizard species, spread over 16 families. A compilation of 22 defense strategies was assembled, with 23% corresponding to passive defenses (crypsis, color polymorphism, ontogenetic polymorphism, aposematism, and mimicry), whereas 77% corresponded to active defenses (scratching, bite, body thrashing, running, diving, cloacal discharge, antipredatory vocalization, tail autotomy, venom, emetic substances, skin loss, skin thorns, slipperiness, aggressive displays, tail luring, tail whip, and thanatosis).

### Passive Defense Strategies

Aposematism or warning coloration is extremely rare among lizard species (Clark et al 2017). The character mapping presented points out aposematism as an autapomorphy for the genus *Heloderma*, including *H. horridum*. Examples of passive defense strategies are shown on figure 3.

Mimicry is a synapomorphic active defense strategy for *G. humeralis* and *C. brachystoma*, and for *Gymnodactylus amarali* and *G. darwinii*. *Diploglossus fasciatus* and *D. lessonae* show mimicry of noxious invertebrates as a synapomorphic passive defense (Fig. 4A).

The cryptic coloration (or camouflage) is present in all studied species, except for *Heloderma horridum*, which is aposematic. Together with tail loss, crypsis seems to be one of the earliest defense strategies in lizards. An unreported case of masquerading is the darker coloration exhibited by *Norops meridionalis* in recently burned areas. The species is found in savanna habitats, usually close to soil or perched at low grasses and shrubs. These lizards commonly use armadillo holes as a shelter during the fire and present a dark color when

emerging from these holes after the fire. The lizard skin becomes dark, and it is not just covered in soot from the fire. The dark color helps them to be camouflaged in the burned vegetation, while the yellowish longitudinal dorsal stripe makes them masquerade as partially burned leaves of grasses and some Cerrado trees, as *Kilmeyera* spp., which releases their leaves after the fire. These leaves often keep the main nervure yellowish. The function of the opaque coloration of the tail and the head showed by the individuals in the recently burned areas remains unknown and is not related to skin shedding. We called this new report pyrogenic camouflage (Fig. 2).

Color polymorphism was detected in *Liolaemus chacoensis*, *Anolis etheridgei*, *A. semilineatus*, *A. sagrei*, and *A. lineatopus*, whereas ontogenetic polymorphism appears in *Salvator merianae*, *Iguana iguana*, *Diploglossus lessonae*, and *A. cuvieri*, indicating an evolutionary convergence for this character (Figs. 4B, 4C). It is possible that many cases of polymorphism in lizards remain underestimated, especially related to ontogeny and color structure quantification such as spots, bars, and stripes.



Figure 2. Camouflage and color change in the Cerrado endemic lizard *Norops meridionalis* is related to seasonal fires. (A) Typical camouflage color showed by the lizard in unburned areas, Águas de Santa Bárbara, state of São Paulo, Brazil (Photo: Bruno F. Fiorillo). (B) Pyrogenic camouflage in *Norops meridionalis* in a recently burned Cerrado area at Emas National Park, state of Goiás, Brazil (Photo: Mario Barroso, September 1998). (C) Pyrogenic camouflage in *Norops meridionalis* captured in a recently burned area at Trijunção Farm, state of Bahia, Brazil (Photo: Reuber Brandão, July 2008).

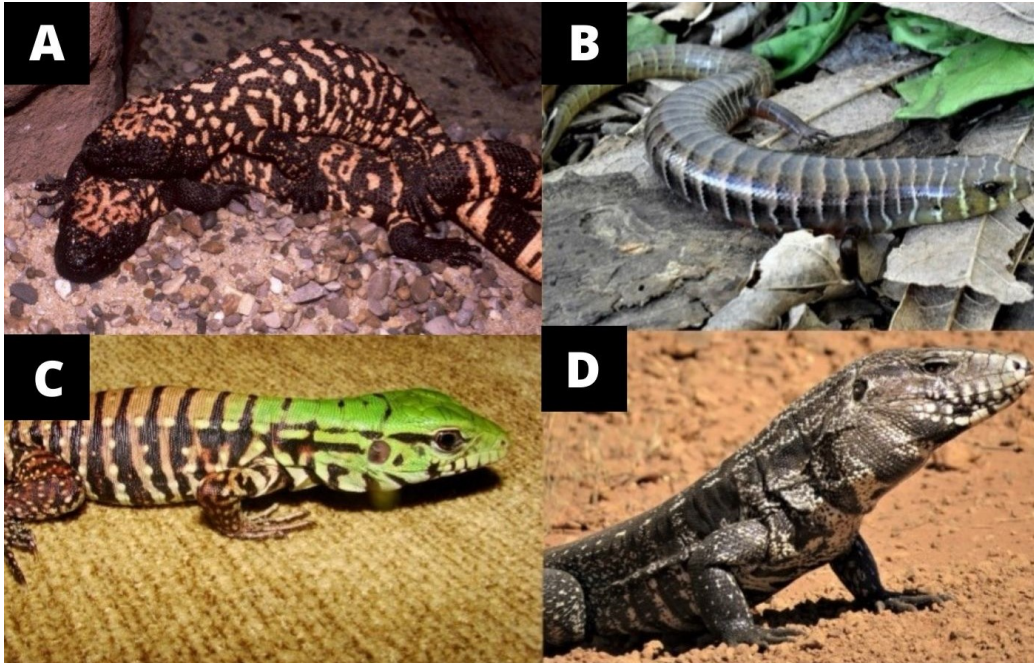


Figure 3. Some examples of passive defense strategies in Neotropical lizards: (A) Aposematism in the venomous lizard *Heloderma suspectum* (Photo: William Quatman). (B) The striking resemblance of noxious millipedes displayed by the Diploglossidae lizard *Diploglossus lessonae* (Photo: Daniel Laranjeiras). Ontogenetic changes in color displayed by (C) young and (D) adult *Salvator merianae* (Photos: Reuber Brandão).

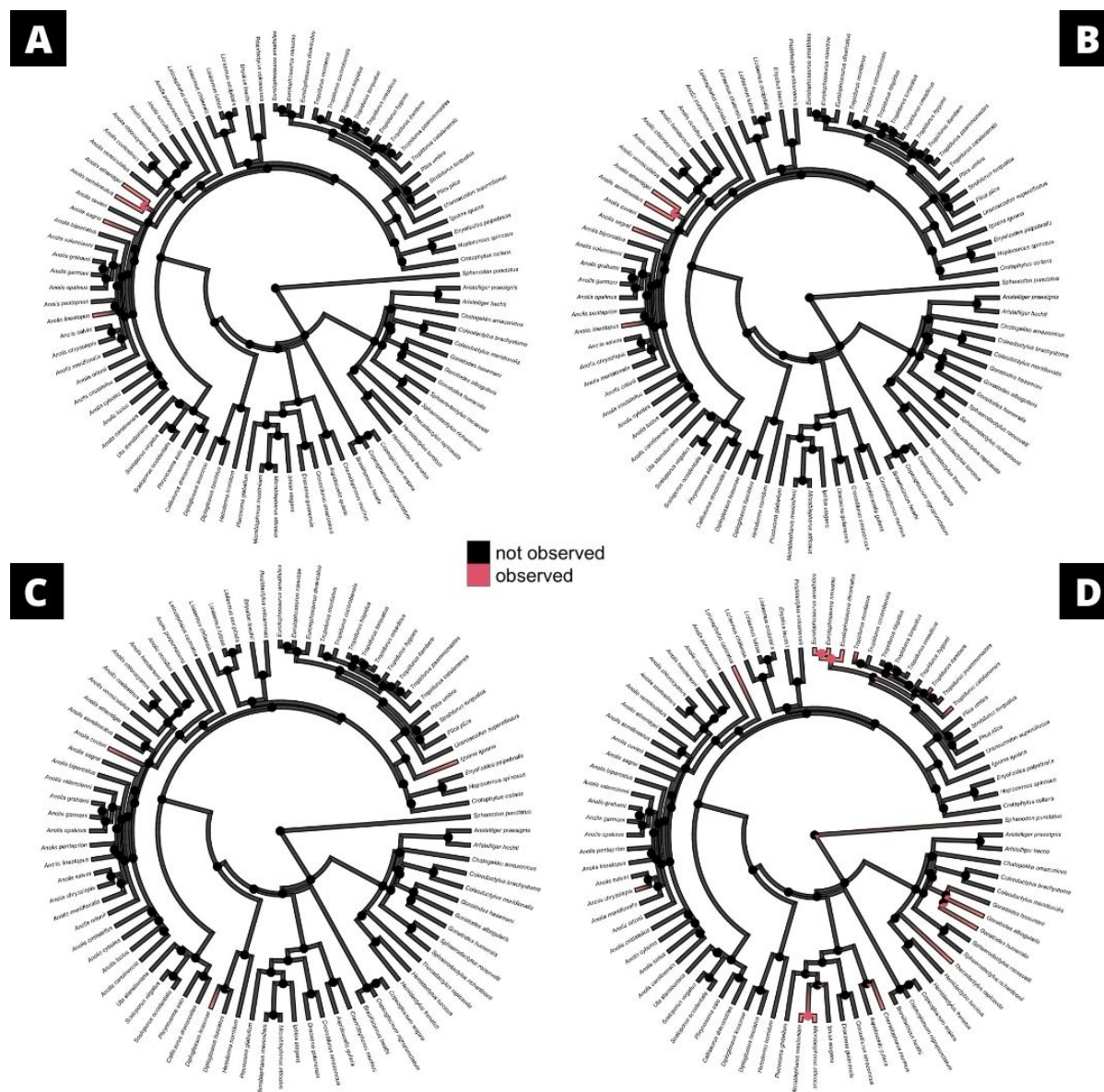


Figure 4. Relationships in defense strategies for Neotropical lizards. Intersection nodes represent the presence probability for that character state. (A) Mimicry. (B) Color polymorphism. (C) Ontogenetic polymorphism. (D) Tail luring.

### *Active Defense Strategies*

Autotomy is a symplesiomorphy in Lepidosauria, as *Sphenodon*, early diverging taxon in the clade, presents fracture for tail loss within its caudal vertebrae (LeBlanc et al. 2018). This

seems to suggest that all lizard species are capable of tail breaking, varying only the frequency they do it. Active defense strategies examples showed by figure 5.

Tail luring is present in many clades, some phylogenetically distant, suggesting evolutionary convergence. *Vanzosaura savanicola*, *Micrablepharus maximiliani*, *M. atticolus*, and *Leiocephalus carinatus* use it more frequently (Fig. 4D). Tropicidurids and gekkonids have tail luring as a common behavior, as well as *Cnemidophorus murinus*. It might be possible that this strategy is selected against visual predators and probably more common than reported in the literature.



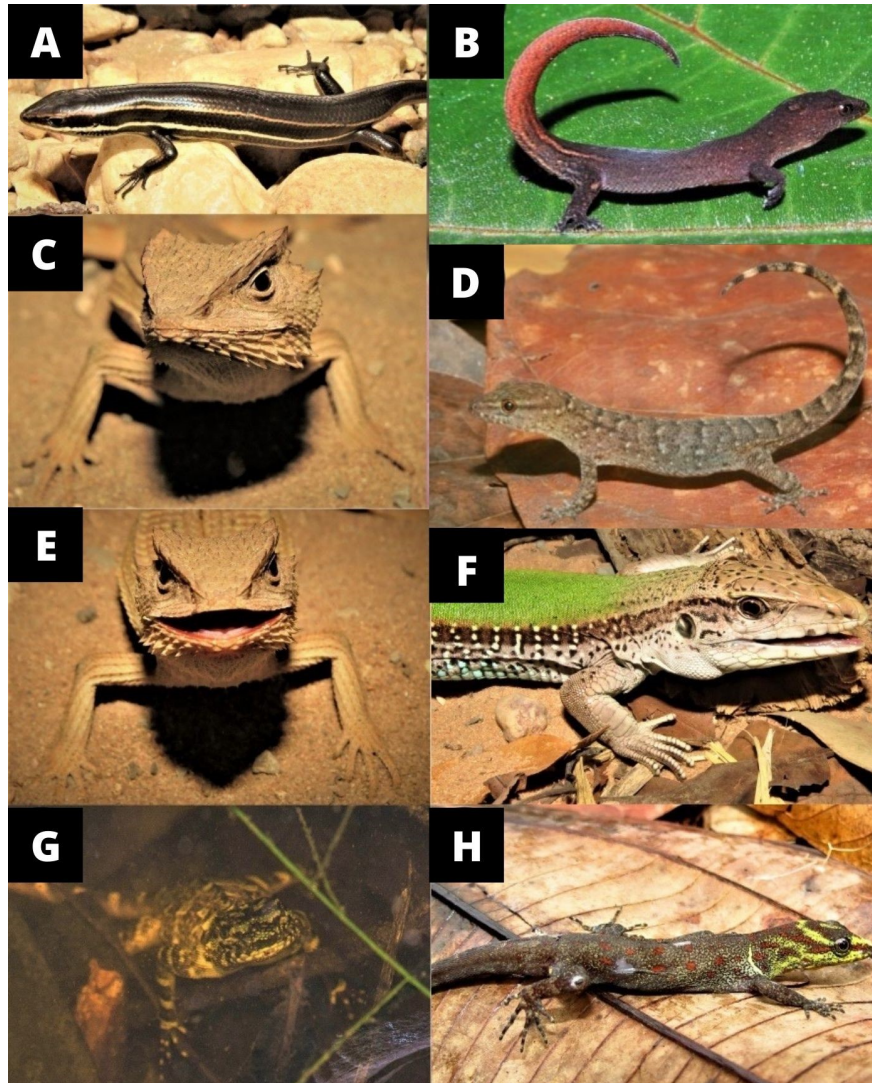


Figure 5. Examples of active defense strategy: (A) The elongated *Aspronema dorsivittatum* showing their smooth and slippery scales (Photo: Reuber Brandão). (B) *Coleodactylus brachystoma* mimicking a scorpion (Photo: Daniel Velho). (C) Detail of *Stenocercus quinarius* head, showing thorns and pointed scales (Photo: Reuber Brandão). (D) *Gymnodactylus darwinii* also curling the tail (Photo: Pedro Peloso). (E) When cornered, *Stenocercus quinarius* assumes a deimatic behavior by opening the mouth and display the vivid reddish edge of its mandible (Photo: Reuber Brandão). (F) Hissing in a large *Ameiva ameiva* (Photo: Reuber Brandão). (G) Some scansorial lizards can dive to avoid tenacious predators, such as this Amazonian *Plica plica* (Photo: Pedro Peloso). (H) Skin tearing showed by the forest dweller gecko *Gonatodes humeralis*. The pieces of lost skin heal within a few days (Photo: Marlon dos Santos).

Skin shedding is a synapomorphic character for sphaerodactylids according to the reconstruction (Fig. 6A). We failed to recover information on *Gonatodes albogularis* and *C. brachystoma*.

Slipperiness is an attribute observed in the mabuyids *Copeoglossum nigropunctatum* and *C. arajara*, arising independently in gymnophthalmids and diploglossids (Fig.6B), whereas thorns appeared in different moments of the phylogenetic history of Neotropical lizards. According to the phylogenetic mapping, this character is present in *Phrynosoma asio*, *Hoplocercus spinosus*, *Iguana iguana*, and *Strobilurus torquatus*, indicating a convergence (Fig. 6C). We also reported thorns for the tropidurid *Stenocercus quinarius*, suggesting a recurrent convergence pattern of the strategy within Neotropical lizards.

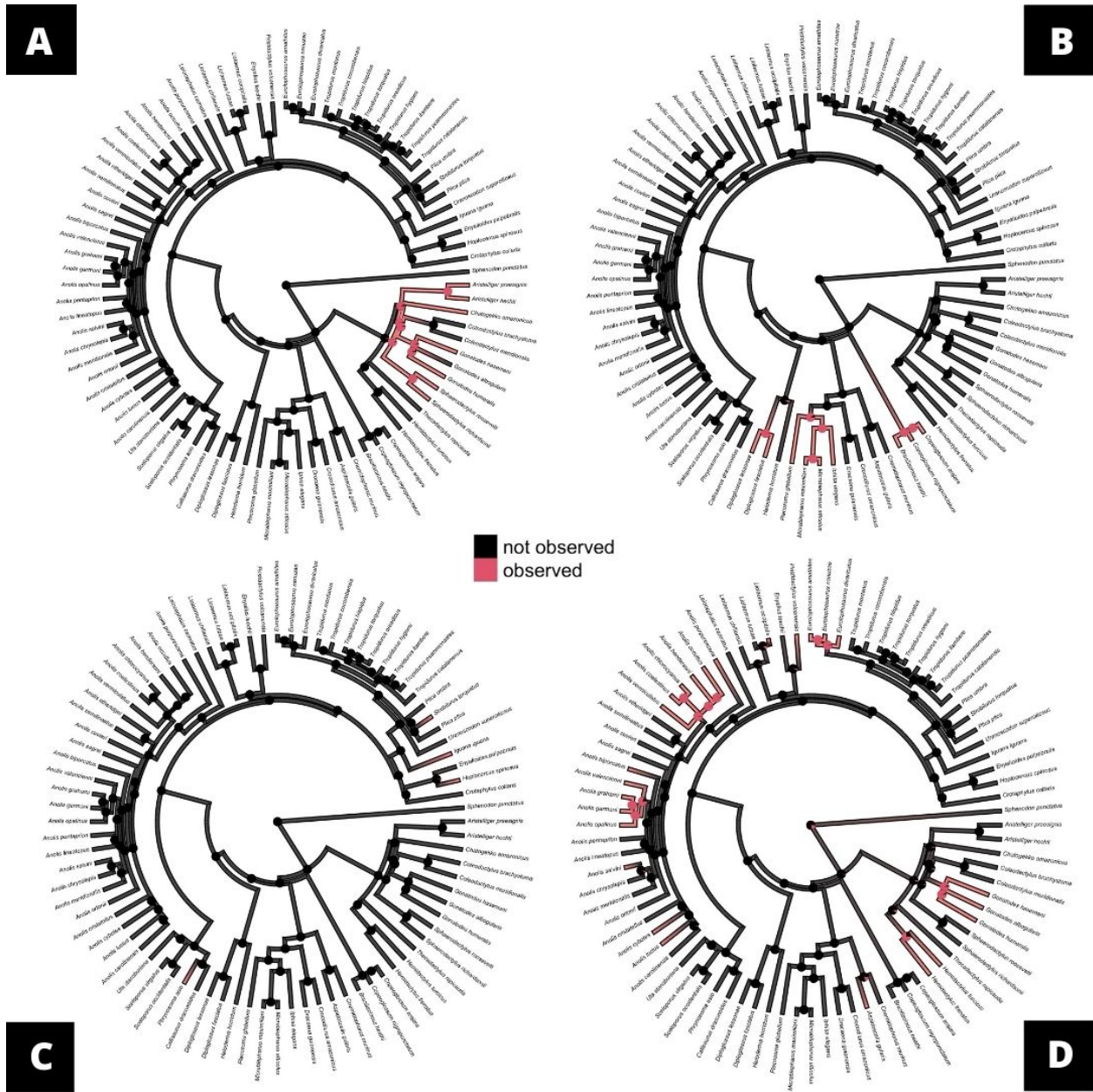


Figure 6. Relationships in defense strategies for Neotropical lizards. (A) Skin shedding. (B) Slipperiness. (C) Presence of thorns. (D) Antipredatory vocalizations.

There are thanatosis reports for the neotropical lizards *Tropidurus montanus* and *Liolaemus occipitalis* (Machado et al. 2007; Santos et al. 2010). However, it should be much more common and widespread within Neotropical lizards, since it is a character shared among organisms, such as planarians, mammals (Hoagland 1927), and lizards. It appears to be a basal

defense mechanism, evolutionarily conserved in several taxa, functioning complementarily and concomitantly with other common strategies, such as aposematism and crypsis (Rogers & Simpson 2014).

The phylogenetic mapping shows an evolutionary convergence for the presence of antipredatory vocalizations (Fig. 6D). Within Squamata, vocalizations are usually limited to lizards, including anguids, gekkonids, helodermatids, varanids, few teiids, and iguanians (e.g., species from *Anolis* genus; Gans 1969; Milton 1979; Phongkangsananan et al. 2014).

Aggressive displays were detected in *Enyalioides palpebralis*, *Iguana iguana*, *Tropidurus itambere*, *Eurolophosaurus divaricatus*, *E. nanuzae*, *E. amathites*, *Anolis pentrapion*, and *A. cristatellus*, as well as in *Heloderma horridum* (Fig.7A). The character mapping indicates, once again, an evolutionary convergence, arising independently in several clades.

There are few lizard species with venom, such as *Heloderma horridum* (Pianka & Vitt 2003; Arbuckle 2009). Thus, when threatening displays do not work, a bite is probably a more effective action. Biting can be related to the production and inoculation of venom, that is an autapomorphy of the *Heloderma* genus, according to our results. Another autapomorphy in our species set is the production of emetic substances by *Phrynosoma asio*.

Character mapping for diving points out another evolutionary convergence (Fig.7B). However, diving is a strategy that depends on water availability or the type of life habit the species presents, as discussed earlier. *Plica plica*, *G. humeralis*, *C. nigropunctatum*, *T. torquatus*, and *T. oreadicus* may use water whether available but this is a rare behavior, whereas riverine lizards, like *Iguana iguana* or the semi-aquatic ones, as *Crocodilurus amazonicus* and *Dracaena guianensis*, show this behavior more frequently.

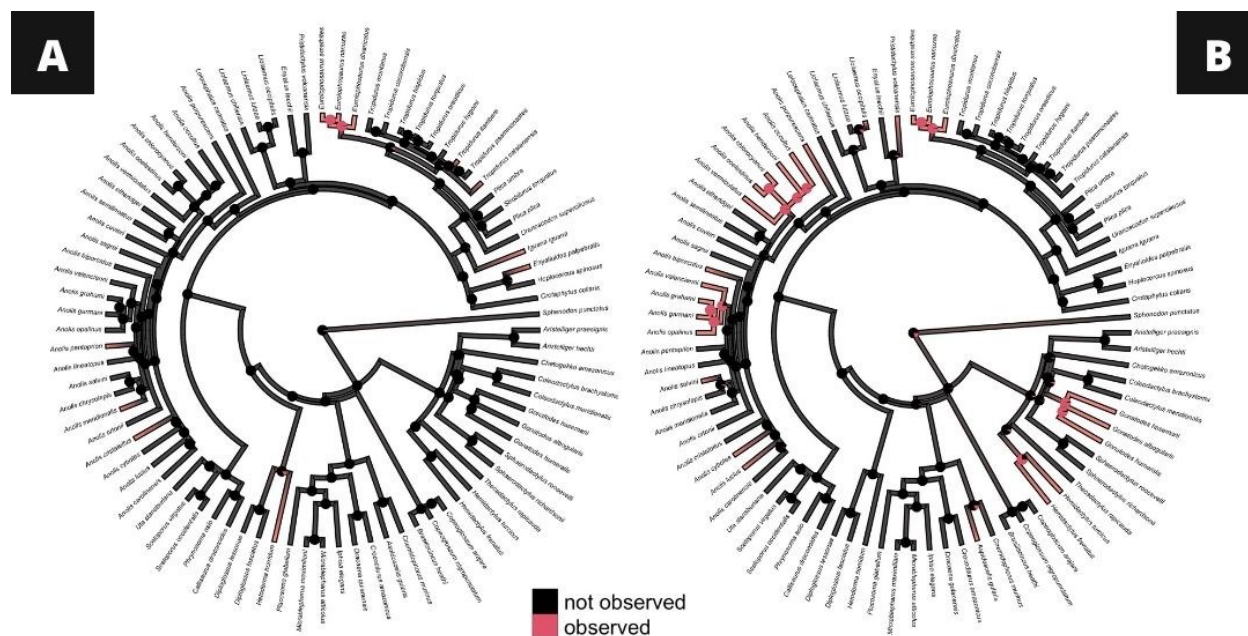


Figure 7. Relationships in defense strategies for Neotropical lizards. (A) Aggressive displays. (B) Diving.

Regarding character state transitions, Bayesian stochastic mapping detected that number of origins is higher than reversal for all phylogenetic relevant characters (mimicry, color polymorphism, ontogenetic polymorphism, tail luring, skin shedding, slipperiness, thorns, antipredatory vocalizations, aggressive displays, and diving). It seems that more complex characteristics once acquired are less likely to be lost, suggesting that this complexity is an advantage for the lizard.

## Discussion

Although our survey has returned 70 publications from this century, 55 from the last and three from the XIXth century, the lack of information about the natural history of Neotropical lizards affects our understanding regarding the evolution of anti-predatory strategies among these animals, limiting further studies. The majority of recent articles focused mostly on exploring classic publications (e.g., McElroy 2019) and studies bringing novel information are rare.

Furthermore, most of published papers are based only on anecdotal observations, and very few studies focus on an analysis of taxa defensive repertoire.

Our character mapping provides valuable information about the evolution of defensive strategies in Neotropical lizards, combining natural history and phylogenetics. It is indispensable to encourage naturalistic observations, especially because natural history studies are the foundation for other areas of scientific investigation. Despite the scarce papers about defense strategies of Neotropical lizards, our study compiles previously described defense strategies of lizards and adds novel information about the subject, based on our empirical observations and analysis. Behaviors such as thanatosis, crypsis, and tail autotomy are symplesiomorphic for lizards, whereas venom and emetic substances are autapomorphic and aposematism seems to be rare.

It is relevant to highlight that trivial observations about an animal behavior might be important to elucidate meaningful aspects of its ecology and evolution. Thus, we strongly recommend that ethological observations describe the event in all possible details, such as the involved species (predator and preys), the context, the habitat, and how the habitat affected the event (if so).

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Table 1. List of all publications returned by the bibliographic survey in scientific databases and libraries. Note that some publications are reference for more than one strategy, e.g., Pianka & Vitt (2003).

<b>Defense Strategy</b>	<b>Publications</b>	<b>Total of publications</b>
Aggressive displays	Abramjan et al. (2015); Bustard (1967); Carpenter (1966, 1977); Edwards & Lailvaux (2012); Font & Kramer (1989); Greene et al. (1978); Hertz et al. (1982); Johnson (1975); Kircher & Johnson (2017); Leal & Rodriguez-Robles (1997); Leal (1999, 2000); Maia-Carneiro et al. (2020); Marcellini (1977); McElroy (2019); Murphy et al. (1978); Pianka & Vitt (2003); Sherbrooke (2008); Shine (1990); Smith & Martins (2006); Vitt & Lacher (1981); Whiting & Miles (2019); Yedlin & Ferguson (1973)	24
Aposematism	Cott (1940); Edmunds (1974); Gambarale & Tullberg (1996); Mappes (2005); McElroy (2019); Ruxton et al. (2014); Clark et al. (2017)	7
Biting	Almeida et al. (2015); Greene (1988); Haddad et al. (2008); Herrel et al. (2009); Martins (1996); McElroy (2019)	6
Body thrashing	Greene (1988); Maia-Carneiro et al. (2020); Martins (1996); Pianka & Vitt (2003)	4
Cloacal discharge	Greene (1988); Maia-Carneiro et al. (2020); Martins (1996); McElroy (2019); Oliveira et al. (2020); Pianka & Vitt (2003)	6
Color polymorphism	Bond & Kamil (2002); Endler (1988); Hoffman & Blouin (2000); Rodrigues et al. (2006); Schoener & Schoener (1976); Zatz (2002)	6
Crypsis	Cott (1940); Cooper (1994); Endler (1988); Hall et al. (2017); Hamilton et al. (2008); Johnson (1970); McElroy (2019); Merilaita (1999); Merilaita & Stevens (2011); Moreno-Rueda et al. (2019); Moreno-Rueda (2020); Pianka & Vitt (2003); Rowland et al. (2007); Ruxton et al. (2004); Samia et al. (2013); Schaefer & Stobbe (2006); Skelhorn et al. (2011); Sousa et al. (2020)	18
Diving	Bauer & Jackson (2008); Boccia et al. (2021); Carvalho et al. (2012); Fernandes et al. (2009); Maciel et al. (2021); Mesquita et al. (2006); Moberly (1968); Schaerlaeken (2012); Vitt & Ávila-Pires (1998); Vitt et al. (1998)	9

Emetic substances	Greene (1988); Hodges (2004); Leaché & McGuire (2006); McElroy (2019); Sherbrooke & Middendorf (2001)	5
Mimicry	Anaissi et al. (2020); Autumn & Han (1989); Bates (1862); Brandão & Motta (2005); McElroy (2019); Costa et al. (2009); Cota & Krebs (2015); Huey & Pianka (1977); Pianka & Vitt (2003); Vitt (1992)	9
Ontogenetic polymorphism	Rand & Andrews (1975); Vitt (1992)	2
Running	Aerts et al., “Bipedalism in Lizards: Whole-Body Modelling Reveals a Possible Spandrel”; Hsieh, “Three-Dimensional Hindlimb Kinematics of Water Running in the Plumed Basilisk Lizard ( <i>Basiliscus Plumifrons</i> ).” Aerts et al., “Bipedalism in Lizards: Whole-Body Modelling Reveals a Possible Spandrel”; Hsieh, “Three-Dimensional Hindlimb Kinematics of Water Running in the Plumed Basilisk Lizard ( <i>Basiliscus Plumifrons</i> ).” Aviléz-Rodríguez & Kolbe (2019); Calsbeek & Irschick (2007); Clemente (2014); Cooper (2016); Cooper & Sherbrooke (2013, 2016); Greene (1988); Hsieh (2003); Hsieh & Lauder (2004); Irschick & Losos (2017); Lema (1983); Maia-Carneiro et al. (2020); Martins (1996); McElroy (2019); Oliveira et al. (2020); Pianka & Vitt (2003); Rocha-Barbosa et al. (2008); Schall & Pianka (1980); Vitt & Ohmart (1977); Wagner & Zani (2017); Zani et al. (2009)	22
Scratching	Greene (1988); Martins (1996); Pianka & Vitt (2003)	3
Skin shedding	Bauer et al. (1989, 1992, 1993); McElroy (2019); Pianka & Vitt (2003)	5
Slipperiness	Greene (1988); Martins (1996); Pianka & Vitt (2003)	3
Tail autotomy	Anderson et al. (2012); Arnold (1984, 2007); Baird & Girard (1852); Bateman & Fleming (2009); Bellairs & Bryant (1985); Clause & Capaldi (2006); Congdon et al. (1974); Cooper (2007); Cooper et al. (2008); Daniels (1983); Domínguez-López et al. (2015); Fleming et al. (2009); Fox & McCoy (2000); Fox et al. (1990, 1994); Galdino et al. (2006); Gillis & Higham (2016); Gillis et al. (2009); Greene (1988); Higham & Russell (2010; 2012); Higham et al. (2013); Hsieh (2016); Jusufi et al. (2008); Kuo et al. (2012, 2014); LeBlanc et al. (2018); Lovely et al. (2010); Martín & López (2003); McElroy (2019); McElroy & Bergman (2013); Niewiarowski et al. (1997); Oliveira et al. (2020); Pafilis et al. (2009); Pianka (1969); Pianka & Vitt (2003); Rumping & Jayne (1996); Russell & Bauer (1992); Russell et al. (2001); Smyth (1974); Sousa et al. (2016); Van Sluys et al. (2002, 2010); Vitt et al. (1977); Vitt & Ballinger (1982); Vitt & Cooper (1986); Vitt (1981, 1983); Wilson (1992); Zani (1996)	50

Tail luring	Alonso et al. (2010); Anaissi et al. (2020); Anaissi & Costa-Campos (2021); Clause & Capaldi (2006); Cooper (2001, 2002, 2007, 2010); Cooper & Vitt (1985); Dial (1986); Eifler & Eifler (2010); Foster & Martin (2008); Fresnillo et al. (2015); Greene (1973); Hasson et al. (1989); Kircher & Johnson (2017); Maia-Carneiro et al. (2020); Mori (1990); Shine et al. (2011); Sousa et al. (2016); Vitt & Cooper (1985); Vitt & Zani (1997); York & Baird (2015); Wilkinson (2003); Watson et al. (2012);	25
Tail whipping	Greene (1988); Martins (1996); Pianka & Vitt (2003)	3
Thanatosis	Anaissi et al. (2020); Bordignon et al. (2018); Bertoluci & Rodrigues (2006); Hoagland (1927); Lipinski et al. (2021); Machado et al. (2007); Machado-Filho et al. (2018); McElroy (2019); Mesquita et al. (2018); Nunes et al. (2012); Patel et al. (2016); Rogers & Simpson (2014); Santos et al. (2010); Toledo et al. (2010)	14
Thorns	Greene (1988); Martins (1996); McElroy (2019); Pianka & Vitt (2003)	4
Venom	Anzueto & Campbell (2010); Arbuckle (2009); Beck (2004, 2005); Fry et al. (2005); Greene (1988); Martins (1996); Pianka & Vitt (2003); Smith (2018); Sprackland (1993); Van Denburgh (1913); Woodson (1947)	12
Vocalization	Alonso & Rodriguez (2004); Bowker (1980); Capshaw et al. (2021); Carothers et al. (2010); Frankenberg (1982); Galdino et al. (2006); Hoare & Labra (2013); Labra et al. (2007); Labra et al. (2013); Marcellini (1974, 1977); Milton & Jenssen (1979); Myers (1971); Phongkangsananan et al. (2014); Ruiz-Monachesi & Labra (2020)	15
Total		252

## CAPÍTULO 2

### **CAN MORPHOLOGY AND NATURAL HISTORY TRAITS INFLUENCE EXTINCTION IN LIZARDS? A LONG-TERM CASE STUDY AT ARTIFICIAL ISLANDS IN THE BRAZILIAN CERRADO**

#### ABSTRACT

Although considered a clean energy source, hydroelectric dams are known as a major responsible for environmental destruction, causing fragmentation, degradation and habitat impoverishment. Different stages of recently isolated communities have been studied, and the impact of species loss is one of the most striking effects. The species loss during the formation of land-bridge islands is expected in theoretical models and reported on empirical studies. Reservoir land-bridge islands became a successful model for accessing the sound impacts of island formation on isolated communities belonging to different taxa. Lizards form a very ecologically diversified group, they are ectotherms, present low dispersal abilities, occupy a variety of trophic niches, and are highly susceptible to habitat structure alterations. Herein, we assess data on abundance and richness of lizard species predating the flooding and after the filling of the Serra da Mesa Dam reservoir to test whether fragmentation of habitat drove local saurofauna to diversity loss. We predict that morphology and natural history could explain the current configuration of communities. Areas that would become islands were sampled in 1996, 1997-1999 (during island formation), 2001, 2011, and in July 2019. We measured eight morphological traits from 369 lizards and used isometric adjusted residuals to check shape differences. The following temporal processes were observed in Serra da Mesa islands: 1) Initial extinction and

abundance decrease of large and long-limbed lizards (Teiidae and Tropiduridae), 2) Higher abundance of small-bodied lizards (Scincidae, Gymnophthalmidae, Gekkonidae, and Sphaerodactylidae). Teiidae and Tropiduridae abundances became low. 3) Richness on the small islands became much lower, depicting communities typically composed of one gekkonid, one scincid, and one gymnophthalmid, whereas the most common lizards before flooding became rare or extinct.

**Keywords:** artificial islands, extinction debt, artificial reservoirs, dam impacts, fragmentation.

## **Introduction**

Although the Theory of Island Biogeography (MacArthur & Wilson 1963; MacArthur & Wilson 1967) has been proposed about 50 years ago, very few studies focused on initial processes related to the formation of land-bridge islands (Wilcox 1978; Faeth & Connor 1979). Although considered a clean energy source, hydroelectric dams are known as a major responsible for environmental destruction, causing fragmentation, degradation and habitat impoverishment (Lees et al. 2016; Jones et al. 2016; Palmeirim et al. 2018). Several factors could act in the adjustment of communities during the flooding of hydroelectric dam reservoirs, as the movement patterns of individuals in the fragments (Bierregaard & Lovejoy 1989), the suppression and creation of habitats, and the following change in the resource availability (Yahner 1991; Malcolm 1997), the reduction or predators loss (Terborgh & Winter 1980), or the impossibility of dispersion among fragments (Adler & Levins 1994). Other factors, as the occurrence of diseases and parasites could also be accountable.

Different stages of recently isolated communities have been studied (Jones et al. 2016), and the impact of species loss is one of the most striking effects (Cosson et al. 1999; Jones et al.

2016). The species loss during the formation of land-bridge islands is expected in theoretical models (Simberloff 1974; Wilcox 1978; Karr 1982) and reported on empirical studies (Jones et al 2016; Palmeirim et al. 2017). Compared with the rarer species, the commonest rodent species in a continuous tropical forest in Thailand showed the highest probability of going extinct after the flooding by a hydroelectric dam reservoir (Lynam 1997). This result suggests that the initial abundance is not a good measure to predict the time of residence in the island. The higher abundance of rarer rodent species in the islands was considered an effect of the decline of predators (Lynam 1997). Terborgh et al. (1997), studying islands isolated only for a few years by a hydroelectric lake in Venezuela, observed that predators were almost absent. These islands showed poorer communities when compared with the margins. A similar result was found by Cosson et al. (1999). These studies, however, did not follow the faunal responses during the flooding process, since the control areas, which were in the lake margins, could also be strongly affected by the lake formation (Pavan 2001).

Due to an extreme level of disturbance along the formation of these archipelagic landscapes, communities face extinctions and turnover of species, resulting in radical local diversity changes (Cosson et al. 1999; Gibson et al. 2013; Palmeirim et al. 2021). Reservoir land-bridge islands became a successful model for accessing the sound impacts of island formation on isolated communities belonging to different taxa, such as mammals (Meyer & Kalko 2008; Palmeirim et al. 2018, 2020), amphibians (Brandão & Araujo 2008), birds (Yu et al. 2012), and trees (Terborgh et al. 2006). Mammals and birds are the taxa mostly used as model for studies about reservoir ecological impact (Jones et al, 2016; Palmeirim et al. 2017). Only recently, lizards became study objects in investigations focusing on land-bridge islands resulting from hydroelectric flooding (Palmeirim et al. 2017, 2021). Lizards form a very ecologically

diversified group, they are ectotherms, present low dispersal abilities, occupy a variety of trophic niches, and are highly susceptible to habitat structure alterations (Ávila-Pires 1995; Gainsbury & Colli 2019; Palmeirim et al. 2021). Besides, they play an important part in ecosystems, acting as prey, predator, and seed dispersers, essential for the ecological equilibrium maintenance (Terborgh et al. 2001). All these features make lizards ideal bioindicators (Gainsbury & Colli 2019).

Low habitat specificity was the main feature of the lizards that remained in fragments studied in Australia (Sarre et al. 1995, Smith et al. 1996, Sarre 1998). Fragment size, connectivity, and distance from the nearest fragment influenced the lizard richness in the fragments investigated by Smith et al. (1996), which is expected according to the Island Biogeography model (MacArthur & Wilson 1967). These more habitat generalist lizards tend to be larger; their diets consist in arthropods and small vertebrates; they forage actively, and they are heliophile in terms of thermoregulation mode (Vitt 1991; Palmeirim et al. 2017). On the other hand, small-bodied heliophobe species, with ambush foraging behavior, and cryptic/crepuscular habits tend to be more habitat specialist (Vitt 1991; Palmeirim et al. 2017). The identification of species characteristics accountable for permanence or extinction on a fragmented area is crucial for an effective conservation planning (Wang et al. 2009; Palmeirim et al. 2017).

Herein, we assess data on abundance and richness of lizard species predating the flooding and after the filling of the Serra da Mesa Dam reservoir to test whether fragmentation of habitat drove local saurofauna to diversity loss. We predict that morphology and natural history could explain the current configuration of communities, considering the fact that larger-bodied lizards with more generalist habits tend to dominate disturbed, reduced, and impoverished areas.

## **Material and Methods**

### **Study area**

The Serra da Mesa dam is located in the northern State of Goiás, Central Brazil, in the core of the Cerrado biome (48° 20'W; 13° 51'S). The Serra da Mesa lake covers 178 km<sup>2</sup> and it was formed after the damming of the Tocantins River, a large affluent of the Amazonas river. The valley flooding isolated the highest hilltops, forming nearly 280 islands. Most of these islands (about 80%) have less than 3 ha, but some are larger than 1.000 ha. The flooding process began in October 1996 and lasted until around January 1999.

Before the flooding, eight hills (future islands) were chosen for trapping, after the end of the flooding process, five islands remained: I-34, I-35, I-37, I-38, and IX (Fig. 1). The islands vary in size from 3 to 35 ha. The choice of these areas was based on vegetation type, level of human disturbance (fire, cattle grazing, logging), and accessibility. Due to fluctuations in water level, island IX connected again with the reservoir margin.



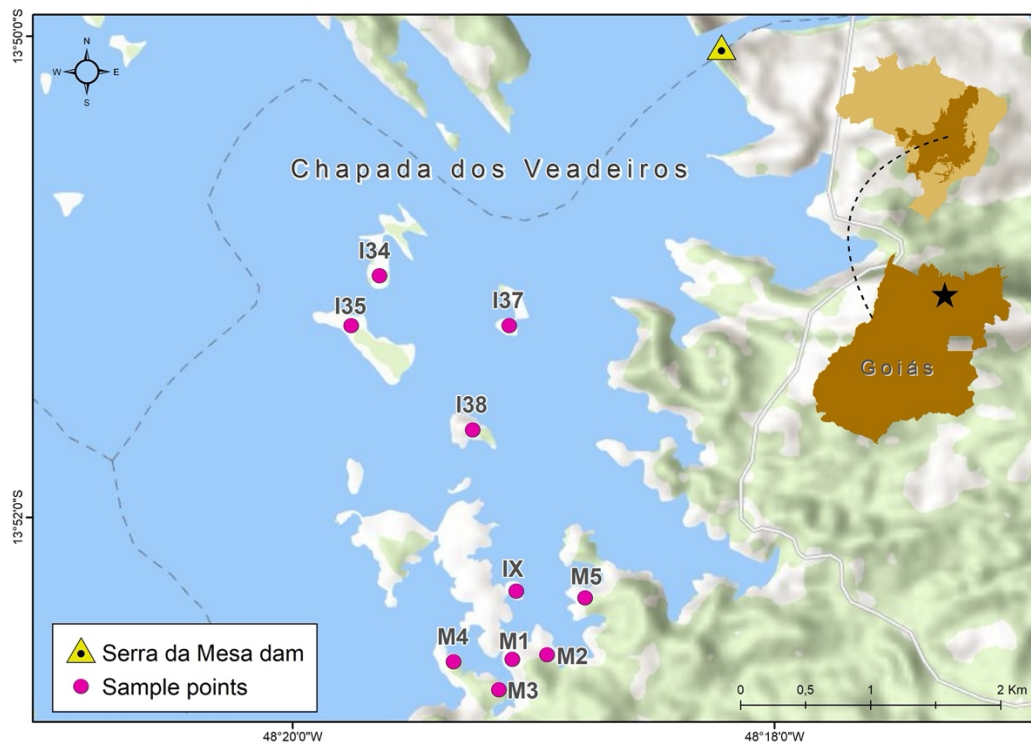


Figure 1. Map of the Serra da Mesa dam in Goiás State, Brazil, showing the sample points.

### Species survey and monitoring

Lizard richness and abundance were obtained through visual survey, pitfall trap captures, and sampling in burned areas. The visual survey was carried out from July to October 1996, then we started to use pitfall traps until January 1999. We installed 20 L buckets in grids of 15 traps, and each trap grid measured 72 m<sup>2</sup> in area. We left the traps open for 13 days, monthly. A total of 315 traps (21 grids) were installed in the studied hills. We took measurements, marked by toe clipping, and released all the captured lizards. For lizards outside the traps, we recorded the habitat, first observation microhabitat, escape microhabitat, escape distance, and the time of activity.

In 2001, 2011, and 2019, we sampled lizards in ten 50x50m squares closed by plastic fences. We used these squares comparing hills and reservoir margins focusing on the effects of

islands formation. We delimited the area with tapelines and closed the square using plastic canvas stretched between wood stakes. After that, we made a 3 meter-width firebreak around the closed areas and burned the vegetation to expose all possible shelters used by lizards. After removing out the vegetation, we carefully searched for lizards, checking all available shelters such as holes, trunk logs, rock crevices, and termite mounds. We controlled for the capture of all lizards in the enclosure using rarefaction curves. There was none dead or wounded lizard due to the use of this sampling method. We named this methodology fire squares. All lizards captured were measured, weighed, euthanized with lidocaine injection in the coelom, fixed in formalin, and posteriorly transferred to 70% alcohol for conservation. All animals were housed at Coleção Herpetológica da Universidade de Brasília (CHUNB).

### **Data analysis**

We calculated richness, abundance, and beta-diversity using the Whittaker index of beta-diversity (Whittaker 1972) to measure differences in local species composition using the equation  $BW=(S/a)-1$ , where **S** is the species richness for each pair of islands, and **a** is the medium richness. The beta-diversity index values range from 0 to 1, where values nearest to 1 show a larger turnover.

Differences in beta diversity, richness, and abundance within islands before, during, and after the flooding were tested with the Mann-Whitney test. Simple Linear Regression analysis tested the relationship between species abundance and time (bimonthly).

The following measurements were taken from 369 lizards: snout-vent length (SVL), head length (HL), head height (HH), mandible length (ML), arm length (AL), leg length (LL), hand length (HAL), and foot length (FL). All morphometric variables were  $\log_{10}$  transformed before

performing the analyses. Then, a Principal Component Analysis (PCA, covariance matrix) was performed, following Ricklefs et al. (1981). This procedure does not remove the size effect, which accumulates a greater variance of the total variance explained by the first component of the PCA. We removed the size effect from the individual measurements by regressing all measurements ( $\log_{10}$ ) against an isometric size, obtaining size-adjusted residuals. This isometric size (SIZE) was obtained by the multiplication of an isometric eigenvalue, defined as  $\mathbf{p}^{-0.5}$  (where  $\mathbf{p}$  is the number of variables) plus the summation of the log-transformed variables (Somers 1986). The size-adjusted residuals were used in a Stepwise Discriminant Analysis (Tabachnick & Fidell 2001) to detect which morphometric variables best take apart the species and families from the lizard community. The classification ratio was determined by cross-validation (Tabachnick & Fidell 2001). Statistical analyses were performed using the software SYSTAT 7.0 and SAS. We considered the significance level of 0.05.

## Results

### *Species richness before flooding*

We recorded 19 lizard species in the sampled area before flooding, distributed among eight families: Teiidae (4 species), Gymnophthalmidae (3), Tropiduridae (3), Hoplocercidae (1), Iguanidae (1), Polychrotidae (3), Scincidae (2), and Gekkonidae (2) (Table 1). We found 15 species at the hilltops and 17 within the flooded area. Two species (*Tropidurus cf. montanus* and *Norops meridionalis*) were recorded only at the hilltops. Four species were only observed in the valley-flooded habitats, mainly in gallery forests and adjacent open Cerrado (*Tupinambis quadrilineatus*, *Tropidurus torquatus*, *Hoplocercus spinosus*, and *Polychrus acutirostris*), which corresponds to 21% of the lizard community. Nearly 79% of all species found in the valleys were also observed at the hilltops.

We detected elevated lizard richness in the sampled area. Seven species (37%) are endemic to the Cerrado biome (Colli et al. 2002), and *Tropidurus* cf. *montanus* is a new, undescribed species. The results show that the saurofauna from Serra da Mesa presents a predominance of heliophile and habitat-generalist species.

### **Changes in abundance and richness during islands formation**

The beta-diversity was calculated for island pairs before and after the flooding, and before and after flooding for the same island. The mean beta-diversity between hills before the flooding was  $0.434 \pm 0.148$ , whereas the mean beta-diversity between islands after the complete flooding was  $0.524 \pm 0.181$ , which shows a tendency of dissimilarity increase after the flooding. This difference, however, was not significant ( $U_{(1,56)} = 276.00$ ;  $p = 0.057$ ).

Between 1996 and 1999 we captured 485 lizards from 13 different species using pitfall traps. The regression between abundance of each species against time (bimonthly), showed that the Teiidae lizards *Ameiva ameiva* ( $r = -0.530$ ,  $p = 0.035$ ), *Ameivula ocellifera* ( $r = -0.498$ ,  $p = 0.050$ ), and Tropiduridae lizards *Tropidurus oreadicus* ( $r = -0.668$ ,  $p = 0.005$ ), and *Tropidurus* cf. *montanus* ( $r = -0.526$ ,  $p = 0.016$ ), decreased their abundance between July 1996 and January 1999 (Fig. 2). The large *A. ameiva* was not registered since 1998 and it was considered extinct at the islands.

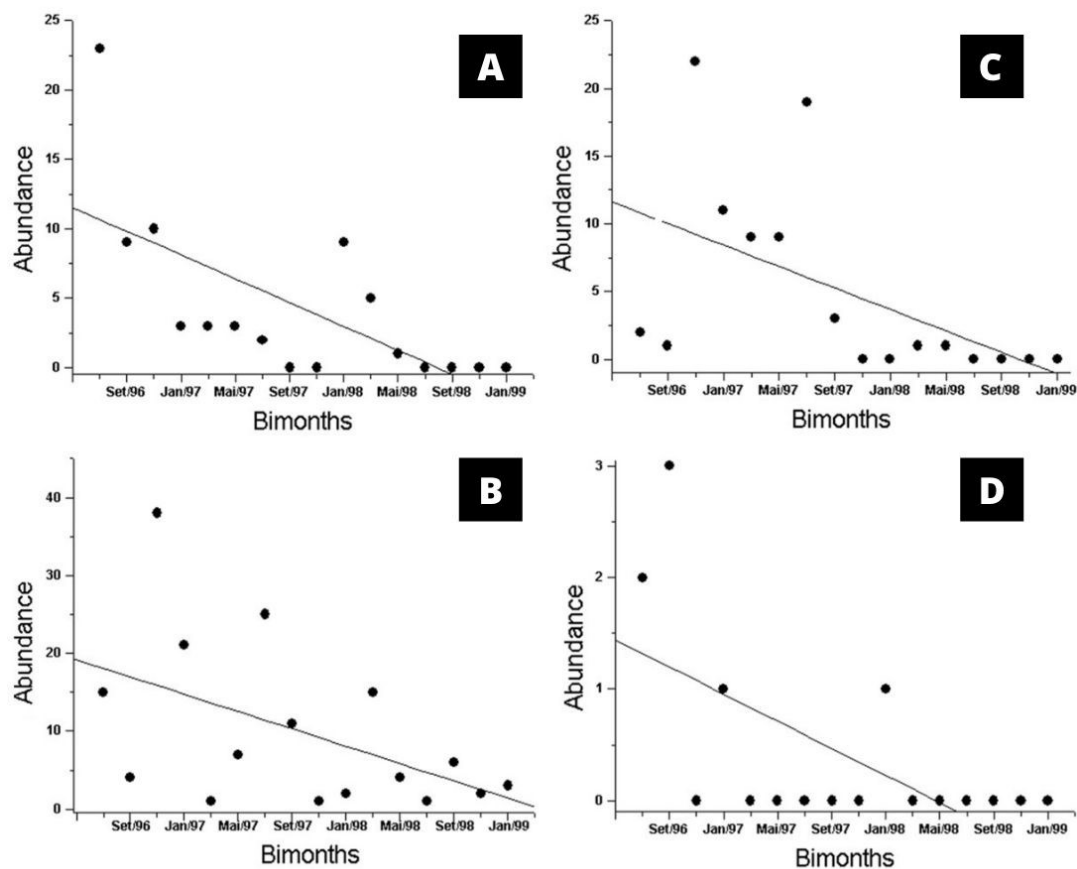


Figure 2. Regressions between abundance and time (bimonthly). A. *Ameiva ameiva* ( $r^2 = 0.281$ ,  $p = 0.035$ ); B. *Ameivula ocellifera* ( $r^2 = 0.248$ ;  $p = 0.050$ ); C. *Tropidurus oreadicus* ( $r^2 = 0.446$ ;  $p = 0.005$ ), and D. *Tropidurus cf. montanus* ( $r^2 = 0.277$ ;  $p = 0.01$ ).

*Ameiva ameiva*, *Ameivula ocellifera*, and *Tropidurus oreadicus* were the most abundant lizards at the hilltops before the flooding. These species and *T. cf. montanus* were the largest lizards from the studied community (excluding tegus and iguanas, not captured by the pitfall traps). Abundance decay of *A. ameiva* and *T. oreadicus* were also detected in lake margins, during the reservoir formation (Pavan 2001).

Smaller, discrete, and rarer lizard species, with more restricted geographic distribution in some cases, did not show a significant drop in abundance during the formation of the island

(Fig.3). There was a significant difference in the  $r^2$  value between the species that declined and the species that did not ( $U(1.13) = 36.00, p = 0.005$ ).

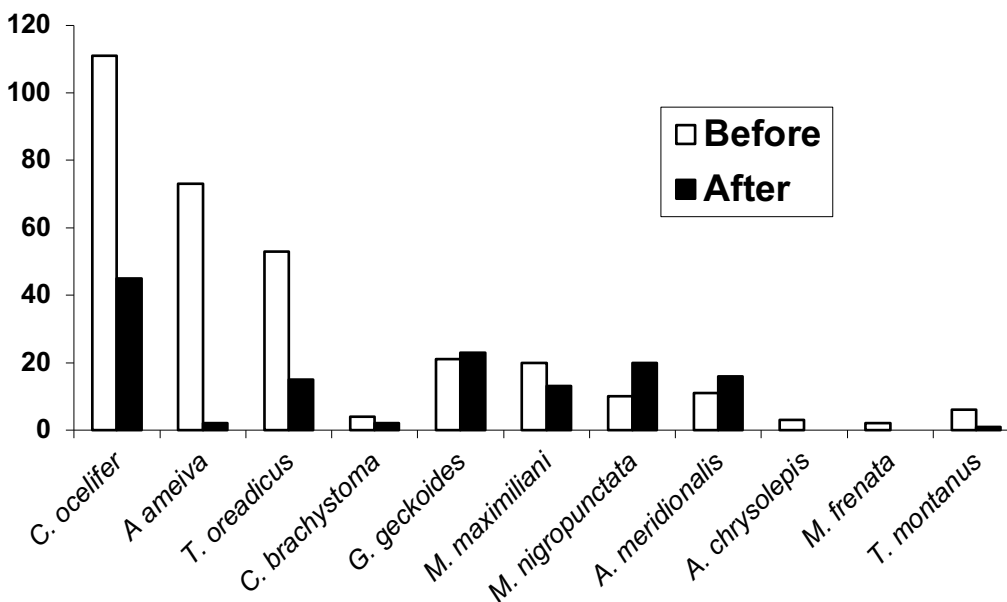


Figure 3. Abundance of lizard species at Serra da Mesa, comparing the first 12 months (before the flooding) with the last 12 months (after the flooding).

During the sampling in 2001, we found 1,002 lizards, belonging to 14 species. The mean abundance of lizards on the islands was nearly two-fold that found in individuals from the margins. Four lizard species were dominant in the island communities: *Micrablepharus maximiliani* (235 individuals or 23.45% of all lizards found), *Gymnodactylus amarali* (197; 19.66%), *Copeoglossum nigropunctatum* (186; 18.56%), and *Coleodactylus brachystoma* (165; 16.47%). These species summed 738 individuals in total or 78.14% of all sampled lizards. These lizards were not abundant in the samplings during the flooding. In contrast, the dominant species during the sampling from 1996 to 1999 (*Ameiva ameiva*, *Ameivulla ocellifera*, and *Tropidurus oreadicus*) corresponded to a small portion of the samples conducted three years after the

complete flooding (the 2001 sample), showing respectively 0% (extinct), 7.3%, and 0.7% of the total abundance in isolated communities. These species presented a severe abundance decline during the flooding.

Along the 2011 samplings in Serra da Mesa, we recorded 284 individuals from 12 species, spread among seven families (Gekkonidae, Gymnophthalmidae, Polychrotidae, Sphareodactylidae, Scincidae, Teiidae, and Tropiduridae). At the continuous areas (margins) 160 specimens were collected, while on the islands we captured 124 individuals from eight species. *Gymnodactylus amarali* was the most abundant lizard in the islands, corresponding to 44.6% of all individuals found. The only lizard species found exclusively on the islands was *Polychrus acutirostris*, whereas *Norops brasiliensis*, *N. meridionalis*, *Tropidurus cf. montanus*, and *Salvator merianae* were restricted to the margins.

In 2019 the samplings recorded 24 individuals distributed in six species. We found in the islands 15 individuals belonging to five species, and *Gymnodactylus amarali* corresponded to 40% of the total. The species *Colobosaura modesta* was only recorded at the margins.

### **Morphology**

The first component of the Principal Component Analysis explained 92.62% of the variance, whereas the second component explained 2.58%. These two components explained 95.20% of all community morphological variance. In component 1, all eigenvectors are positive and high, due to the size effect (isometric factor). In component 2, snout-vent length and head width showed the highest positive values, whereas foot and leg length showed the highest negative values (allometric factor, Table 2; Fig.4).

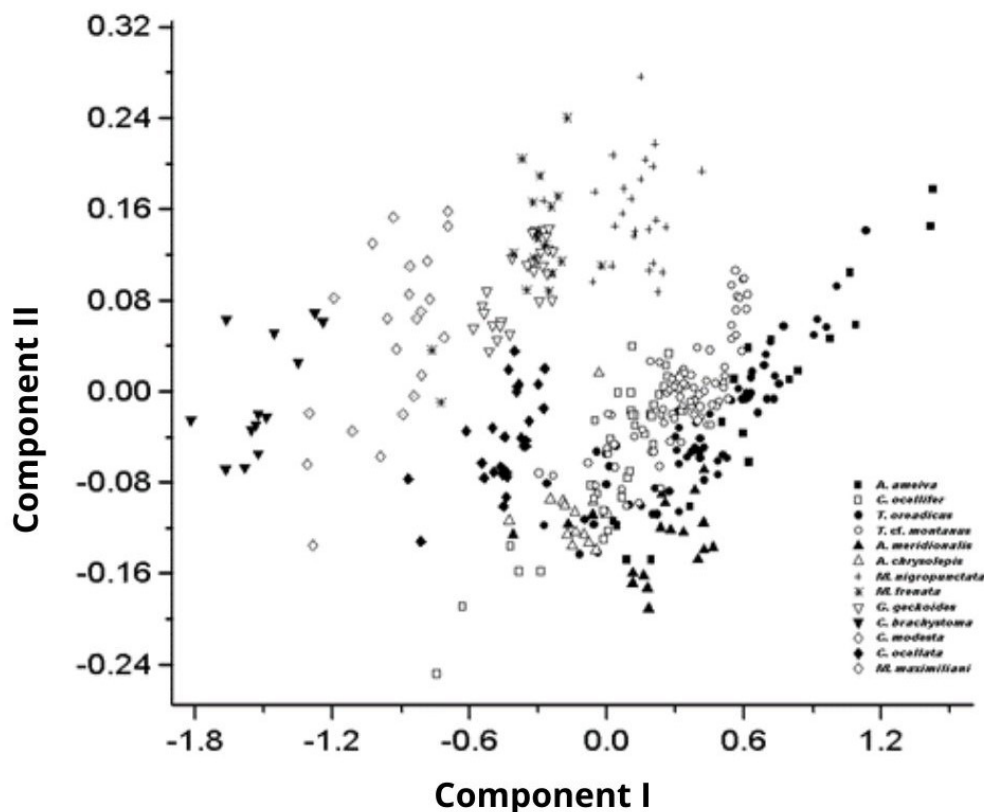


Figure 4. Principal Component Analysis with the Log<sub>10</sub> of the morphometrical measures, showing the relation between form and size of the species.

The Stepwise Discriminant Analysis of size-adjusted residuals selected eight variables that best take apart the species, classifying correctly 87.26% of them. A classification model, based on the sequential addition of isometric size variables, leg residuals, and snout-vent length, correctly classified 38.48%, 67.75%, and 78.32% of the species (Table 3; Fig.5). The same analysis was performed for lizard families. Eight variables were selected and 94.85% of families were correctly classified. A similar classification model, based on sequential addition of leg length residual, isometric size, and snout-vent length residual, correctly classified 58.89%, 76.96%, and 83.74% of lizard families (Table 3; Fig.6).



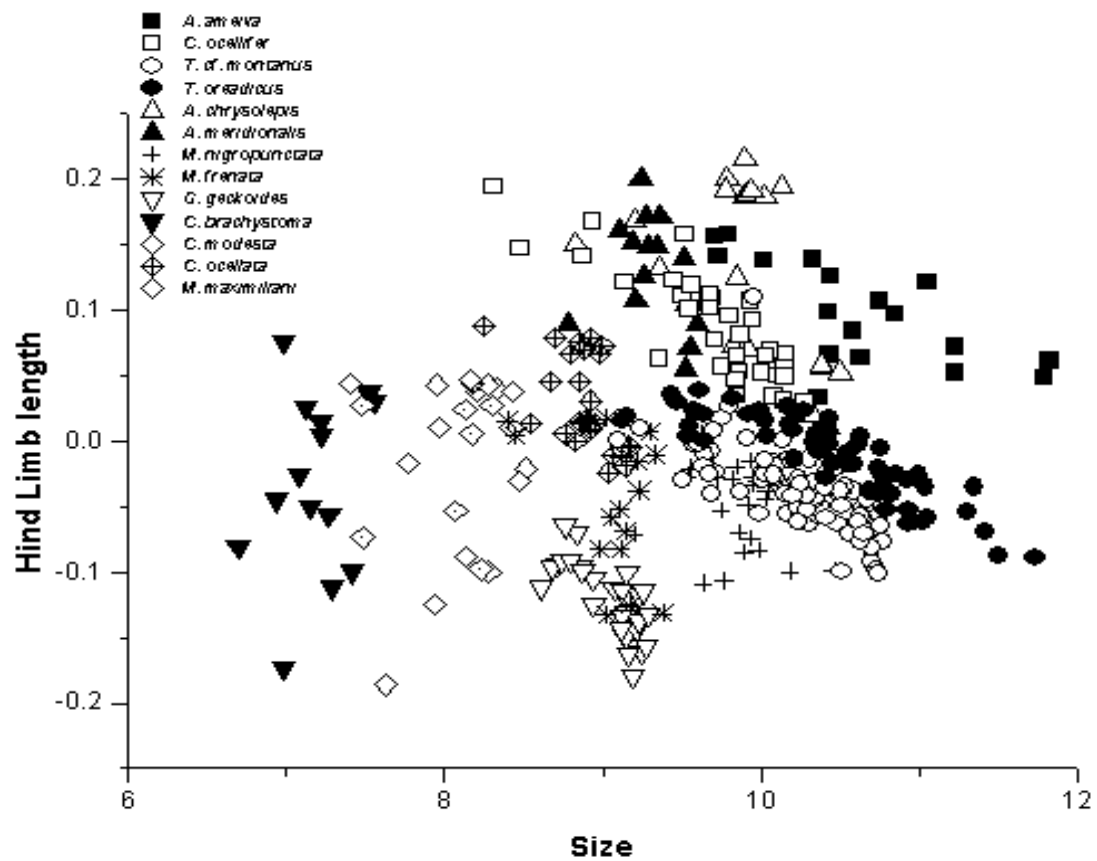


Figure 5. Species classification of lizards from Serra da Mesa based on the hind limb length and the isometric size.

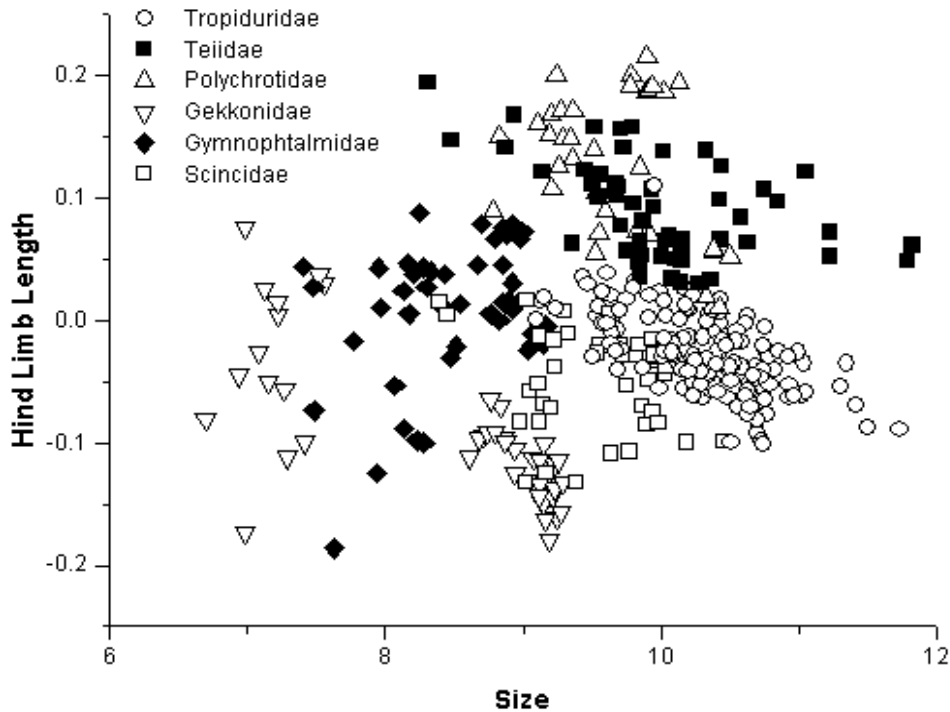


Figure 6. Family classification of lizards from Serra da Mesa based on the hind limb length and the isometric size.

Although all morphological measurements have contributed to the community classification, body size and hind limb length presented the highest discriminatory power. The Discriminant Analysis showed that lizard species from Serra da Mesa could be separated into larger species with longer limbs (Teiidae and Tropiduridae), smaller species with shorter limbs (Gekkonidae, Gymnophthalmidae, and Scincidae), and plant climbing (Polychrotidae lizards). These three groups (showed in Fig. 7) could be considered morphological guilds (sensu Araújo 1991, Araujo 1992, Ricklefs et al. 1981).

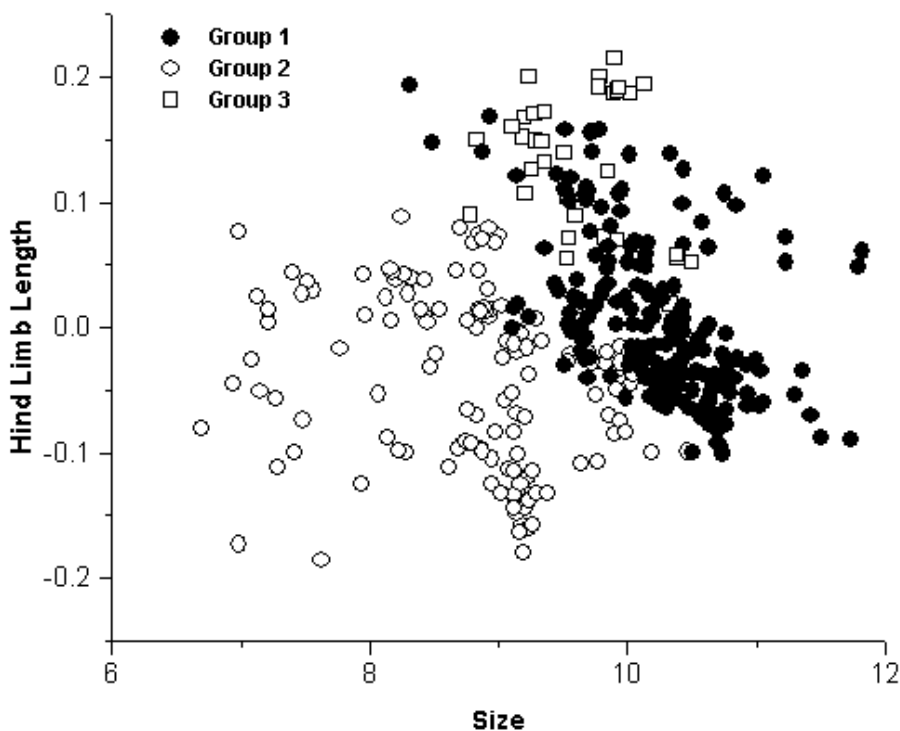


Figure 7. Group (morphometric guilds) classification of lizards from Serra da Mesa based on the hind limb length and the isometric size.

## Discussion

The flooding process imposed a ruthless impact upon the region, especially in terms of habitat loss and availability. During the flooding, forested and humid habitats in the valleys disappeared, resulting that only open and dry Cerrado habitats at the hilltops remained. Serra da Mesa was once formed by forested low valleys (gallery forests) and wet habitats (swamps, also known as “veredas”), whereas open Cerrado covered the hilltops. It was expected that, during the lake formation, species occurring in the flooded valley would be displaced to the hilltops, which were occupied by heliophile and/or habitat-generalist species. Due to this migratory movement, it would be expected an increase in species richness and abundance at the hilltops. Moreover, a

posterior adjustment on the species-area rate would also be expected due to ecological release (sensu Diamond 1972; Terborgh et al. 1997). In case of removal or reduction of a constraining interspecific interaction (e.g., reduction of predation pressure), niche expansions and shifts are expected according to this concept (Herrmann et al. 2020)

The mean islands beta diversity between before and after the flooding process was different from zero, which points out changes in the species composition during the flooding process. Species assemblages can be different in two ways: when species from one site are replaced by different species in another site, which is known as turnover (Baselga & Orme 2012); and the second way, that consists in the addition (or eradication) of species at only one of the sites, turning the less species rich area into a subset of the more diverse one (Baselga & Orme 2012). The latter case is called nestedness, and it is the pattern we detected in Serra da Mesa. It was expected a decrease in the beta diversity between island pairs due to the selection of more sensitive species. However, the increase in the beta diversity value in the islands immediately after flooding was caused by the migration of species from the valley, changing the island lizard communities. This result suggests that the adjustment in the species-area relationship did not occur during the first two years of monitoring, and crowding effects were likely related to the reduction of area.

The species that showed abundance declines during the flooding (including the local extinction of one species), were larger-bodied, numerically dominants before the flooding, and had a diurnal activity. The species that remained in the monitored islands were the smaller, rarer in the communities before the flooding, and with discrete activity. This result differs explicitly from what has been observed in other studies carried out in forest fragments (Smith et al. 1996; Sarre et al. 1995; Sarre 1998), and in the islands and margins of hydroelectric dam lakes

(Terborgh et al. 1997; Cosson et al. 1999; Palmeirim et al. 2017). The species that declined during the Serra da Mesa flooding (from 1996 to 1999) are commonly found in Cerrado remnants at the Brasília neighboring (Colli 1992; Brandão & Araujo 2001; Colli et al. 2002), suggesting that the island formation in Serra da Mesa experienced different processes when compared to other fragmentation events in the Cerrado.

Araujo (1991), studying a less rich lizard community of Restinga habitat, pointed out the presence of two species groups, based on ecomorphological characters. The first group was composed by larger lizards with longer limbs (Teiidae and Tropiduridae), whereas the second group was composed by smaller species, with shorter limbs (Gekkonidae and Scincidae). These two groups showed strong habitat use differences. While the second group used the interior of vegetation bushes and bromeliad plants (“bromelicolous lizards” sensu Araujo 1991), the first group used the bush edges and open dunes (“sand runners”). The sand runner lizards were more conspicuous when compared with the secretive “bromelicolous” species. A similar separation was observed for the richer Cerrado lizard communities (Araujo 1992). The smaller lizards with shorter limbs (Gekkonidae, Scincidae, and Gymnophthalmidae) could be considered “hidden lizards” (similar to the “bromeliad lizards” of Araujo 1991). These species used mostly dead leaves and trunks, decayed logs, termite mounds, and tree barks. The small size of these lizards reduces their ability to run or jump, as well as the size of prey that they can subdue. Bigger lizards with longer limbs (Teiidae and Tropiduridae) could be considered “runner lizards”. These species could run very fast and use exposed soil, rocks, and trunks. The third group was composed by lizards with elongated body, and long limbs and fingers (Polychrotidae). These species were associated mainly with the vertical dimension of the habitat (“vegetation lizards”).

The elongated and light body, and the long limbs and fingers, allow these lizards to climb the vegetation and show great jump ability.

The lizards *Ameiva ameiva*, *Ameivula ocellifera*, and *Tropidurus spp.* are the more conspicuous lizards in Central Brazil (Rodrigues 1987; Colli et al. 2002). In the Cerrado biome, smaller lizards with shorter limbs are less conspicuous than larger lizards with longer limbs, mostly due to their low movement ratio and secretive habits. These “hidden lizards” also show strong association with certain kinds of retreat sites, like termite mounds, “leaf-cut” ant mounds, and debris (Colli et al. 2002). Gekkonids also show nocturnal and crepuscular activity (Vitt 1991). In summary, these lizards are more difficult to be observed in nature. The morphological analysis detected the decline of species having larger body size and hind limb length in the islands, whereas the remaining species showed the opposite, smaller body size and shorter hind limbs. These results suggest a directional selection event in the lizard community due to the Serra da Mesa reservoir flooding. Thus, our study reveals that in the Serra da Mesa community, the smaller, discrete, and rarer species have advantages to survive when compared with the larger, generalists and more conspicuous lizards.

Predation probably was the most crucial factor affecting lizard communities in the Serra da Mesa islands. During the flooding, a large number of eagles, hawks, and falcons (Accipitridae, Falconidae) were spotted in the islands and several events of predation were observed. Besides the birds, some mammals, and snakes also moved to higher sites as the water level became higher. Due to physiological differences, the prey number ingested by snakes and birds is quite different. Therefore, birds were expected to be the most efficient lizard predators. Moreover, many bird species also prey on snakes, contributing to the snake population decline. Some bird species considered important reptile predators, such as the red-legged seriema

(*Cariama cristata*) and the curl crested jay (*Cyanocorax cristatellus*), became very common in the islands along the flooding process. Excluding owls, birds are diurnal and visually oriented predators. Indeed, diurnal, conspicuous, and more abundant lizards, as *Ameiva ameiva*, *Ameivula ocellifera*, and *Tropidurus spp.*, were more prone to be found by birds than species with crepuscular behavior, with smaller size and/or discrete habits, like *Coleodactylus brachystoma*, *Gymnodactylus amarali*, *mabuids*, and *Micrablepharus maximiliani*. Rarer, cryptic, and smaller species could be less attacked by visually oriented predators than abundant, conspicuous, and larger species. The decline of species with these later characteristics gives support to the directional selection event observed.

Considering the effects of habitat use in the fragmentation process, it was expected that larger, heliophile and habitat generalist species would show a higher chance of permanence in the islands than smaller, heliophobe and rarer species. Although some heliophobe species declined, some heliophile and habitat-generalists presented a marked decline in their abundances, especially *T. oreadicus*, *T. cf. montanus*, and *A. ocellifera*. The same occurred with the generalist *Ameiva ameiva*, whereas rarer species (as *Coleodactylus brachystoma*) did not decay. Refuting our prediction that heliophile, larger and generalist lizards would take over the islands as a consequence of habitat suppression and isolation, in the Serra da Mesa case, predation might have acted as the principal factor for species selection in the years of the islands formation (between 1996 and 1999).

There is strong evidence that species from valleys were not successful in the islands colonization. This probably happened due to metabolic limitations, or to the low colonization success of the lizards that moved to new habitats (Massot et al. 1994), since resident species have advantages to maintain their populations. Besides predation, a general reduction in food and

spatial resources during the islands formation could have favored smaller species, with small energy needs (e.g., less diary food intake). These species may present advantages in more simple habitats. Curiously, Gekkonid and Scincid lizards are the most common lizards in ocean islands (Carlquist 1965).

The prediction concerning island dominance by more generalists, opportunistic and abundant species was not confirmed. This pattern, observed in previous studies (e.g., Case 1975; Sarre et al. 1995; Smith et al. 1996; Sarre 1998; Cosson et al. 1999; Palmeirim et al. 2017), was not corroborated, showing that several factors could act in fragmentation processes and/or land-bridge island formation. These factors could be density-dependent, as predation and competition, which control the population sizes. Other density-independent factors, such as fire, flooding, and invasions could be also very important for changes in fragmented communities, and in resource availability. Moreover, as opposed to results reported by Gainsbury & Colli (2003), where extinctions in Amazonian Cerrado enclaves were pointed out as stochastic consequence of historical factors, our results show that fragmentation is a very complex event, and ecological factors, such as predation, could determine community structure in reservoir land-bridge islands.

The dramatic reduction in lizard richness and abundance observed in Serra da Mesa islands suggests that small fragments are not efficient for conservation of Cerrado lizards. Hydroelectric constructors, for the sake of biodiversity conservation, must consider the fact that island size is crucial for maintenance of a reasonable number of fauna species. A careful planning before the flooding initiation would be determinant in order to mitigate wildlife depletion. Furthermore, our results highlight the role of species natural history for extinction events in these areas. Species associated to thermally buffered microhabitats, such as the nocturnal *Gymnodactylus amarali*, which spend their time inside termite mounds (Vitt et al.



2007), are potentially more resilient in the Serra da Mesa islands. However, permanence over time might be compromised by the effects of isolation (Amorim et al. 2017).

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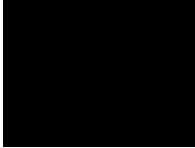

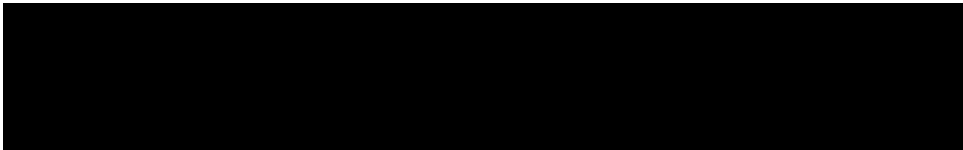
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Table 1. Lizard species found in the study area, distributed by sampling period in island habitats. H – Species recorded in top hills; V – Species recorded in valleys (that became flooded); P – Species recorded on islands in 2019; E – Species extinct. The habitats used by the lizards are gallery forest (GF), open grassland (OG) veredas (VE), and cerrado-cerradão (CE-CD). The species habits are terrestrial (te), fossorial (fo), saxicolous (sa), herbaceous (he) and arboreal (ar). They were classified as habitat-generalist (GN), heliophilous (HE), and umbrophilous (UM).

TAXA	Occurrence	May to Oct 1996 (before reservoir formation)	Oct 1996 to Jan 1999 (during reservoir formation)	2001 (Three years after island formation)	2011 (13 years after island formation)	2019 (21 years after island formation)	Permanence	Habitat use
<b>TEIIDAE</b>								
<i>Ameiva ameiva</i>	H, V						E	MG, CL, VE, CE-CD
<i>Ameivulla ocellifera</i>	H, V						P	CE - CE
<i>Salvator merianae</i>	H, V						E	MG, CL, VE, CE-CD
<i>Tupinambis quadrilineatus</i>	V						E	MG, CL, VE, CE-CD
<b>GYMNOPHTALMIDAE</b>								
<i>Cercosaura ocellata</i>	H, V						E	MG, CL, VE, CE-CD
<i>Colobosaura modesta</i>	V							MG

<i>Micrablepharus maximiliani</i>	<b>H, V</b>		<b>P</b>	<b>CL, VE, CE-CD</b>
<b>TROPIDURIDAE</b>				
<i>Tropidurus cf. montanus</i>	<b>H</b>			<b>E</b> <b>CE-CD</b>
<i>Tropidurus oreadicus</i>	<b>H, V</b>			<b>E</b> <b>CL, VE, CE-CD</b>
<i>Tropidurus torquatus</i>	<b>V</b>		<b>E</b>	<b>MG</b>
<b>HOPLOCERCIDAE</b>				
<i>Hoplocercus spinosus</i>	<b>V</b>		<b>E</b>	<b>MG, CE-CD</b>
<b>IGUANIDAE</b>				
<i>Iguana iguana</i>	<b>H, V</b>		<b>E</b>	<b>MG, CL, VE, CE-CD</b>
<b>POLYCHROTIDAE</b>				
<i>Norops meridionalis</i>	<b>H</b>		<b>E</b>	<b>CL, VE, CE-CD</b>
<i>Norops brasiliensis</i>	<b>H, V</b>			<b>E</b> <b>MG, CE-CD</b>
<i>Polychrus acutirostris</i>	<b>V</b>			<b>E</b> <b>CL, VE, CE-CD</b>
<b>SCINCIDAE</b>				
<i>Copeoglossum nigropunctatum</i>	<b>H, V</b>		<b>P</b>	<b>MG, CL, VE, CE-CD</b>

<i>Mabuya frenata</i>	V	[REDACTED]	[REDACTED]		CL, VE, CE-CD
<b>GEKKONIDAE</b>					
<i>Coleodactylus brachystoma</i>	H, V	[REDACTED]		E	MG, CE-CD
<i>Gymnodactylus amarali</i>	H, V	[REDACTED]		P	CE-CD
<hr/> <i>Total</i>		19			

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Table 2. Eigenvalues of Principal Component Analysis with the effect of the size on lizard measurements (Log10 of measurements).

<b>Variable</b>	<b>Component 1</b>	<b>Component 2</b>	<b>Component 3</b>
LOGCRA	0.170	0.052	-0.012
LOGCC	0.172	0.041	-0.015
LOGLC	0.186	0.023	0.041
LOGAC	0.203	0.016	0.001
LOGCM	0.175	0.032	-0.014
LOGCB	0.199	-0.026	0.033
LOGCP	0.209	-0.032	0.017
LOGMA	0.197	-0.041	0.002
LOGMP	0.214	-0.042	-0.053
<b>Variance explained</b>	<b>92.62%</b>	<b>2.58%</b>	<b>1.32%</b>

Table 3. Results of Stepwise Discriminant Analysis for size-adjusted measurements of lizard species and families from Serra da Mesa.

<b>Species</b>			
<b>Variable</b>	<b>F</b>	<b><i>p</i> (Wilk's Lambda)</b>	<b>error-rate</b>
Body Size	136.65	0.17837	0.6152
Posterior limb length	105.05	0.03920	0.3225
Snout-vent length	75.35	0.01102	0.2168
Leg length	46.43	0.00428	0.1870
Head length	38.45	0.00185	0.1545
Anterior limb length	22.37	0.00105	0.1463
Head width	20.47	0.00062	0.1491
Head high	16.94	0.00039	0.1274
<b>Families</b>			
<b>Variable</b>	<b>F</b>	<b><i>p</i> (Wilk's Lambda)</b>	<b>error-rate</b>
Posterior limb length	133.64	0.3520	0.4011
Body size	152.74	0.1132	0.2304
Snout-vent length	126.04	0.0412	0.1626
head length	54.96	0.0234	0.1084
head width	38.21	0.0153	0.0894
Leg length	37.42	0.0100	0.0705
Arm length	25.30	0.0074	0.0596
Anterior limb length	11.58	0.0064	0.0515

## CAPÍTULO 3

### **MULTILOCUS ENVIRONMENTAL ADAPTATION AND POPULATION STRUCTURE IN POPULATIONS OF THE CERRADO GECKO *GYMNODACTYLUS AMARALI* (SAURIA: PHYLLODACTYLIDAE) FROM SERRA DA MESA HYDROELECTRIC PLANT, CENTRAL BRAZIL**

#### ABSTRACT

In order to understand how populations adapt to different environmental conditions, studies of local adaptation have been largely used as an interface to address ecological and evolutionary questions. Ecological specialization resulting from local adaptation may culminate in speciation, when local adaptation is a significant component of responses to environments going through changes. In this study, we investigate populations of *Gymnodactylus amarali* (Phyllodactylidae) isolated in rapidly created artificial islands. We combined a genotyping-by-sequence (GBS) survey and redundancy analyses to investigate genotype-environment associations (GEA) while accounting for spatial genetic structure. Our hypothesis is that *G. amarali* populations in the islands are going through a local adaptation process and consequently becoming genetically different from the populations in the mainland. Our DAPC detected the presence of a distinct genetic lineage in Serra da Mesa, which is differentiated from nearby “mainland” populations. The RDA pointed out local genetic adaptations correlated with temperature and precipitation, suggesting three environmentally distinct lizard populations. At least three locally structured populations show significant local adaptation to environmental variation, with numerous SNPs correlated with climatic conditions at each site. Although we lack

sufficient data from before the reservoir construction, we still present robust evidence of the huge impact caused in the local *G. amarali* populations. Our results add valuable information about evolutionary ongoing processes to the previous reports accounting for severe ecologic and morphologic changes of this gecko.

**Keywords:** Redundancy Analysis, Central Brazil, Reservoir, Habitat isolation.

## **Introduction**

Spatial environmental variation is global and inescapable, which makes adaptation to local biotic and abiotic conditions common and necessary for most populations (Savolainen et al. 2013). In order to understand how populations adapt to different environmental conditions, studies of local adaptation have been largely used as an interface to address ecological and evolutionary questions (Hofmeister et al. 2020). A local population in a place where environmental constraints and forces such as divergent selection are operating might quickly evolve advantageous adaptations to proximate environmental conditions (Kawecki and Ebert 2004). As a result of this process, a pattern where the genotypes in each population would have a higher relative fitness on average in their local habitat compared to the genotypes from other locations should emerge (Kawecki and Ebert 2004). Both the process and the pattern leading to it is the definition of local adaptation (Williams 1966; Kawecki and Ebert 2004).

Ecological specialization resulting from local adaptation may culminate in speciation, when local adaptation is a significant component of responses to environments going through changes (Savolainen et al. 2013). For example, climate change caused by human activities is ruthlessly impacting biodiversity on our planet (Scheffers et al. 2016). Organisms carrying genetic variation for climate-related traits are expected to possess the capacity of adapting

rapidly to changing environments (Bay et al. 2018). Commonly, these traits which allow local adaptations are polygenic quantitative traits, and it is a highly demanding task to identify the loci that control variation in such traits (Savolainen et al. 2013). A very important first step aiming for establishing evidence of local adaptation is the measurement of genomewide patterns of variation using large-scale single nucleotide polymorphism (SNP) genotyping arrays (Schweizer et al. 2016).

High degrees and rapid onset of local adaptation are usually expected in isolated populations, which are generally free from the homogenizing effects of high gene flow (Hofmeister et al. 2020). However, most studies in this field focused on rapid adaptation to local conditions in response to new selection regimes that some taxa encountered in the process of range expansion (e.g.: cane toads, sticklebacks, honeybees, steelhead trout, deer mice; consult Hofmeister et al. 2020 for references). In this study, we investigate populations of the gekko *Gymnodactylus amarali* (Phyllodactylidae) isolated in rapidly created artificial islands resulting from the flooding of the Serra da Mesa Hydroelectric Plant reservoir, in Central Brazil.

The Serra da Mesa reservoir filling started in 1996: 170,000 ha of area was flooded, valleys were submerged, and hilltops became ~ 290 islands (Amorim et al. 2017). Local adaptations may appear rapidly according to biogeography and studies on contemporary adaptation (Savolainen et al. 2013). Amorim et al. (2017) demonstrated that only 15 years of isolation were enough for *G. amarali* to present significant head size increase and consequent ecological niche breadth expansion. Lizards living on the islands have disproportionally larger heads compared to adjacent mainland populations. Furthermore, all five island populations presented this shift in morphology independently (Amorim et al. 2017). Due to ecological

release, after the extinction of larger lizards on the islands, all five populations went through a process of parallel local adaptation (Amorim et al. 2017).

Herein, we aimed at testing for correlations between SNPs and environmental predictors and genetic divergence between island and mainland populations in this termite specialist gecko. We combined a genotyping-by-sequence (GBS) survey and redundancy analyses to investigate genotype-environment associations (GEA) while accounting for spatial genetic structure. Our hypothesis is that *Gymnodactylus amarali* populations in the islands are going through a local adaptation process and consequently becoming genetically different from the populations in the mainland. We find support for both spatial genetic structure (i.e., geographic lineages) and local environmental adaptations to climatic factors among sites, including significant variation for Serra da Mesa populations.

## **Material and Methods**

### ***Sequencing and Bioinformatics***

We obtained 46 tissues of *Gymnodactylus amarali* from the CHUNB and LAFUC collections at the Universidade de Brasília, from the municipalities of Colinas do Sul (one individual), Minaçu (20 individuals), and from five islands and five margin sites in and around the Serra da Mesa reservoir (25 individuals), Goiás state, Brazil (see Appendix S1 for sample numbers, localities, and associated data). We extracted genomic DNA using Qiagen DNEasy kits and visualized the results on a 2% agarose gel. We sent ~30mg to the UWBC Biotechnology center for genotype-by-sequencing (GBS) analysis (Elshire et al. 2011). The samples were optimized using the ApeKI enzyme for digestion, bead cleanup for size selection, amplification using 18 PCR cycles, and a post-PCR normalization step prior to sequencing. We sequenced

each sample for an average of ~6.5 million 150bp paired-end reads using an Illumina NovaSeq6000.

We processed the raw reads to extract SNP calls using ipyrad 0.9.59 (Eaton and Overcast 2020) using the denovo pairgbs pipeline on the GW HPCC *Pegasus* cluster (MacLachlan et al. 2020). We used ‘C[W]GC’ to identify the ApeKI restriction overhang, and employed strict filtering and trimming for adapter sequence and quality of reads. We generally used the default parameters for SNP calling (e.g., a depth of 6 for majority-rule and statistical base-calling), with a 90% clustering threshold as a stringent compromise between over-splitting and over-lumping of loci as recommended by the authors. We retained loci called for ~80% of individuals (i.e., 37 of 46), resulting in 2,068 loci and 2,808 SNPs, for a total alignment length of up to 113,439bp per individual.

### ***Population structure and multilocus adaptation***

We first tested for population structure using the DAPC (Discriminant Analysis of Principal Components) algorithm in the R package ‘adegenet’ (Jombart and Collins 2017), which produces a principal-component reduction of the SNP matrix for which discriminant functions can be used to estimate membership probability in an optimally-determined number of clusters. DAPC is a powerful tool to summarize the genetic divergence found between groups while disregarding within-group variation (Jombart et al. 2010). We used the full SNP matrix (46 individuals x 2,808 SNPs) and determined the optimal number of clusters by the “elbow” method of calculating the lowest BIC (Bayesian Information Criterion) score across candidate values of K from 1 to 12. These were then compared to the sites (Colinas do Sul, Minaçu, and the 10 sites within Serra da Mesa, five islands and five locations on the reservoir margin) to determine the

extent of local population structure within *Gymnodactylus amarali* in the study region (see Domingos et al. 2014).

We then tested for multilocus adaptation using Redundancy Analysis (RDA) to detect loci under selection in a genotype-environment association framework (Rellstab et al. 2015; Forester et al. 2018). Recent studies showed that RDA-based methods are more efficient for detection of local adaptation signatures, presenting a combination of low false-positive and high true-positive rates throughout weak, moderate, and strong multilocus selection when compared to other methods (Forester et al. 2016), whereas RDA genome scans presented greater statistical power than scans based on PCA, by allowing individual-based simulations (Capblancq et al. 2018).

We predicted that temporal, spatial, and climatic axes in concert may all have resulted in weakly covarying signatures in the molecular data, for which we tested the response of the SNP data to the multivariate environment for detection of candidate genes (Schweizer et al. 2016). We employed this multivariate ordination technique in the R package ‘vegan’ (Oksanen et al. 2007). The response variable was the 46 individuals by 2,808 SNP matrix, with the 50,087 missing values imputed as the most common genotype at each SNP across individuals, as RDA requires complete entries for all values; for a full description of this method, see Forester et al. (2018).

### ***Environmental predictors***

Savannas, deserts, semi-arid regions, and other open habitats are known as high diversity areas for lizard faunas. The Brazilian Cerrado is an unique savanna hotspot (Nogueira et al. 2009; Azevedo et al. 2016), with both daily and seasonal shifts in temperature and moisture (Vitt et al. 2007). The study species *Gymnodactylus amarali* is a termitaria specialist, living in a microhabitat that buffers the temperature effects. However, populations from areas where termite



mounds are absent were reported using rocky habitats as refuge (Vitt et al. 2007), which exposes them to temperature and moisture variations. Furthermore, most Cerrado lizards reproduce during the rainy season and this reproductive seasonality is determined by fluctuations in arthropod abundance, which are related to rainfall fluctuations (Colli et al. 2002). Most reproductive individuals of *G. amarali*, however, were observed during the dry season (Colli et al. 2003).

Thus, our data set was designed to reflect the relationship between genetic divergence and the environment used by *G. amarali*. For predictor variables, we included a set of weakly-correlated climatic variables from the 30-second BIOCLIM dataset (Fick and Hijmans 2017). For the latter, we first identified environmental variation at each sampling location using the R package “raster” (Hijmans and van Etten 2012), then we extracted values for all 19 variables at the 10 sites and estimated collinearity with  $r < 0.7$  as a cutoff (Dormann et al. 2013) This yielded a reduced set of four weakly correlated climatic variables consisting of annual mean temperature (BIO1), isothermality (BIO3), annual precipitation (BIO12), and precipitation seasonality (BIO15). These variables presented relatively low variance inflation factors ( $< 10$ ): BIO1 (VIF=8.03), BIO3 (2.85), BIO12 (8.28), and BIO15 (6.43). Annual mean temperature and isothermality are parameters associated to the temperature that lizards endure in that region, whereas annual precipitation and precipitation seasonality inform about the humidity available in the environment.

## Results

### *Discriminant Analysis of Principal Components*

Using the function ‘find.clusters,’ we detected three clusters in coincidence with the elbow in the curve, which matches the smallest BIC (Fig.1). Then, the number of clusters detected was used to run the DAPC. The scatterplot we obtained shows a clear-cut separation among the three clusters, each one representing a *G. amarali* population (Fig.2). The individual island and reservoir margin populations are not differentiated from each other, but all Serra da Mesa individuals are differentiated from nearby “mainland” populations. There are two “mainland” genetic clusters, one consisting of the single sample from Colinas do Sul and seven of the Minaçu specimens, and another consisting of the other 13 Minaçu samples. Thus, there is sympatric genetic diversity of two genetic lineages in at least one of the “mainland” sites, while the Serra da Mesa populations are genetically distinct. A map illustrates both “mainland” clusters occurring at Minaçu, which are genetically distinct from Serra da Mesa (Fig.3). In the graph, individuals are represented as dots while the ellipses represent the groups (Fig. 4).

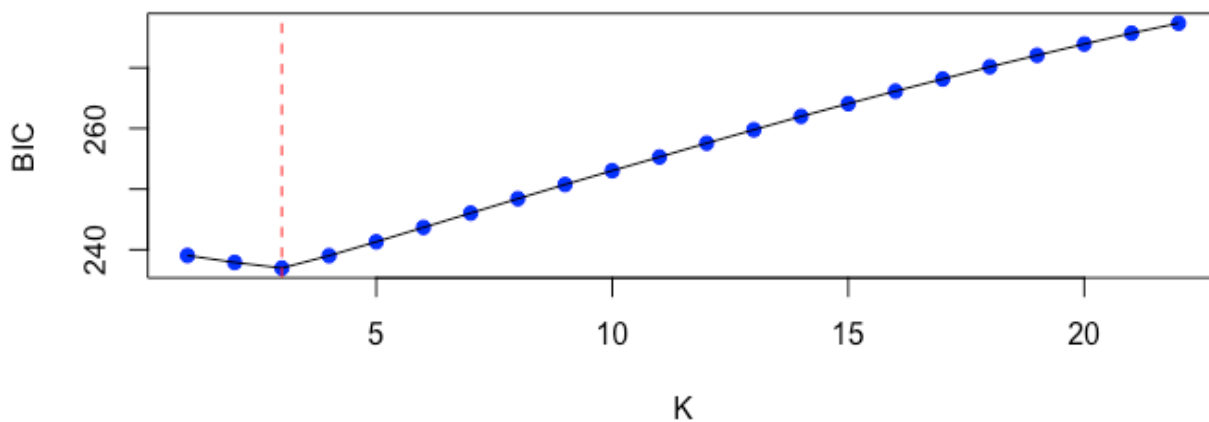


Figure 1. Plot of BIC values for different values of  $K$ , showing optimal result of three genetic clusters corresponding to populations from Colinas, Minaçu, and Serra da Mesa.



Figure 2. Axes 1 and 2 of Discriminant Analysis of Principal Components (DAPC) of 46 individuals from Serra da Mesa and the other two localities: Colinas do Sul and Minaçu. The groups are represented as inertia ellipses and the dots are the individuals. Analysis eigenvalues are showed inset.

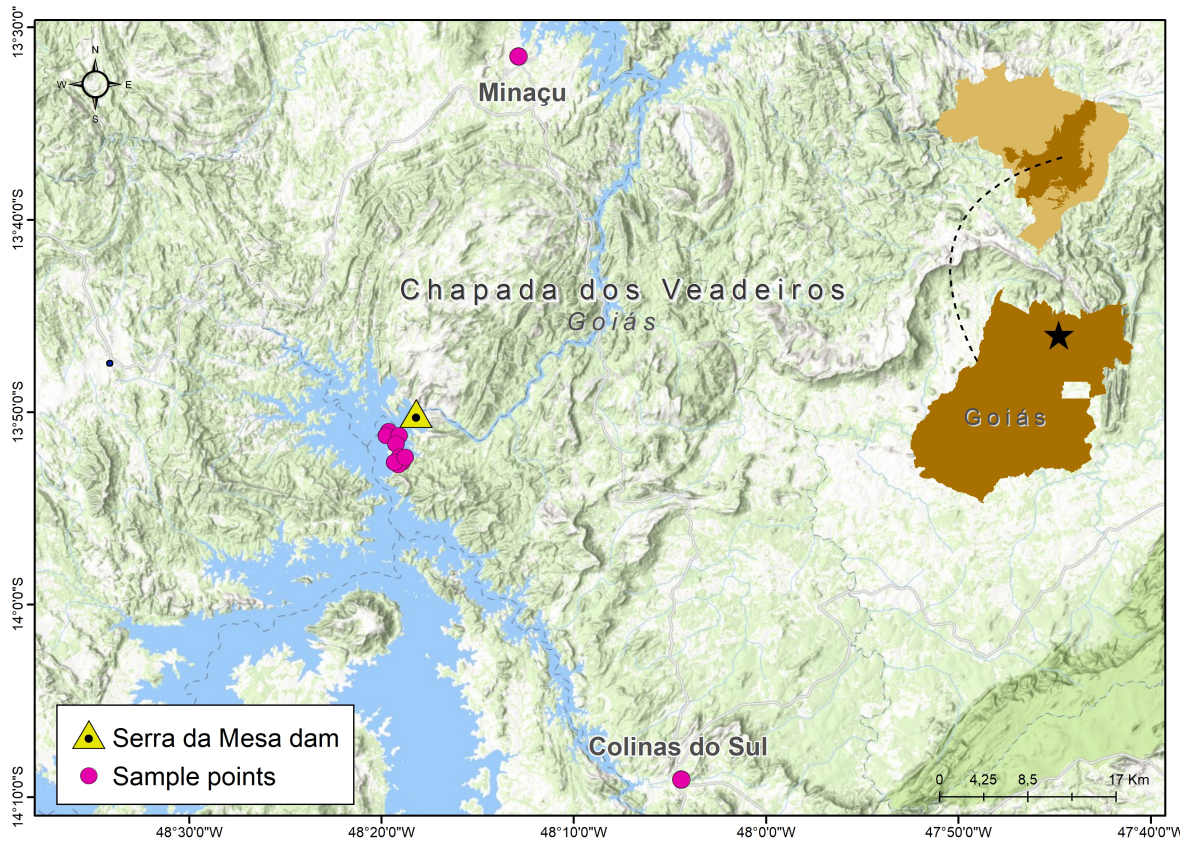


Figure 3. Map showing the three detected clusters: two “mainland” clusters, Minaçu and Colinas, which are genetically distinct from Serra da Mesa.

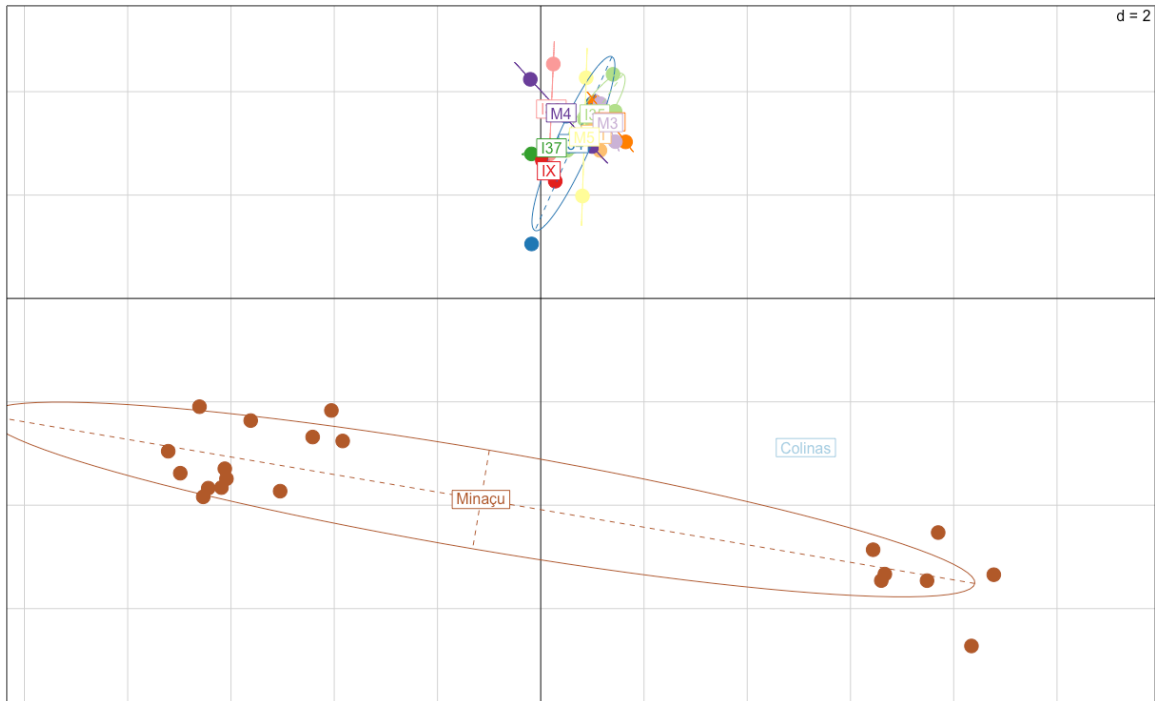


Figure 4. Axes 1 and 2 of the SNPs PCA generated using GBS, coded by the initial sites. Individuals are represented as dots, and ellipses represent the groups.

### ***Redundancy Analysis***

The proportion of the variance explained by the environmental predictors in the Redundancy Analysis is 37,5% for RDA1, 30,7% for RDA2, and 16,4% for RDA3.

Isothermality loads positively whereas annual precipitation, annual mean precipitation, and precipitation seasonality show negative loadings in axis 1. In axis 2, annual precipitation loads negatively whereas annual mean temperature, precipitation seasonality, and isothermality have positive loadings (Fig.5). The main contrast was related to precipitation and temperature, which is in accordance with the Cerrado seasonality. A similar pattern is observed for the comparisons with RDA1 vs RDA3 (Fig.6).

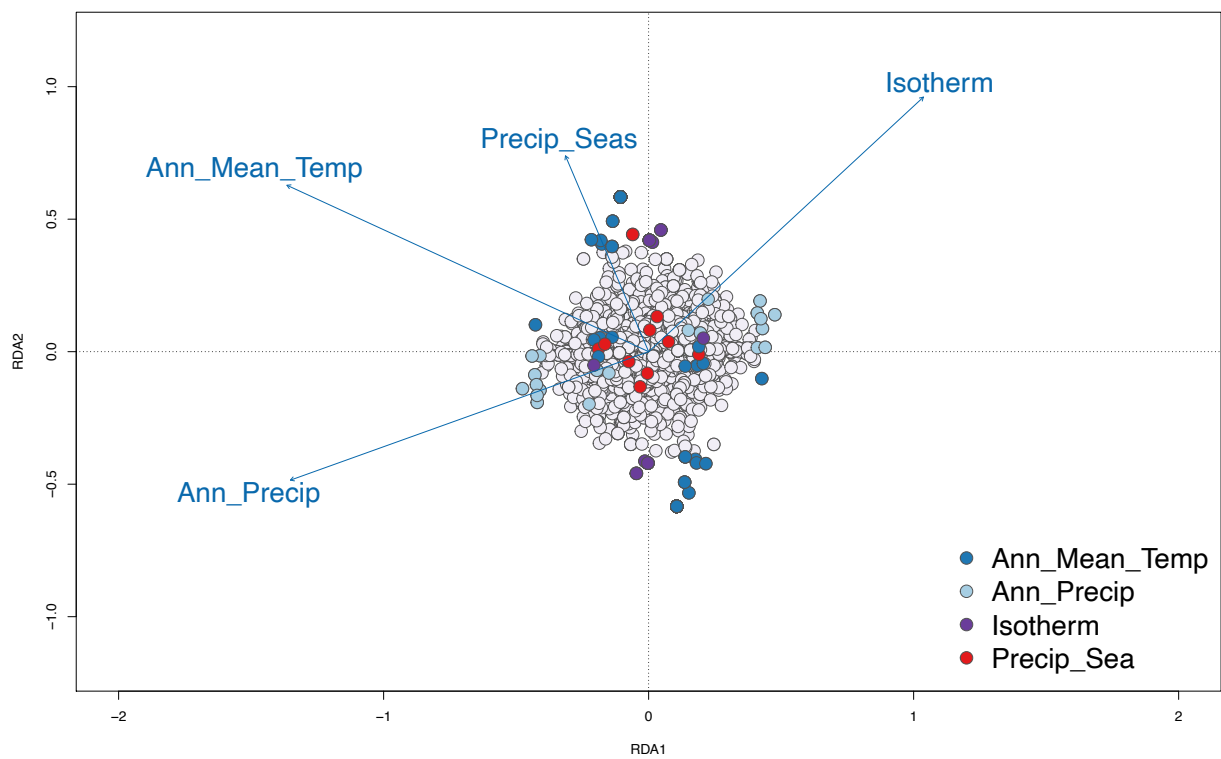


Figure 5. RDA Triplot of specimens, SNPs (small light grey points), and variables (vectors) on axes 1 and 2, by environmental factors.

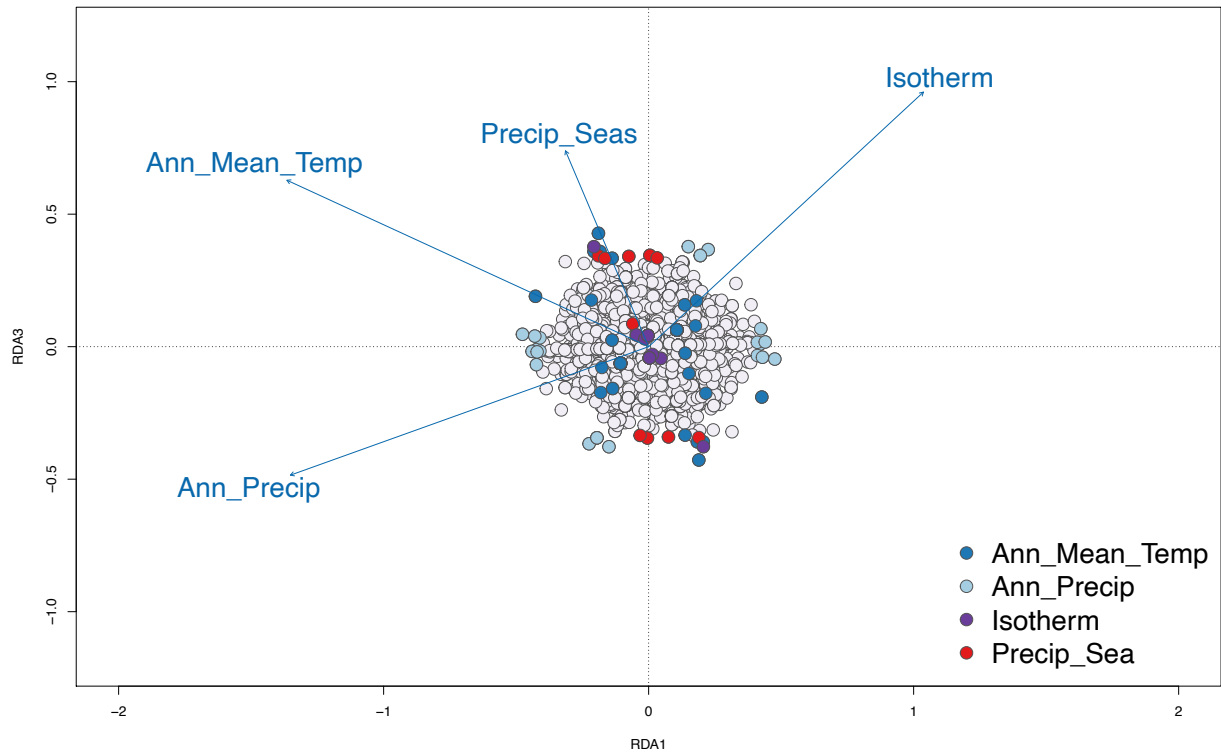


Figure 6. RDA Triplot of specimens, SNPs, and variables on axes 1 and 3, by environmental factors

About 8% of the 2,808 SNPs sampled are associated with environmental variation. There are SNPs heavily associated with all four variables, revealing that the estimated genotypes are correlated with local temperature and precipitation. Among the 230 candidate SNPs detected, the majority were correlated with temperature variables: 170 SNPs correlated with annual mean temperature (BIO1) and 27 SNPs correlated with isothermality (BIO3). The remaining SNPs were associated with precipitation: 23 SNPs associated with annual precipitation (BIO12) and 10 with precipitation seasonality (BIO15). The Serra da Mesa population is clustered in the right quadrant showing a strong positive correlation with temperature (isothermality), whereas the Minaçu population is clustered in the left quadrant, presenting a positive correlation with both annual mean temperature and annual precipitation. Although clustered together with Minaçu

population in the DAPC, the single individual from Colinas appears isolated. The distance from the other two populations demonstrates a magnitude of divergence and a strong correlation with the environmental predictors as well (Fig.7).

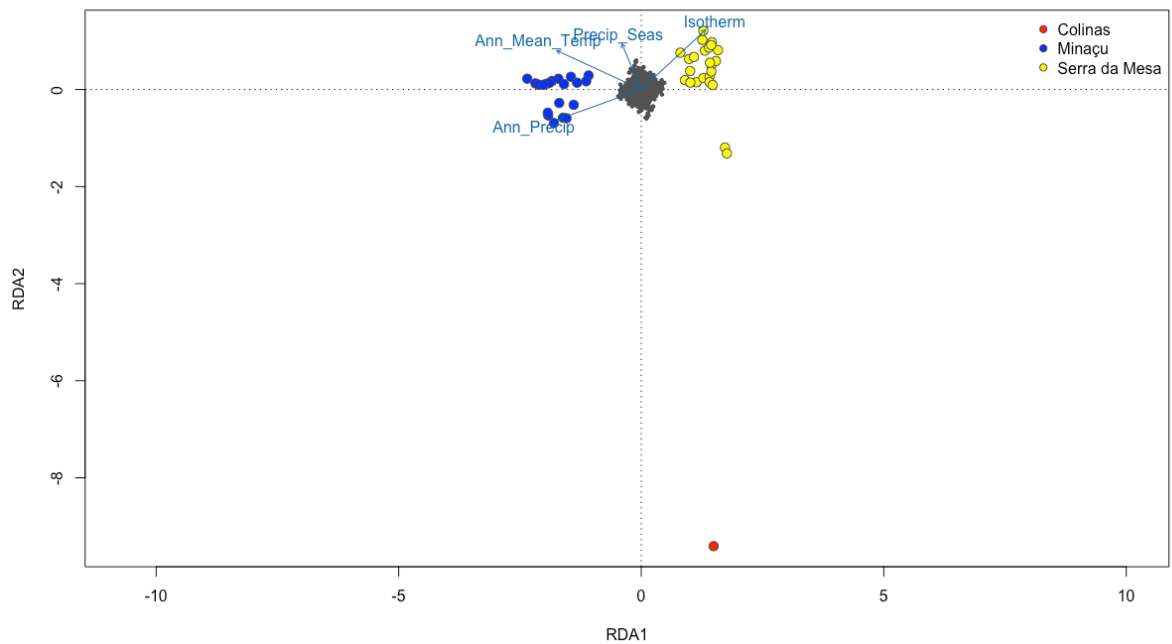


Figure 7. RDA Triplot of specimens, SNPs (small grey points), and variables (vectors) on axes 1 and 2, by site.

## Discussion

Cases of heritable phenotypic differentiation between local populations have always been a subject that attracts the attention of evolutionary biologists and naturalist (Kawecki and Ebert 2004). Local adaptation plays a crucial role in initiating the divergence of incipient species (Kawecki and Ebert 2004). Several examples of adaptation have been reported, such as the genomic mapping of the color polymorphism in the peppered moth *Biston betularia*, coat color variation in different mouse species in response to the variation of the environment background color, and trichome variation to improve herbivory resistance in *Arabidopsis lyrate* (Savolainen et al. 2013). Recent studies with *Anolis* lizards also reported rapid directional changes. These



lizards, after experiencing extreme cold temperatures, presented a greater resistance to the cold due to a shift in gene expression (Campbell-Staton et al. 2017). Another interesting case involving *Anolis* describes their improved capacity of surviving hurricanes in the Caribbean region because of their larger toepads (Dufour et al. 2019). All these examples show visibly rapid local adaptation on human timescales, often in response to human pressures.

Recently published studies on local adaptation by GEA were focused on birds (Bay et al. 2018); (Hofmeister et al. 2020), wolves (Schweizer et al. 2016), and plants (Vangestel et al. 2018). All these papers investigated genomic variations of metapopulations across the range of distribution of different species. Although it is not possible to claim that human interference was responsible for the genetic differentiation observed, we present herein results with anthropogenically isolated organisms, where gene flow was interrupted, and rapid genetic morphological and ecological differentiation has previously been detected (Amorim et al. 2017).

DAPC detected the presence of a distinct genetic lineage of *G. amarali* in Serra da Mesa, which is differentiated from nearby “mainland” populations. Our results showed a clear separation among three populations we examined: one in Serra da Mesa, one shared between Colinas and Minaçu (spanning either side to the north and south of Serra da Mesa), and one restricted to Minaçu. This fine-scale population structure was not detected in previous range-wide phylogeographic analyses of the species (see Domingos et al. 2014). We found evidence of local adaptation to environmental conditions for all populations. RDA pointed out local genetic adaptations correlated with temperature and precipitation, suggesting that lizards are adapting to the climate at each site, and highlighting the effect of Cerrado seasonality on local adaptations of lizard populations in this climate contrasting biome (Françoso et al. 2020). Previous studies with

*G. amarali* in Serra da Mesa reported head size increase (Amorim et al. 2017) and negative allometry in the hemipenis lobe in the “island” populations (Coelho 2020).

Adaptive phenotypic plasticity may lead to adaptive phenotypic differentiation, even without genetic divergence (Kawecki and Ebert 2004). Thus, although the geckos living in the islands and the ones from the margins were clustered together, the aforementioned ecological release detected in the islands yielded the reported morphological differences. This was not reflected in our genetic analyses, which suggested a cluster of locally adapted genotypes at Serra da Mesa across both the “islands” and the reservoir margin. It is possible that the genetic divergence and local adaptation of these populations predates the dam, or that ongoing gene flow to and from the islands overrides any hyper-local adaptations. While some of our samples pre-date the dam, we lack sufficiently time-stratified sampling to detect temporal trends in local adaptation or genetic differentiation. Similarly, additional geographic sampling is needed to determine if the locally adapted genotypes at Serra da Mesa occur elsewhere, and how frequently and widely distributed such locally climate-adapted population structure occurs.

Although the emergence of the local adaptation concept is relatively old, there is still much room for further investigation. We still do not know to which loci the environmental variables are correlated in *Gymnodactylus amarali*. Finding the SNPs associated with Gene Ontology categories, as for instance, the morphological categories enriched by temperature and precipitation, would be a desirable next step. We provide here another piece for the puzzle, complementing Amorim et al. (2017) findings, aiming at a deeper comprehension of what is underlying the rapid evolution of *G. amarali* in the Serra da Mesa reservoir.

In summary, we here show that both island and reservoir margin populations are genetically distinct from nearby “mainland” sites (but not from each other). At least three locally

structured populations (one at Serra da Mesa and two at nearby mainland localities) show significant local adaptation to environmental variation, with numerous SNPs correlated with climatic conditions at each site using GEA methods. Having in mind the lack of sufficient data from before the reservoir construction, we still present here evidence of the impact caused in the local *G. amarali* populations by this enterprise. Our results add valuable information about evolutionary ongoing processes to the previous reports accounting for severe ecological and morphological changes of this gecko (in preparation; Amorim et al. 2017; Coelho 2020). Further study is now needed to untangle the root genomic and developmental causes of short- and long-term genetic and phenotypic variation in these unique “island” populations.

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## CONSIDERAÇÕES FINAIS

A região de Serra da Mesa era originalmente formada por florestas de galeria e veredas em seus vales, enquanto os topos de morro eram formados por Cerrado aberto. Após a inundação, os vales úmidos foram submersos e apenas os topos dos morros permaneceram. Houve uma grande perda de qualidade e variedade de habitat disponível para fauna local. Como consequência, esperava-se um aumento de abundância e riqueza de espécies nos topos de morro devido ao processo migratório natural. Uma vez que a região mais alta de Serra da Mesa já era ocupada por espécies de lagartos heliófilos e generalistas, um resultado esperado era de que estas se mantivessem no ambiente. Entretanto, algumas destas espécies heliófilas e generalistas também sofreram grande declínio em sua abundância.

Aves e cobras eram os principais predadores locais de lagartos, de acordo com eventos observados nas ilhas. Porém, muitas dessas aves também se alimentam de cobras, reduzindo a predação de lagartos à ação quase exclusiva de aves. As espécies de aves predadoras eram em sua maioria diurnas e com orientação visual. Este fato seria crucial para permanência de espécies menores e crípticas, uma vez que espécies mais conspícuas ficariam mais expostas a estes predadores. A lista de espécies coletadas na última expedição feita em junho de 2019 corrobora esta hipótese. *Ameivula ocellifera*, *Micrablepharus maximiliani*, *Gymnodactylus amarali*, *Copeoglossum nigropunctatum*, *Colobosaura modesta*, e *Tropidurus oreadicus* são lagartos que apresentam como principal estratégia de defesa a coloração críptica. Além da coloração críptica, a atividade crepuscular, o pequeno porte, a utilização do folhíço e de cupinzeiros como refúgio tornam estes lagartos mais difíceis de serem detectados por aves. A sobrevivência destas espécies sugere que houve seleção direcional nestas ilhas.

Além da seleção direcional, outros dois processos naturais foram apontados por este estudo. A adaptação local ao clima e a divergência genética da população de *G. amarali* de Serra da Mesa em relação às populações do continente também podem ser consequência da influência humana trazida pela construção da represa. Embora não haja dados anteriores à construção da barragem, outros estudos recentes na região trazem resultados que suportam esta possibilidade. O aumento do tamanho da cabeça e do lobo hemipeniano destes geconídeos em populações insulares, somados aos resultados trazidos neste estudo, permitem afirmar, de maneira mais assertiva, o impacto causado por uma intervenção desta magnitude no meio ambiente natural.



Desta forma, estudos futuros com foco nas origens genômicas e nas implicações funcionais das adaptações locais detectadas seriam importantes para aprofundamento do nosso conhecimento à cerca dos processos naturais com os quais *G. amarali* vem lidando ao longo dos anos, em Serra da Mesa. Além disso, autoridades e corporações responsáveis pelo planejamento de empreendimentos energéticos, os quais impliquem no alagamento de uma extensa área, deveriam, obrigatoriamente, ter em mente que o tamanho dos fragmentos de habitat remanescentes é fator determinante para a manutenção de um número maior de espécies locais. Fragmentos/ilhas com área reduzida foram, mais uma vez, apontados como ineficientes para a conservação de lagartos.