UNIVERSIDADE FEDERAL DA PARAÍBA

CENTRO DE CIÊNCIAS EXATAS E DA NATUREZA

DEPARTAMENTO DE SISTEMÁTICA E ECOLOGIA

PROGRAMA DE PÓS GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

Padrões globais do nicho alimentar de lagartos

TESE DE DOUTORADO

LUCAS BARBOSA DE QUEIROGA CAVALCANTI

João Pessoa - PB, Março de 2018

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Padrões globais do nicho alimentar de lagartos

Aluno:

Ms. LUCAS BARBOSA DE QUEIROGA CAVALCANTI

Orientador:

Dr. DANIEL OLIVEIRA MESQUITA

Tese a ser apresentada para obtenção do título de doutor no Programa de pós graduação em Ciências Biológicas (Zoologia) da Universidade Federal da Paraíba Campus I.

João Pessoa - PB, Março de 2018

Ata da 108ª Apresentação e Banca de Defesa de Doutorado de Lucas Barbosa de Queiroga Cavalcanti

Ao(s) Vinte e seis dias do mês de março de dois mil e dezoito, às 14:00 horas, no(a) Sala do PPGCB, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a tese de doutorado de **Lucas Barbosa de Queiroga Cavalcanti**, candidato(a) ao grau de Doutor em Ciências Biológicas. A banca foi composta pelos seguintes professores/pesquisadores: **Dr. Daniel Oliveira Mesquita (orientador), Dr. Pedro Cordeiro Estrela (titular), Dr. Gustavo Henrique Calazans Vieira (titular), Dr. Pablo Ariel Martinez (titular) e Dr. Timothy J. Colston (titular).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra para o(a) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Lucas Barbosa de Queiroga Cavalcanti**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"Padrões globais no nicho alimentar de lagartos".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito APROVADO. Perante a aprovação, declarou-se o(a) candidato(a) legalmente habilitado(a) a receber o grau de **Doutor em Ciências Biológicas**, área de concentração **Zoologia**. Nada mais havendo a tratar eu, **Dr. Daniel Oliveira Mesquita**, como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 26/03/2018.

Dr. Daniel Oliveira Mesquita (orientador)

Dr. Pedro Cordeiro Estrela (titular)

Dr. Gustavo Henrique Calazans Vieira (titular)

Dr. Pablo Ariel Martinez (titular)

Dr. Timothy J. Colston (titular)

Ciente do Resultado:

Lucas Barbosa de Queiroga Cavalcanti

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Resumo

Entender como os fatores históricos e recentes podem moldar as características ecológicas das espécies é crucial para elucidarmos processos ecológicos e evolutivos. Utilizando um banco de dados global dos aspectos alimentares de 722 populações de 323 espécies de lagartos (dentre 32 famílias), testou-se a influência da filogenia nas preferências alimentares dos lagartos numa escala global, assim como sua relação com o clima, modo de forrageio, habitat, distribuição (tropical/temperada) e tamanho do corpo. A história evolutiva foi o fator determinante nas preferências alimentares dos lagartos, explicando 53,79% da variação total dos dados. Também foi encontrado sinal filogenético na ingestão de presas tanto numa perspectiva univariada como multivariada. Lagartos Iguania tendem a comer mais besouros e himenópteros que não Iguania. Sugere-se que os Iguania possuem adaptações que facilitam o desenvolvimento da herbivoria. Lagartos não Iguania geralmente são de dois grupos: (1) aqueles que se alimentam de cupins (especialmente as espécies de deserto) ou (2) aqueles que se alimentam de presas energéticas (como ortópteros, aranhas e baratas). Ainda, encontramos evidência de influência climática nas preferências alimentares, sento a fauna de artropodes de folhiço bem mais comuns na dieta dos lagartos que habitam climas mais quentes e úmidos. Artrópodes com resistência a ambientes frios foi mais ingeridos por largartos de climas mais frios. A ingestão de cupins (assim como carrapatos e louva-deus) foi associada a climas sazonais e quentes, como desertos e regiões áridas, sendo uma fonte de alimento em ambientes mais hostis. Herbivória foi associada a ambientes sazonais, provavelmente como fonte de alimento e água. O modo de forrageio não foi um bom preditor das preferências alimentares, e foi relacionado apenas com solpugidas e carrapatos, as quais não são tipos de presas primários. A especialização do habitat também parece predizer aspectos secundários da alimentação, especialmente em espécies arbóreas e semi-aquáticas. Lagartos tropicais tendem a ingerir uma quantidade mais variada de artrópodes, enquanto Squamata são mais comuns na dieta de lagartos de regiões temperadas (provavelmente pela presença de espécies de lagartos predadoras de tamanho de corpo maior). O tamanho do corpo foi positivamente correlacionado com maiores tamanhos de presa (mais eficientes energeticamente) e com herbivoria (fonte de comida alternativa e também digerem melhor as plantas). A hipótese prévia de que a dieta dos lagartos é basicamente predita pelos aspectos evolutivos foi corroborada, no entanto são sugeridas novas intepretações para estes padrões e ressalta-se a importância de outras características ecológicas como variáveis ambientais na modulação tanto de presas secundárias como primárias na dieta dos lagartos.

Keywords: habitos alimentares, squamata, sinal filogenético, pPCA, caracteres ecológicos

Abstract

The understanding of how both recent and historical factors can mold species ecological traits is crucial for elucidating ecological and evolutionary processes. Compiling a global dataset of dietary aspects of 722 populations of 323 lizard species (across 32 families), we tested the influence of phylogeny on dietary preferences of lizards in a worldwide scale, as well as its relationship with climate, foraging mode, habitat, distribution (tropical/temperate) and body size. Phylogenetic history was the major factor defining dietary preferences on lizards, accounting for 53.79% of total variation. We also found significant phylogenetic signal in prey ingestion on both univariate and multivariate analysis. Iguanian lizards eat more beetles and hymenopterans than non-iguanians. We suggest that iguanians evolved traits that facilitate the ingestion of these preys, while non-iguanians does not have these traits and tend to avoid them. Iguanians also seems to have adaptations that facilitate the development of strict herbivory. Non-iguanians lizards are usually from two groups: (1) those that feed on termites (especially desert species) or (2) feed on other energetic prey items (such as orthopterans, spiders and roaches). Also, we found evidence for significant climatic influence in dietary preferences, with litter fauna arthropods being more often found on the diet of lizards inhabiting wet/warmer climates. Cold resistant arthropods (beetles and millipedes) were also more ingested in colder climates. Termite ingestion (together with mites and mantids) was associated to seasonal warmer seasonal environments, such as deserts and arid areas, thus providing abundant food source on harsh environments. Herbivory was associated to seasonal environments, probably as an alternative source of food and water. Foraging mode was not a good predictor of dietary preferences, as they were only related to solpugids and mites (~ 3%), neither being primary prey categories. Habitat specialization also seems to predict specific secondary preys, especially on arboreal and semi-aquatic lizard species. Tropical lizards seems to ingest a wide variety of arthropods, while squamates are more ingested by temperate lizard species (probably due to the presence of larger body-sized lizards on temperate zones. Body size was positively correlated to larger prey groups (more energetic efficient) and herbivory (alternative food source and better plant digestion). We support the previous hypothesis that lizard species diet is mostly predicted by evolutionary history, providing interpretations for these patterns and highlighting the importance of other ecological traits as well as environmental variables also modulating the ingestion of both principal and secondary preys among lizard clades.

Keywords: feeding habits, squamata, phylogenetic signal, pPCA, ecological traits

Introdução:

As características ecológicas das espécies são cruciais para o entendimento de adaptação, plasticidade e evolução das mesmas. Inicialmente, acreditava-se que os principais fatores que definiam as características ecológicas das espécies eram as interações interespecíficas (dentro de uma escala temporal recente), principalmente predação e competição. Tal linha de pensamento persistiu por quase toda a segunda metade do Século XX e foi base para a explicação de estudos ecológicos dos mais diferentes táxons (Zaret & Rand 1971; Pianka 1973; Cody 1974; Lynch 1979). No entanto, a partir da década de 90, o desenvolvimento de métodos filogenéticos comparativos, possibilitou a descoberta de grandes divergências ecológicas entre os clados de determinados grupos, e a semelhança das mesmas entre espécies mais próximas evolutivamente (Cadle & Greene 1993; Losos 1996; Webb 2000) (Cadle & Greene 1993; Losos 1996; Webb 2000). Isto possibilitou a constatação de que certas características ecológicas de determinadas espécies eram na verdade resultado de uma história evolutiva, ao contrário do que se imaginava anteriormente. Hoje em dia, com o avanço destes estudos, está cada vez mais evidente que muito do que observamos nos nas características ecológicas das espécies possui reflexos da filogenia nos caracteres ecológicos que permitem ou limitam a coexistência das espécies (Kelt *et al.* 1996; Vitt & Pianka 2005; Helmus *et al.* 2007; Colston *et al.* 2010).

Existem duas hipóteses para explicar as diferenças ecológicas observadas nas espécies que compõem as comunidades, e ambas podem estar agindo concomitantemente. A primeira hipótese considera como fator determinante efeitos recentes, como disponibilidade de recursos, competição e predação. Estas características podem ocasionar a existência de divergências ecológicas (e.g., segregação de nicho) nas espécies que coexistem. Logo, as características ecológicas observadas seriam derivadas de fatores recentes, assim como as divergências nos nichos seriam resultado da interação entre as espécies. Esta hipótese é chamada de hipótese ecológica ("competition-predation hypothesis" ou "competition hypothesis"), e explica alguns resultados observados em comunidades biológicas (Morin 1983; Lenihan *et al.* 2011; Buchmann *et al.* 2012), assim como possui relação direta com outras teorias ecológicas, como a teoria do fantasma da competição passada (Connell 1980), princípio da exclusão competitiva (Hardin 1960) e da heterogeneidade de hábitat (e.g.: Benton *et al.* 2003). Além destas relações ecológicas, o ambiente é outro fator contemporâneo que pode exercer forte influência nos caracteres ecológicos das espécies. É conhecido que diferenças características estruturais ambientais e climáticas são muitas vezes fortes preditores da abundância e ocorrência de determinadas espécies dentro de uma microescala. Por exemplo, um recente estudo sobre efeito de borda na Amazônia apontou que diferenças microclimáticas foram excelentes preditores da abundância e riqueza de Mutilídeos, e que estas caracterísicas de microclima refletem bem as variações na estrutura do hábitat (Vieira *et al.* 2015). Numa escala global, o clima também pode ser um importante preditor de características ecológicas. Um estudo realizado considerando quase 300 espécies de lagartos aponta que o clima possui uma forte influência em características da história de vida deste grupo. Por exemplo, a precipitação é positivamente correlacionada com o número de ninhadas por ano, assim como lagartos de regiões tropicais tendem a ter ninhadas menores que aqueles de regiões temperadas (Mesquita *et al.* 2016).

A segunda hipótese sugere que determinadas divergências evolutivas resultam em características ecológicas que são mantidas até os dias atuais. Neste caso, se considera que as preferências de nicho que permitem a coexistência das espécies podem ser explicadas pela historia evolutiva das mesmas. Um exemplo prático seria o conservatismo de nicho (Wiens & Graham 2005), onde espécies tenderiam a apresentar características ecológicas ancestrais, logo, as espécies mais aparentadas tenderiam a apresentar maior semelhança em seus caracteres ecológicos, enquanto espécies mais distantes filogeneticamente apresentariam mais divergências. Esta segunda hipótese chama-se de hipótese histórica ("deep history hypothesis") e também serve de base para explicação de padrões ecológicos de diversos táxons, desde vertebrados (Kelt *et al.* 1996; Vitt & Pianka 2005), invertebrados (Helmus *et al.* 2010)(Helmus *et al.* 2010), e até mesmo bactérias (Horner-Devine & Bohannan 2006). Por exemplo, um estudo utilizando 196 espécies de serpentes de seis continentes diferentes demonstrou que 70% das variações do nicho alimentar entre os clados de serpentes foram explicadas por sete divergências na história evolutiva das serpentes (21% do total de clados) (Colston *et al.* 2010).

Répteis Squamata são excelentes modelos para estudos de grande escala que buscam as origens de características ecológicas, pois: (1) sua história evolutiva é datada entre o Jurássico e o fim do Triássico, no início das principais separações de massas de terra que originaram os atuais continentes (Evans 1988); (2) eles se diversificaram por todos os atuais continentes (Vitt *et al.* 2003); (3) eles ocupam uma gama diversificada de nichos ecológicos (Pianka 1973; Pianka & Vitt 2003; Vitt *et al.* 2003) e (4) são abundantes e fáceis de se manipular (Vitt *et al.* 2007). Há cerca de uma década, Vitt *et al.* (2003) observaram, com base em dados de várias regiões do globo, que diversas características ecológicas atualmente observadas em lagartos (proporção de espécies nas taxocenoses, dieta e uso de microhábitat) possuíam fortes divergências entre as espécies, e que suas origens estavam diretamente ligadas à história filogenética do grupo. Estas divergências no nicho ecológico teriam se originado durante a diversificação entre os dois grupos irmãos mais basais de Squamata, Iguania e

Scleroglossa, e em seguida, a separação de Scleroglossa em Gekkota e Autarchoglossa. Durante a primeira divergência, os Scleroglossa se modificaram da condição ancestral da captura da presa pela língua para a captura pela mandíbula, o que possibilitou um maior sucesso na alimentação. Na divergência entre Gekkota e Autarchoglossa, o sistema quimiosensorial se desenvolveu de modo diferente, assim como a língua. Os Gekkota se diferenciaram da condição ancestral (diurno) e se tornaram primariamente noturnos, com um sistema nasal olfatório bem desenvolvido e a língua com finalidade da limpeza ocular. Nos Autarchoglossa, o sistema vomeronasal se tornou bem desenvolvido, e a língua adquiriu um papel principal na discriminação química de presas. Esta discriminação provavelmente permitiu o desenvolvimento do forrageio ativo (condição ancestral: senta-espera) e um aumento na seletividade das presas, contribuindo para o seu sucesso em ambientes terrestres. Enquanto isto, os Iguania, com algumas exceções (e.g., Chamaleonidae), retiveram todas as características ancestrais de Squamata (hábito diurno, captura da presa pela língua, busca visual e forrageio senta-espera), logo, isto teria ocasionado a diversificação de Iguania para a utilização de estratos mais elevados no microhábitat (e.g., afloramentos rochosos e árvores). Na dieta, estas adaptações são refletidas na seleção de presas, sendo que os Scleroglossa parecem evitar presas com defesas químicas, como Coleoptera e Hymenoptera (principalmente formigas), que são as presas mais comuns na maioria dos Iguania. Além disto, os Scleroglossa se alimentam mais de presas de alto teor energético e que se encontram mais escondidas em geral, como Aranae e Orthoptera. Com isto, as adaptações de Scleroglossa parecem ter contribuído para o grande sucesso evolutivo e ecológico do grupo, visto que a proporção de espécies de Scleroglossa para Iguania em taxocenoses de Squamata é em geral sempre elevada (mesmo quando se desconsidera as serpentes). Tais comparações realizadas neste estudo consideraram a proposta filogenética baseada em dados morfológicos (Estes *et al.* 1988). No entanto, atualmente existem grandes divergências entre as propostas filogenéticas, mais especificamente entre as hipóteses moleculares e morfológicas (Estes *et al.* 1988; Townsend *et al.* 2004; Gauthier *et al.* 2012; Pyron *et al.* 2013). Logo, estas incongruências nas propostas filogenéticas podem alterar a explicações para os resultados observados no estudo de Vitt *et al.* (2003).

Em seguida, os mesmos autores realizaram um estudo com base nessas teorias, utilizando dados de dieta de 184 espécies de lagartos, dentre 12 famílias em quatro continentes (Vitt & Pianka 2005). Este estudo criou uma hipótese filogenética para as espécies utilizadas e observou com base em modelos nulos que a variação do nicho alimentar entre os clados era explicada por seis divergências (80% da variação total), e a maior variação (27% do total) foi encontrada exatamente na separação dos clados Iguania e Scleroglossa, e que estava relacionada com a quantidade de presas com proteção química, baixa em Scleroglossa e alta em Iguania (formigas, besouros e outros Hymenoptera), corroborando com seus resultados anteriores (Vitt *et al.* 2003). Como consequência, criou-se uma expectativa que de maneira geral, os padrões ecológicos dos lagartos refletissem essas fortes divergências ecológicas explicadas pela história evolutiva no seu padrão de uso de recursos. No entanto, recentes estudos na região Neotropical apontam que os efeitos filogenéticos não foram fatores preditores do padrão de uso de recursos por lagartos em taxocenoses locais (Werneck *et al.* 2009; Garda *et al.* 2013). Ainda (na maioria dos casos), em alguns eixos do nicho ecológico (e.g., uso de microhábitat e dieta), não foi observado segregação do mesmo entre as espécies (Mesquita *et al.* 2006a; Mesquita *et al.* 2006b; Werneck *et al.* 2009). Junto a este fato, recentes estudos filogenéticos com base em análises moleculares vêm demonstrando uma grande incongruência com a hipótese filogenética morfológica (Estes *et al.* 1988; Townsend *et al.* 2004; Gauthier *et al.* 2012; Pyron *et al.* 2013). O mais recente estudo, considerando mais de 4000 espécies de Squamata, e com base em 12 marcadores moleculares aponta algumas divergências do modelo "clássico" Iguania-Scleroglossa, comum em estudos morfológicos (Gekkota surge como grupo irmão dos antigos Autarchoglossa e Iguania, e Anguimorpha surge como grupo irmão de Iguania) (Pyron *et al.* 2013). De contrapartida, um estudo igualmente recente (Gauthier *et al.* 2012), baseado em análises de cerca de 940 sinapomorfias de mais de 600 fenótipos de 192 espécies de Squamata (51 extintas e 141 atuais), obtiveram resultados que corroboram com as propostas morfológicas mais antigas (Estes *et al.* 1988). Além disso, as diferentes topologias provindas das filogenias com base em dados moleculares permitiram reinterpretações da evolução de determinadas características ecológicas. A alta ingestão de formigas (Formicidae) pelos Iguania, por exemplo, poderia estar mais relacionada com a congruência entre a diversificação concomitante dos dois grupos de organismos do que por segregação de nicho (Sites Jr *et al.* 2011).

Estas recentes mudanças na filogenia podem alterar substancialmente os resultados observados anteriormente nos aspectos ecológicos dos lagartos, visto que as explicações sugeridas pelos autores estão intrinsecamente baseadas nas propostas filogenéticas morfológicas para Squamata (Vitt *et al.* 2003; Vitt & Pianka 2005). Por fim, a aplicação de recentes técnicas para acessar a informação filogenética contida nas características ecológicas das espécies também pode auxiliar na resolução de como e a que nível, estas forças históricas realmente interferem nos padrões ecológicos. Ainda, em último caso, pode auxiliar na resolução das divergências de resultados entre os padrões ecológicos observados em taxocenoses de lagartos locais e o padrão global sugerido para os principais grupos de Squamata. Logo, se faz necessária a obtenção de dados ecológicos do maior número espécies de regiões do mundo todo (a fim de representar o maior número possível de famílias), possibilitando uma melhor análise destes padrões. Ainda, a execução de análises da influência histórica com base nas novas propostas filogenéticas para Squamata por meio de métodos mais sofisticados, assim como a análise de fatores ecológicos em conjunto, podem ser aspectos essenciais para confrontar possíveis diferenças dos resultados observados anteriormente das características ecológicas dos lagartos observadas nos dias atuais.

Dentro deste contexto, esta tese está estruturada em dois capítulos (com um apêndice suplementar auxiliar), intitulados:

Capítulo 1: Tracking the Global Patterns on the Dietary Niche of Lizards: Recent Approaches and New Interpretations.

Este manuscrito tem por entender como os fatores climáticos, caracteres biológicos e a história evolutiva estão influenciando as preferências alimentares de lagartos, a partir de dados de dieta de lagartos de todo o globo e com o uso de técnicas filogenéticas comparativas. Sugestão de revista para submissão: Global Ecology and Biogeography ISSN: 1466-8238

Capítulo 2: Myrmecophagy in Lizards: Evolutionary and Ecological Implications.

Este manuscrito tem por entender como evoluiu a mirmecofagia em lagartos e como a biológia das espécies junto aos fatores ambientais estão moldando os padrões de ingestão de formigas pelos lagartos nos dias, igualmente a partir de dados de dieta de lagartos de todo o globo e com o uso de técnicas filogenéticas comparativas. Sugestão de revista para submissão: Ecology Letters ISSN: 1461-0248

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TRACKING THE GLOBAL PATTERNS ON THE DIETARY NICHE OF LIZARDS:

RECENT APPROACHES AND NEW INTERPRETATIONS

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Abstract

The understanding of how both recent and historical factors can mold species ecological traits is crucial for elucidating ecological and evolutionary processes. Compiling a global dataset of dietary aspects of 722 populations of 323 lizard species (across 32 families), we tested the influence of phylogeny on dietary preferences of lizards in a worldwide scale, as well as its relationship with climate, foraging mode, habitat, distribution (tropical/temperate) and body size. Phylogenetic history was the major factor defining dietary preferences on lizards, accounting for 53.79% of total variation. We also found significant phylogenetic signal in prey ingestion on both univariate and multivariate analysis. Iguanian lizards eat more beetles and hymenopterans than non-iguanians. We suggest that iguanians evolved traits that facilitate the ingestion of these preys, while non-iguanians does not have these traits and tend to avoid them. Iguanians also seems to have adaptations that facilitate the development of strict herbivory. Non-iguanians lizards are usually from two groups: (1) those that feed on termites (especially desert species) or (2) feed on other energetic prey items (such as orthopterans, spiders and roaches). Also, we found evidence for significant climatic influence in dietary preferences, with litter fauna arthropods being more often found on the diet of lizards inhabiting wet/warmer climates. Cold resistant arthropods (beetles and millipedes) were also more ingested in colder climates. Termite ingestion (together with mites and mantids) was associated to seasonal warmer seasonal environments, such as deserts and arid areas, thus providing abundant food source on harsh environments. Herbivory was associated to seasonal environments, probably as an alternative source of food and water. Foraging mode was not a good predictor of dietary preferences, as they were only related to solpugids and mites (~ 3%), neither being primary prey categories. Habitat specialization also seems to predict specific secondary preys, especially on arboreal and semi-aquatic lizard species. Tropical lizards seems to ingest a wide variety of arthropods, while squamates are more ingested by temperate lizard species (probably due to the presence of larger body-sized lizards on temperate zones. Body size was positively correlated to larger prey groups (more energetic efficient) and herbivory (alternative food source and better plant digestion). We support the previous hypothesis that lizard species diet is mostly predicted by evolutionary history, providing interpretations for these patterns and highlighting the importance of other ecological traits as well as environmental variables also modulating the ingestion of both principal and secondary preys among lizard clades.

Keywords

feeding habits, Squamata, phylogenetic signal, pPCA, ecological traits

Introduction

The understanding of which factors directly affects species ecological traits is crucial for researches in ecology. Previously, scientists believe that the major factors defining ecological traits were interspecific iterations (in a recent scale), especially predation and competition. A plenty of ecological studies corroborated this idea, thus generating many important ecological theories, such as the “ghost of competition past”, “competitive exclusion principle” and “habitat heterogeneity theory” (Morin 1983; Lenihan *et al.* 2011; Buchmann *et al.* 2012). Such approach persisted throughout the second half of the 20th century, and was the basis for many ecological studies among different taxa (Zaret & Rand 1971; Pianka 1973; Cody 1974; Lynch 1979). Nevertheless, during the 90s, the fast development of comparative phylogenetic methods allowed more detailed analysis of similarities and divergences among clades and closely related species (Cadle & Greene 1993; Losos 1996; Webb 2000). With the development of these studies, it is even clearer that many observed ecological aspects are reflections of historical phylogenetic effects (Kelt *et al.* 1996; Vitt & Pianka 2005; Helmus *et al.* 2007; Colston *et al.* 2010). For instance, considering these historical influences, we can highlight the phylogenetic niche conservatism, where some species tend to possess ancestor biological traits (Wiens & Graham 2005). Within these, closely related species under these conditions are expected to present similarities on their ecological traits than to more evolutionarily distant ones.

In the last decade, Vitt *et al.* (2003) investigated a multicontinental dataset of lizards’ ecological traits and suggested strong historical influence bounded to the major divergences they found on species traits. They stated that these ecological niche divergences had been originated during the diversification of the two major basal groups of Squamata between Scleroglossa and Iguania and after between

Autarchoglossa and Gekkota (based on morphological phylogenetic hypothesis for squamates, see Estes *et al.* 1988). The development of an efficient chemosensory system (vomeronasal apparatus on autarchoglossans and olfactory system on gekkotans) and the shift from lingual prey capture to a jaw prehension (Cooper 1995) should have permitted the scleroglossans to easily access preys that were previously more difficult to access (cryptic and sedentary), promoting a higher prey selectivity due to chemical discrimination (Cooper Jr 1994, 1995; Vitt *et al.* 2003). The accessibility of new prey' types was even more conspicuous on the autarchoglossans, due to the shift from an ambush sit-and-wait foraging mode into an active one. Iguanians, however, retained mostly of ancestral traits: lingual prey prehension, sit-and-wait foraging mode and visual prey discrimination (Cooper Jr 1994, 1995; Vitt *et al.* 2003). As a consequence, these lizards usually presents a diet with larger amounts of high mobile preys (often with noxious chemicals) such as coleopterans and hymenopterans (mostly ants), avoided by most active foragers (Huey & Pianka 1981; Vitt *et al.* 2003; Vitt & Pianka 2005). All the synapomorphies of autarchoglossans would make them better competitors than iguanians on terrestrial habitats, what could have driven the latter to an exploration of more vertical habitats, such as rocky outcrops and trees to avoid competition (Vitt *et al.* 2003).

Later, they corroborated these propositions performing a study using dietary information of 184 lizard species from 12 families from four continents (Vitt & Pianka 2005). They observed that six major divergences explained near 80% of total variation on diet among clades. Besides, the divergence with higher variation explained (27%) was in the dichotomy Scleroglossa and Iguania (considering the morphological phylogenetic hypothesis), segregating into dietary preferences. This variation was mostly associated to the iguanian diets with higher amounts of Coleoptera, Formicidae and other Hymenoptera compared to scleroglossans. Nevertheless, recent phylogenetic hypotheses for squamates based on molecular data are incongruent with the classic morphological hypotheses (Townsend *et al.* 2004; Vidal & Hedges 2009; Pyron *et al.* 2013). Moreover, Iguania is considered to be derived rather than ancestral on the molecular hypothesis, which can change drastically how we interpreted the evolution of dietary associated biological traits between the major groups of Squamata. Recently, researchers have already considered new insights reinterpreting the evolution of traits in squamates considering the new molecular-based phylogenies (Sites Jr *et al.* 2011). For instance, they suggest that high Formicidae ingestion on Iguania can be related to the congruent time of divergence of both groups.

Nevertheless, not only feeding related biological traits can be associated to dietary niche on lizards. Other biological traits, such as body size and habitat preferences can be directly related to dietary preferences in lizard species. It has been observed that larger lizards ingests larger preys, probably to acquire energy from food sources more efficiently (Costa *et al.* 2008b). Also, plant consumption is often associated to an increasing in body size for lizards (Pough 1973; Cooper Jr & Vitt 2002). Larger herbivore lizards should be more common than smaller ones because of the longer digestion period (helping plant matter absorption) plus as a complementation of energetic needs (in omnivores). Habitat preferences can also be related to diet in lizards. On desert communities, termites and ant brood are more associated to the diet of fossorial lizard species, as these preys are often found on soil fauna (Abensperg-Traun & Steven 1997). Also, some neotropical termite specialist geckos lives inside termitarias, using them as shelter, foraging site and for thermoregulation (Colli *et al.* 2003; Vitt *et al.* 2007a).

Besides both phylogenetic and biological traits roles on lizard' dietary aspects, recent factors such climatic variables could also exert significant influence on the ecology of lizards. It is know that structural habitat characteristics in a microscale are good predictors of occurrence and abundance of lizard species (Vitt *et al.* 2007b; Garda *et al.* 2013). Climate is also a very important predictor on global patterns of lizard life history traits (seasonality reduces the number of clutches per year while increases number of eggs per clutch; Mesquita *et al.* 2016). Also, climate characteristics seem to affect lizard diet as well. It has been observed in Australia that termite ingestion by lizards increases from mesic to xeric environments (Abensperg-Traun 1994), as these preys are a quite abundant food source on these harsh areas, such as deserts. Herbivory has also been positively associated to arid, seasonal environments, as food scarceness and water requirements would drive lizards to exploit new food sources, such as plant material (Cooper Jr & Vitt 2002; Pietczak & Vieira 2017). Moreover, warmer areas should also favors herbivory as it would facilitate plant digestion (Zimmerman & Tracy 1989).

In this study, we test the following hypotheses: (1) Major divergences on Squamata clades reflect on dietary divergences among lizard species (phylogenetic dependent dietary niche). Prediction: iguanians ingest higher rates of coleopterans and hymenopterans; (2) dietary preferences are correlated to foraging mode, habitat, distribution and body size. Predictions: ingestion of high mobile prey is higher in sit-and-wait ambushers lizards/fossorial lizards ingest higher rates of termites/herbivory is higher in tropical lizards/larger lizard species ingest higher rates of larger prey groups and/or plant matter; (3) Dietary preferences are correlated to climatic variables. Prediction: termite and/or plant matter ingestion is higher in seasonal/dry/warm environments.

Materials and Methods

Dietary database and data collecting

We compiled data from a total of 722 populations of 323 lizard species, sampling 29 families from all continents except Antarctica (Figure 1, Appendix Table 1). Dietary data were obtained from two major sources. (1) Bibliographic searches of online scientific databases from Google Scholar™ and Zoological Record™. We used the keyword “lizard” together with the following keywords: “diet”, “feeding habits”, “feeding ecology”, “dietary aspects” within the year range of 1900 to 2015. (2) Personal data collect by all authors during the last four decades.

We used data from direct observation of stomach contents, fecal analysis and even observations. In each observed population, four variables were calculated: occurrence (number of individuals ingesting a given prey category), number, volume and mass of prey. Whenever data were separated into ontogenetic and/or sexual categories (e.g.: juvenile/adults, males/females), we calculated weighted averages for each prey category using sample sizes as weights. We also recalculated percentages to remove unidentified prey or to combine prey categories, in order to standardize our data set. With respect to data that we collected, diet analysis was performed by direct observation of prey items in lizard stomachs. We dissected all specimens and removed their stomachs for analysis under a stereomicroscope. We identified and categorized each prey item. For each prey category, we calculated absolute and relative occurrence, number and volume (mm^3). To calculate volume, we measured width and length from each intact prey using an electronic calliper (0.01 mm) and then applied the following ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right) \times \left(\frac{w}{2}\right)^2,$$

where l is the prey length and w is the prey width. After collecting data, we performed weighted averages for each prey category to combine populations from a given species using sample sizes of each population as weights. Finally, we estimated volumetric values for populations where volume data was missing, using linear equations based on the relationship between occurrence and volume from species containing both kinds of data. We choose occurrence as an estimator of volume because this variable is not influenced by prey raw numbers in lizard diets. Finally, we used volumetric percentages of ingestion for each prey category to test the hypotheses that we present. We found a total of 61 prey categories, mostly arthropods (Table 1).

Ecological and climatic variables

We assembled a dataset for the following variables for each population that we sampled: Latitude and Longitude (on decimal degrees), foraging mode (active or sit-and-wait), maximum SVL (in mm), and habitat (arboreal, semi-arboreal, bromelicolous, terrestrial, fossorial, semi-aquatic and saxicolous). Data for these same variables were extracted from bibliographic sources that included dietary data or supplemented by database papers and/or species description papers. Climatic predictors were generated for 19 climatic variables from *Worldclim* (Hijmans *et al.* 2005). To avoind using high number of climatic variables, most of them higly correlated, we scaled the variables and then performed a principal components analysis (PCA), using the canonical axis that accounted most of the total variation. We extracted the first two canonical axes from temperature and precipitation variables. Temperature principal components together explained 99% of data total variation. TEMP1 was positively correlated with seasonality and negatively correlated to high temperatures, representing a gradient of stable warm climates to colder seasonal ones. TEMP2 was positively correlated with isothermality and negatively correlated to high temperatures, representing a gradient of warm seasonal climates to stable colder ones. Precipitation principal components explained together 96% of all variation. PREC1 is positively correlated to precipitation seasonality while negatively correlated with total precipitation, representing a gradient of wet and stable climates against dry seasonal ones. PREC2 is positively correlated to precipitation seasonality on wet months, thus demonstrating a gradient of wet stable climates to seasonal climates but presenting high precipitation values during rainy season. We then used these four climatic variables for conducing the following analysis describe below (see second paragraph from next section).

Statistical Analysis

To test for phylogenetic signal on each prey category, we used K statistics from the *phytools* package for R (Revell 2012). We also performed the multivariate phylogenetic signal (K-mult, Adams 2014) using the *geomorph* package for R (Adams & Otárola-Castillo 2013) to access phylogenetic signal considering the entire dietary dataset. We used a phylogenetic tree of sampled species containing branch lengths and a matrix containing prey type ingestion percentages for each sampled species and prey categories. Values near zero for K indicate phylogenetic independence of data while values near 1 indicate that a given character follows a Brownian Motion (BM) evolutionary model (Freckleton *et al.* 2002; Blomberg *et al.* 2003; Losos 2008). $K > 1$ indicates that closely related taxa are more similar than expected in a BM model. Posteriorly, we tested for significance on phylogenetic signal (null hypothesis $K = 0$) based on randomizations species names in the phylogeny using likelihood relationships tests (Blomberg *et al.* 2003). The phylogeny used for this test was extracted from Pyron *et al.* (2013).

To account for historical and recent effects on dietary preferences, we performed a phylogenetic principal component analysis (pPCA) (Jombart *et al.* 2010) using the dietary data from all sampled species. Phylogenetic principal component analysis (pPCA) (Jombart *et al.* 2010) is a multivariate method that correlates a phylogenetic tree containing branch lengths with a set of ecological traits (dietary) for each species found in an given pool and then tests for phylogenetic autocorrelation (Gittleman & Kot 1990), which is dependency of a given trait value due to phylogenetic lineages. A positive phylogenetic autocorrelation indicates similarities among close taxa for a given trait, while negative phylogenetic autocorrelation indicates divergences among close taxa. The pPCA summarizes the patterns of phylogenetic autocorrelation, identifying principal components representing the highest phylogenetic correlation (historical influence, global structure) and the lowest phylogenetic autocorrelation (recent influence, local structure). Then, we can access the global and local structure scores to identify which traits (variables) and which taxa are involved. For phylogenetic relationships, we used a phylogenetic tree based on a recently published phylogeny hypothesis for Squamata using molecular markers (Pyron *et al.* 2013)containing the sampled species.

To test for the influence of climatic variables and ecological traits on prey type's ingestion, we built ordinary least squares models (OLS). We also built phylogenetic regression models using phylogenetic generalized least squares models (PGLS) (Grafen 1989). To implement PGLS models, we created covariance matrices based on Brownian Motion expectations from a phylogenetic tree of sampled species extracted from Pyron *et al.* (2013). These models remove the effect of evolutionary history thus providing data independency. Phylogenetic regressions were performed with the *ape* package for R (Paradis *et al.* 2004).

We conducted all statistical analyses using R version 3.4.3 (R Development Core Team 2017) with a significance level of 5% to reject null hypotheses. Means are presented ± 1 SD.

Results

We found a total of 61 prey categories (Table 1) on the 323 lizard species we sampled. The most frequent ingested preys were Coleoptera, Aranae, Orthoptera, Hemiptera and insect larvae, all of them being ingested in any amount by approx. 80% of all sampled species.

Phylogenetic signal and historical effects on diet

Univariate phylogenetic signal test indicated significant phylogenetic signal in many prey groups ingestion (Table 2). Multivariate phylogenetic signal was also significant, indicating phylogenetic dependency on lizards' dietary aspects (K-mult = 0.357, $p = 0.01$). These results provide evidence of deeply rooted influence of evolutionary history on the dietary preferences of lizards. The phylogenetic principal component analysis (pPCA) indicated two global axes explaining most variation of observed data. Both principal components contained the highest values of positive phylogenetic autocorrelation (similarities among close related species) explaining 53.79% of total variation. First global axis explained 29.26 % of variation while the second global axis explained 24.53 % of total variation. The prey categories determining the first global axis were plant, Formicidae (major) and Isoptera, Hymenoptera, Coleoptera (lesser) (positive scores; black circles, Figs. 2 and 3); and Aranae, Orthoptera, Blattodea, Insect larvae and Squamata (negative scores; white circles, Figs. 2 and 3). The prey categories determining the second global axis were a constrast between Isoptera (major), Insect larvae, Coleoptera (lesser) (positive scores; black circles, Figs. 2 and 3); and plant material, Aranae, Orthoptera, Blattodea, Squamata (major), Hymenoptera and Formicidae (lesser) (negative scores; white circles, Figs. 2 and 3).

Relationship between diet vs. climatic variables

The results from both PGLS and OLS regression presented significant relationships between the ingestion of certain prey groups by lizards and climatic variables, suggesting a relationship between climate and dietary preferences (Table 3). Prey groups negatively related to TEMP1 (hot, stable temperatures) were Blattodea, Mollusca, plant material and Trichoptera, while those positively related (colder, variable temperatures) were Coleoptera, Gastropoda and Hemiptera. Prey groups negatively related to TEMP2 (hot, variable temperatures) were Acari, Isoptera and Mantodea, while those positively related (colder, stable temperatures) were Diplopoda and plant material. For precipitation climatic variables relationships, prey groups negatively related to PREC1 (wet, stable precipitation) were Blattodea, Gastropoda, Hemiptera, Mollusca, Opiliones, Orthoptera and Trichoptera, while the only positively related (dry, seasonal precipitation) was plant material. Prey groups negatively related to PREC2 (wet, stable precipitation) were Hymenoptera, Thysanura and Trichoptera while those positively related (seasonal climates with high precipitation on wet season) were Hemiptera and Orthoptera. These results suggest that the ingestion of certain prey itens is associated to specific climatic patterns, from both temperature and precipitation.

Relationship between diet vs. foraging mode, habitat, distribution and body size

The regression results of both PGLS and OLS presented significant relationships between the ingestion of certain prey groups by lizards and ecological variables, thus suggesting a relationship between ecological traits and dietary preferences (Tables 4, 5 and 6). For foraging mode analysis, only two preys presented significant differences in ingestion on PGLS: Acari and Solifuga, both more ingested by active foraging lizards (Acari: 0.31 ± 1.66 *vs*. 0.21 ± 0.86 and Solifuga: 0.34 ± 1.85 vs. 0.24 ± 0.98; active foragers and sit-and-wait ambushers, respectively). Considering habitat type, prey groups that presented significant relationship in ingestion on PGLS were Amphibia, Amphibia eggs, Anura, Aves, Chelonia, Crustacea, Embioptera, Odonata, Orthoptera, Phasmatodea and Plecoptera (Table 5), suggesting a high ingestion of certain preys on arboreal habitats (Aves, Phasmatodea), bromeliads (Anura, Orthoptera) and aquatic environments (Crustacea, Odonata, Embioptera and Plecoptera). Considering distribution (temperate/tropical), prey groups that presented significant relationships in ingestion on PGLS were Blattodea, Chilopoda, Hymenoptera, Orthoptera, reptile eggs and Squamata (Table 6), where tropical lizards ingests higher values of Blattodea, Chilopoda, Hymenoptera, Orthoptera and reptile eggs while temperate lizards ingests higher values of Squamata. Finaly, PGLS analysis pointed prey groups that presented significant positive relationship with body size, which were: Amphibia, Amphibia egg, Chelonia, Crustacea, Diplopoda, Embioptera, Gastropoda, Mammalia, plant material, Plecoptera, reptile egg and Vertebrata, while negative relationship between ingestion and body size was only significant in Hemiptera. These results suggest that larger lizards ingest larger prey sized groups and herbivory, as with few exceptions, most of these preys are vertebrates and/or invertebrates with large species representatives.

Discussion

Evolutionary history and diet

Evolutionary history plays a major role on defining the dietary niche on lizards. Both results based on phylogenetic signal and pPCA indicated the presence of phylogenetic roots on the dietary variation among lizards. This result is in agreement with all previous studies concerning the global arrangement of lizards' dietary aspects (Vitt *et al.* 2003; Vitt & Pianka 2005), even using diferent phylogenetic hypothesis. Nevertheless, new analysis has enabled us to reconsider some interpretations, especially the major hypothesis around the dietary shift between iguanian and non-iguanian lizards. In general, predacious iguanians seem to have preferences for high mobility preys that often contain noxious chemicals, such as hymenopterans (especially ants) and beetles (Vitt *et al.* 2003; Vitt & Pianka 2005), and our results corroborate this statement. This has been often associated to their ecological traits, such as foraging mode (sit-and-wait), prey discrimination (mostly visual) and lingual capture (Huey & Pianka 1981; Schwenk 2000; Schwenk & Wagner 2001).

Previously, Iguania clade was considered to retain ancestral states when compared to scleroglossans (on classic morphological data based Squamata phylogenies; See Estes *et al.* 1988), and this divergence between dietary aspects from both groups was related to the avoidance of noxious preys and higher accessibility to other sedentary, cryptic prey types by scleroglossan lizards, promoted by several synapomorphies (i.e.: both visual and chemical prey discrimination, jaw prey capture and active foraging mode on autarchoglossans) (Schwenk 2000; Vitt *et al.* 2003; Vitt & Pianka 2005). This combination of iguanian traits (or the lack of scleroglossan ones) would lead to a diet with larger amounts of these high mobile, noxious preys on Iguania. However, last decade studies reconstructing Squamata phylogenies based on molecular data points Iguania as a more derived clade, instead of ancestral (Townsend *et al.* 2004; Vidal & Hedges 2009; Pyron *et al.* 2013). This ancestor-derived shift allowed new hypotheses for theses dietary observations, as iguanian traits once considered to be ancestral are now treated as derived. Sites Jr *et al.* (2011) suggests that the ingestion of ants on Iguania can be explained by the close diversification period of both iguanians and Formicidae from Cretaceous to Eocene, so iguanians could have evolved to prey upon ants, instead of an inability to access other prey.

The same idea can be applied to explain the ingestion of beetles and other hymenopterans. Personal data also support this idea (Chapter II), as ant specialist lizards are strictly iguanians, plus the only non-iguanian clade that presents a higher ingestion of ants (lacertids) is from an region (Europe) were iguanian, possible competitors, are almost absent. It is important to highlight that both situations can overlap. It is expected that non-iguanians with chemical discrimination of preys should avoid undesirable prey items (i.e.: Moreno-Rueda *et al.* 2017) as they should forage for high energetic prey (Vitt *et al.* 2003). Nevertheless, we suggest that cause-effect relationship around the higher presence of beetles and hymenopterans on iguanians can have other origins (i.e.: evolutionary adaptations to feed on these preys) rather than only an inability to access sedentary and cryptic preys. For instance, territoriality (more conspicuous on iguanians) and lingual prehension of preys could facilitate the defense of foraging sites (i.e.: hymenopteran nests) and the manipulation of high mobile small preys. In addition, these suggestions are roughly speculative and needs more studies.

On Iguania, we also observed the higher importance of plant ingestion. Although most omnivorous species are not in Iguania clade, all strict/frequent herbivore families are iguanians (Iguanidae and Liolemidae) plus plant ingestion in this clade is higher than in others (Cooper Jr & Vitt 2002; Espinoza *et al.* 2004; Pietczak & Vieira 2017). Also, almost no other species possess morphological and physiological adaptations (i.e.: intestinal flora, colic valves) to herbivory than iguanids (Iverson 1982; Cooper Jr & Vitt

2002). Depistes this older evolutionary background, herbivory has also evolved more recently on island lizards, such as the teiid *Cnemidophorus murinus* (Dearing & Schall 1992)

Concerning the historical influence on the diet of non-iguanian lizards (and some representatives of iguanian Dactyloidae family), they can be separated into two sets: (1) termite eaters and (2) “other prey” eaters (orthopterans, roaches, spiders, squamates and larvae). Many gekkotans (some gekkonids, mostly diplodactylids) and non-mabuyinae skinks have a strong association to termite feeding. More interesting, almost all these species are from subtropical deserts. This pattern was already observed by Vitt *et al.* (2003). Termites are known to be very important on the dietary niche structure of desert lizard assemblages (Pianka 1986), with the presence of some species specialized into feeding on them (i.e.: *Ctenotus* spp., Scincidae; Pianka 1969). It seems that in lizard assemblages from these harsh environments, termite feeding influence is not only quite important nowadays, but had also been deeply rooted on the evolutionary history of desert non-iguanian lizards, molding even the dietary preferences of entire families (i.e: Diplodactylidae).

With the exception of squamates (more confined to larger species of lizards, i.e.: Varanoidea clade), all other preys (roaches, spiders and larvae) are very common on most non-iguanian lizards (and Dactyloidae), and are indeed more cryptic, sedentary preys especially during daylight. Within these, active foraging lizards can rely on chemical discrimination to find these preys more easily. In addition, most of these preys items seems to be highly energetic (Slobodkin 1962), corroborating the theories proposed for prey preferences on active foragers (Vitt *et al.* 2003; Vitt & Pianka 2005). Although gekkotans foraging mode (sit-and-wait ambushers) seems to contrast this idea, most of these preys that are hidden during daylight are actually active at night (most geckos are nocturnal), so their high mobility at geckos' activity period should facilitate prey detection. As a whole, it is clear that most dietary divergences observed on lizard species nowadays have deep evolutionary origins, as observed from other studies from the last decades (Cooper Jr & Vitt 2002; Vitt *et al.* 2003; Vitt & Pianka 2005). Most of this variation can be associated to divergences to morphological, physiological and behavioral differences among clades, especially (1) foraging mode, (2) prey capture apparatus and (3) prey discrimination. However, the link between the actual scenery to the phylogenetic history that originated this framework of lizards' dietary preferences and how these traits evolved it is still very blurred. Probably, focusing on the study of these traits with both anatomic and embryonary development studies in a wide range of species/clades could be a keypiece for further considerations on these matters.

Relationship between diet vs. climatic variables

Climatic variables seem to predict the ingestion of at least 15 prey types in lizards. Prey groups associated to hot, stable and wet areas (tropical forests) were Blattodea, Mollusca and Trichoptera which are common organisms in many communities from tropical forested environments (Barker 2001; Bell *et al.* 2007; De Moor & Ivanov 2008). Roaches usually lives on leaf litter, which is an important element for many lizards of tropical forests to forage for food (Bell *et al.* 2007). Molluscs and caddisflies are both highly associated to water (Barker 2001; De Moor & Ivanov 2008), so they are expected to be more abundant on wet areas, reflecting on their presence on lizards' diet that occur on these conditions. Coleopterans and diplopods ingestion was more associated to colder environments (beetles were also associated to seasonality while millipedes to stable ones). Both these arthropods are quite common in harsher, colder environments (Sinclair 1999; Kime & Golovatch 2000; Golovatch & Kime 2009). Besides, some beetles have both physiological and morphological apparatus to resist cold (Sinclair 1999). Within these, they could be suitable preys for lizards were other arthropods are absent due to thermal conditions. Gastropods and hemipterans were also more common on the diet of lizards from colder places, but were also associated to wet areas as well. Terrestrial gastropods are known to be also abundant in temperate biomes (Solem 1984; Barker 2001). Yet, they are still very associated to water and wet areas, such as many hemipterans (both larval and adult stages, Schuh & Slater 1995; Polhemus & Polhemus 2008). Acari, Isoptera and Mantodea were preys related to warm environments with thermal seasonality, such as subtropical deserts, savannahs and semiarid areas.

The relationship of lizards' termite ingestion with climate has already been studied on Australia (Abensperg-Traun 1994). The results were somehow similar to present study, were termite ingestion decreases from arid to mesic zones (Abensperg-Traun 1994). As cited before, termites are one of the key elements on the trophic structure of desert lizard assemblages (Pianka 1986). Plus, some studies on deserts and other seasonal environments points that termite diversity seems to predict (or covariate with) lizard diversity (Morton & James 1988; Colli *et al.* 2006; Costa *et al.* 2008a). All these findings, together with the high importance of evolutionary history on termite feeding (see above) puts the ingestion of these preys in a mix of both recent and historical influence. Mites are also an important element of microarthropod soil fauna in desert communities (Crawford 1981), thus being potential preys for desert lizards. Mantids are also known to inhabit warm seasonal zones all around world, but there is little information about them (Crawford 1981), making difficult to achieve more elucidations of why they are more present on the diet of lizards inhabiting these environments. Plant material ingestion had also relationship with many climatic variables and is in line to what has been previously proposed. It has been long suggested that herbivory in lizards is associated to warm, dry and seasonal climates for a couple of reasons: (1) warmer environments would facilitate plant digestion (Pough 1973; Cooper Jr & Vitt 2002) and (2) dry/seasonal environments would drive herbivory as a complement for the scarceness of other food types and to fulfill metabolic water needs (Cooper Jr & Vitt 2002; Pietczak & Vieira 2017). We found that herbivory is indeed associated to dry areas with seasonal precipitation, but they are related to both cold and warm climates as well. This is not a surprising result, considering that some lizards from colder climates are almost strictly herbivores (i.e.: liolemids, Espinoza *et al.* 2004). So, it is probable that herbivory in lizards from dry seasonal environments is higher due to water needs and alternative food source and temperature is not a restricting factor of herbivory.

Finally, orthopterans, harvestmen, thysanurans and non-ant hymenopterans are all associated to wet areas with stable precipitation (mostly forest environments). With few exceptions, all these arthropods groups have species that are common in the litter fauna of humid areas (Specht 1988; González & Seastedt 2000), an already cited foraging site for forest lizards (Scott Jr. 1976). In conclusion, climatic variables can predict the ingestion of both main and secondary prey items on lizards' diet. From 15 preys associated to climate, six were among those from the two pPCA axes. Besides these results, it is still pretty clear that evolutionary history is the major predictor of lizard dietary aspects. However, climatic variables can act as maintainer factors of the ingestion of certain prey types, making the influence of nowadays factors on lizards' diet also present.

Relationship between diet vs. foraging mode, habitat, distribution and body size

It has been long hypothesized that foraging mode has many consequences on the trophic niche of species. In general, sit-and-wait foragers would feed on more mobile, active preys (Huey & Pianka 1981; Cooper Jr 1995). Considering active foragers (which can search more efficiently for their food), they would tent to ingest more sedentary prey, with better energetic content and palatability (Cooper Jr 1994, 1995; Vitt *et al.* 2003). Nevertheless, from mostly of our 61 prey categories, only two presented different rates of ingestion between foraging modes (Acari and Solifuga). These are both arachnids and are more often on active foragers' diet, which is expected. As many species of these preys are usually hidden during daylight, they are expected to be more ingested by active foraging lizards than to sit-and-wait ambushers. However, mites and sun-spiders are not very common preys in a global perspective. They are found on less than 30-12% of lizard species we sampled (Acari and Solifuga, respectively). Within these, we can assume that foraging mode is not a good predictor of dietary preferences on lizards, despites the majority of previous studies contrasting these findings (i.e.: Cooper Jr 1995). This can be happening for two reasons. The major one is that dietary aspects of lizards are very explained by phylogeny, as well as foraging mode. Gekkota and Iguania clade are majorly sit-and-wait predators, while all the other clades are more prone to an active foraging mode (Perry 1999; Pianka & Vitt 2003). Within this, removing the effects of evolutionary history when performing foraging mode vs. dietary preferences analysis can cause a high loss of variation. Our OLS results corroborate this proposition. When not accounting for phylogeny, many important prey items shows significant difference between active and sit-and-wait foraging (ants and other hymenopterans are higher on sit-and-wait foragers while spiders and roaches more common on active foragers). The second reason is that most of lizard preys are arthropods, and these taxa are very ecologically diversified. Arthropods (especially insects) are indeed very diverse, and they have a plenitude of different behaviors, activity periods and other ecological aspects (Speight *et al.* 1999; Price *et al.* 2011). Along with this fact, the majority of dietary studies on lizards identify prey items until order taxonomic level. It is possible that order taxonomic level could not be efficiently accurate to access the relationships between foraging mode and dietary preferences, as it can lower the resolution of ecological divergences among ingested invertebrates. Nevertheless, most of lizard studies (as well as other taxa) uses order as a standard when accounting for prey categories on dietary ecology researches (i.e.: Pianka 1973; Pianka 1986; Vitt *et al.* 1999; further information, see appendix 1), and it has already been used with confidence since decades, so it is probably an adequate identification method, at least for comparison purposes.

Habitat preferences are related to the ingestion of a set of prey categories, according to our results. Most of these differences are associated to aquatic and arboreal habits. Orthopterans and anurans were more commonly found on the diet of bromelicolous lizards. Bromeliads often form tanks where water and detritus accumulate, thus creating specifics microhabitats for arthropods (such as orthopterans) and even some anurans (Armbruster *et al.* 2002; Frank & Lounibos 2009). As a consequence, these bromelicolous organisms could be preyed by lizards that forage on these plants. Also, our results points that orthopterans were abundant on the diet of arboreal and semi-arboreal lizards while anurans also presented relative high values on semi-aquatic lizards' diets, and bromeliads engulfs both of these habitats. Nevertheless, our sample size and number of bromelicolous species is very low. For bromelicolous lizards, we only sampled two *Mabuya* species, both from Brazil, so there is a chance that our data can be biased. For the arboreal species, birds and phasmids were more ingested by lizards inhabiting these habitats than in others. Considering the ecology of birds and walking-sticks, (usually found perched, foraging on tree branchs and shrubs) they would be also expected to be more often on the diet of arboreal lizard species.

Finally, dragonflies, crustaceans, webspinners and plecopterans were more common in the diet of semi-aquatic species of lizards. In parallel to those preys found on arboreal species, these are prey items highly associated to freshwater habitats, thus making them more accessible to semi-aquatic lizards (Fochetti & De Figueroa 2008; Kalkman *et al.* 2008), except for webspinners. Curiously, saxicolous lizards seem to ingest more amphibians, amphibian brood and chelonians than in other habitats. Nevertheless, these preys were only found on *Varanus* species and the formers were only present in the diet of a single species of our database (*Varanus albigularis*, see Dalhuijsen *et al.* 2014) from all 323 sampled, so this result could be also biased by sampling. As a whole, it is known that habitat specialization has been correlated to dietary specialization in many vertebrate taxa. For instance, some ground-dwelling frogs commonly feed on mites although this is not a common prey found on anuran diet (Simon & Toft 1991). In gasterosteid fishes, habitat shifts can even lead to changes in trophic positions (Matthews *et al.* 2010). Based on our results, it seems that in lizards, more strict habitat specializations can allow/facilitate the access of some types of preys more than in other habitats. Interesting, most of these prey items are secondary components of lizards' diets (with the exception of orthopterans), so it is probable that habitat specialization can act as a predictor of lizards' complementary diet (while most of the main diet composition is explained by evolutionary history, as discussed above).

We found significant differences between distribution and the ingestion of some prey items. The ingestion of roaches, centipedes, orthopterans, non-ant hymenopterans, and reptile eggs were significantly higher in tropical region. This is somehow expected, as most of these preys are arthropods that are way more diverse on tropics than on temperate regions (i.e.: Lewis 1981; Austin & Dowton 2000; Bell *et al.* 2007). Besides, some of these preys are conspicuous elements of litter fauna, which is a very common habitat on many tropical biomes. For temperate regions, only one type of prey was found in significant higher amount: Squamata. Unlike the other preys, this is probably not associated to diversity but rather on lizard's body size differences between temperate and tropical regions. Although most lizards do not follow the Bergmann's rule (increasing on body size in higher latitudes; Ashton & Feldman 2003; Pincheira-Donoso *et al.* 2008), many larger species from our data are from temperate regions. These differences, together with positive correlations between lizard's body size and Squamata ingestion (see further on discussion) suggests that higher amounts of squamates on temperate lizards diet are probably associated to the presence of larger bodied lizard species on these regions, as squamates are more common on the diet of larger lizard species.

Body size and dietary preferences are two traits correlated in many taxa (Mittelbach 1981; Fleming 1991; Emmerson & Raffaelli 2004). Among predaceous lizards, a larger body size is often associated with larger preys (maximizing energetic acquirement from food), even leading larger lizard species to a narrower niche breadth (Costa *et al.* 2008b). In agreement, we found a positive relationship between many prey types: amphibians and amphibian brood, chelonians, crustaceans, millipedes, webspinners, gastropods, mammals, plecopterans, squamates, vertebrates and plant. Although we did not directly account for prey size, most of these preys are vertebrates and/or arthropods which present some large-sized species, which can corroborate the findings that the ingestion of larger prey on lizards is often associated to an increasing on species body size. Another interesting fact was that herbivory was associated to an increasing on body size. Classical studies pointed that herbivory in lizards (and reptiles in general) is related to an increasing on body size to fulfill the physiological requirements of plant digestion (Pough 1973; Cooper Jr & Vitt 2002). Indeed, lizard herbivory is positively related to body size and warmer climates in many cases (Zimmerman & Tracy 1989; Van Damme 1999; Cooper Jr & Vitt 2002). This was hypothesized as an alternative for scarceness of large preys and/or difficulty for small species to degrade plant material when compared to larger species (Cooper Jr & Vitt 2002; Pietczak & Vieira 2017). In contrast, there are plenty of studies confronting these results, as some herbivore lizard species have developed small bodies and are found on cooler climates (i.e.: liolemids, Espinoza *et al.* 2004; Vitt 2004). However, most of these studies are regional and were made based on the qualitative observation of herbivores and non-herbivores rather than a continuum of plant ingestion, plus some are absent of phylogenetic comparative analysis. In a broader scale, our results suggests that larger body sizes on lizards seems to facilitate herbivory (but not only in warmer climates, as discussed above) although many other variables that we could not analyze (e.g.: body mass, physiological activity, ontogenetic variation) can be in play when accounting for plant ingestion.

Surprisingly, only Hemiptera ingestion was negatively correlated with body size. We associate most of this result to a lack of hemipterans on larger lizards' diets. From all sampled lizard species with body size > 100 mm (120 spp.), about 30% (41 spp.) had no hemipteran on their diet, while the other ones ingested in very few amounts, averaging around 4% of total diet (range 0-26%). This avoidance is still pretty unclear, as we did not found relationship of this manner on relatively smaller preys than hemipterans (i.e.: mites, springtails) and neither on preys with similar defense mechanisms found on bugs (such as beetles and hymenopterans).

Conclusion

Such as previously proposed, phylogenetic history is the major predictor of present-day dietary divergences found among lizard species, and is more conspicuous on more older clades rather than in recent ones. Most of these variations can be traced by divergent biological traits (foraging mode, prey capture and discrimination system) between the different clades, where iguanians eats more high mobile, noxious preys (beetles and hymenopterans) than non-iguanians. Althougth most of this variation was previously pointed as a consequence of a difficulty on iguanians to access and discriminate more palative, sendentary preys as efficient as scleroglossans, we suggest a different scenario: the possibility that iguanians (considering them as a derived clade on new molecular phylogenies) had evolved to prey upon these mobile/noxious insects more efficiently. Also, our results suggests that iguanians also tend to develop strict herbivory more than other clades. Despites the conspicuous effects of evolutionary history on dietary preferences of lizards, environmental variables and other ecological traits can also predict the rates of ingestion of many prey items. On harsher climate regimes, some prey items are ingested more often than others (i.e.: termites on warmer climates and beetles on colder ones; plant matter on seasonal environments), and can be associated to alternative nutrient source where other food/water sources are scarce/unavailable. Habitat specializations can also predict higher ingestion of some prey groups, majorly on arboreal and semi-aquatic lizards. At last, body size had positive correlations to herbivory and large prey groups, thus indicating dietary shifts for better energetic acquisition on larger lizard species. Interesting, foraging mode was not a good predictor of dietary preferences as classically hypothesized. This provides indications of how we should be aware of phylogenetic dependent traits and how the absence of phylogenetic comparative methods can lead us to misinterpretations. Finally, we undoubtedly points phylogenetic history as the main driven factor of dietary divergences among present-day lizard species, although we still draw attention to the need of directional studies to better elucidate the cause-effect relationships that explain these dietary divergences. Furthermore, we also provided some evidence of how ecological traits and environment variables can also act as maintainers of lizards' dietary preferences, enlightening the understanding of recent and historical factors influence on dietary niches from a global recent perspective.

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Tables and Figures

Table 1: Sampled prey categories (N = 61) based on 722 populations from 323 lizard species around the globe, with respective absolute frequency (number of species that ingested that prey).

CATEGORY	Absolute frequency	CATEGORY	Absolute frequency
Acari	78	Isopoda	98
Archeognatha	2	Isoptera	170
Ambplypigy	4	Lepidoptera	159
Amphibian	1	Mammalia	1
Amphibian (eggs)	1	Mantodea	71
Amphipoda	2	Mollophaga	8
Anura	22	Mollusca	39
Arachnida	13	Myriapoda	7
Aranae	267	Neuroptera	32
Aranae egg	11	Odonata	42
Aves	7	Oligochaeta	28
Blattodea	185	Opiliones	39
Chelonia	5	Orthoptera	254
Chilopoda	106	Phasmatodea	44
Collembola	49	Plant material	135
Coleoptera	268	Plecoptera	18
Crustacea	15	Pseudoscorpiones	61
Dermaptera	47	Psocoptera	22
Diplopoda	93	Reptile (eggs)	13
Diplura	2	Rodentia	1
Diptera	175	Scorpionida	75
Embioptera	12	Siphonaptera	1
Ephemeroptera	4	Solifuga	34
Formicidae	227	Squamata	43
Gastropoda	66	Thysanura	42
Hemiptera	246	Thysanoptera	14
Hymenoptera	188	Trichoptera	6
Hyrudinea	1	Uropygi	1
Insect (eggs)	34	Vertebrata	51
Insect larvae	241	Zygoptera	1
Insect pupae	30		

Table 2: Phylogenetic signal estimates for each prey category found on sampled lizard species around globe (N=323). Bold values presenting “*” are statistically significants while bold only values represents marginal significance.

CATEGORY	Blomberg’s K	p	CATEGORY	Blomberg’s K	p
Acari	0.595148	**0.003***	Isopoda	0.111337	0.918
Archeognatha	0.371948	**0.076**	Isoptera	0.29491	**0.001***
Ambplypigy	0.224129	0.434	Lepidoptera	0.306759	**0.025***
Amphibia	0.233543	0.494	Mammalia	0.180663	0.631
Amphibia (eggs)	0.233543	0.464	Mantodea	0.155787	0.745
Amphipoda	0.272001	0.396	Mollophaga	0.246654	0.333
Anura	0.307337	0.196	Mollusca	0.210799	0.351
Arachnida	0.200825	0.476	Myriapoda	0.258778	0.287
Aranae	0.232928	**0.036***	Neuroptera	0.114017	0.887
Aranae (eggs)	0.179019	0.588	Odonata	0.409441	**0.002***
Aves	0.224962	0.475	Oligochaeta	0.467492	**0.030***
Blattodea	0.229242	**0.047***	Opiliones	0.29912	**0.021***
Chelonia	0.241907	0.418	Orthoptera	0.189788	0.351
Chilopoda	0.190809	0.461	Phasmatodea	0.277845	0.223
Collembola	0.511848	**0.007***	Plant material	0.472674	**0.001***
Coleoptera	0.277376	**0.001***	Plecoptera	0.198625	0.591
Crustacea	0.278932	0.217	Pseudoscorpiones	0.243318	0.252
Dermaptera	0.288177	**0.042***	Psocoptera	0.182912	0.606
Diplopoda	0.327303	**0.008***	Reptile (eggs)	0.472062	**0.033***
Diplura	0.233318	0.444	Rodentia	0.123294	0.834
Diptera	0.369383	**0.007***	Scorpionida	0.285323	0.158
Embioptera	0.193372	0.555	Siphonaptera	0.07651	0.948
Ephemeroptera	0.378762	0.160	Solifuga	0.551044	**0.003***
Formicidae	0.320095	**0.001***	Squamata	0.218106	0.352
Gastropoda	0.371238	**0.009***	Thysanura	0.152606	0.771
Hemiptera	0.228629	**0.049***	Thysanoptera	0.209928	0.379
Hymenoptera	0.293868	**0.008***	Trichoptera	0.269853	0.185
Hyrudinea	0.305472	0.313	Uropygi	0.290157	0.374
Insect (eggs)	0.190272	0.526	Vertebrata	0.382061	**0.015***
Insect larvae	0.221572	**0.099**	Zygoptera	0.215491	0.530
Insect pupae	0.229837	0.223			

Table 3: Results from phylogenetic regressions (PGLS) and ordinary regressions (OLS) from the relationship between dietary preferences and climatic variables for sampled lizard species around globe (N=323). Bold values presenting "*" are statistically significants, bold values presenting "**" are those with p-values <0.001 while bold only values represents marginal significance. $^{\mu}$: Estimated values of prey category ingestion based on the increasing of one unity on the climatic variable.

CATEGORY	R^2	F	P	intercept	TEMP1$^{\mu}$	TEMP2$^{\mu}$	PREC1$^{\mu}$	PREC2$^{\mu}$	AIC
ACARI									
- *PGLS*	0.01007	1.808	0.326	0.925025	-0.00276	**0.064724***	0.039514	-0.0511	953.7764
- *OLS*	0.01446	2.166	**0.07263***	**0.2681****	-0.01495	**0.10676****	0.05881	-0.03512	
ARCHEOGNATHA									
- *PGLS*	-0.00703	0.4454	0.7757	0.0572815	-0.00782	-0.00284	0.001834	-0.00379	-29.673
- *OLS*	-0.00504	0.6015	0.6618	0.0186408	-0.00043	0.007043	-0.00062	-0.00983	
AMBPLYPIGY									
- *PGLS*	0.004104	1.328	0.2595	0.0143821	-0.0044	-0.0003	-0.00174	-0.00202	-362.564
- *OLS*	0.00105	1.084	0.3647	**0.0138353***	-0.00378	-0.00068	-0.00169	-0.00249	
AMPHIBIA									
- *PGLS*	0.005724	1.458	0.2149	0.0105872	-0.00507	0.006969	0.006599	**-0.01354**	-171.756
- *OLS*	0.005724	1.458	0.2149	0.010587	-0.00508	0.006969	0.006599	**-0.01354**	
AMPHIBIA (EGGS)									
- *PGLS*	0.005724	1.458	0.2149	0.0158807	-0.00761	0.010454	0.009899	**-0.02031**	82.87584
- *OLS*	0.005724	1.458	0.2149	0.015881	-0.00761	0.010454	0.009898	**-0.02031**	
AMPHIPODA									
- *PGLS*	0.003585	1.286	0.2753	0.0145472	-0.00243	0.012138	0.006144	-0.02033	165.8862
- *OLS*	0.003585	1.286	0.2753	0.014547	-0.00243	0.012138	0.006144	-0.02033	
ANURA									

- *PGLS*	-0.00582	0.5404	0.7062	0.5433463	-0.04068	-0.00623	-0.07917	-0.0546	1635.307
- *OLS*	0.003355	1.268	0.2826	0.52131**	-0.05638	-0.01776	-0.11103	0.02211	
ARACHNIDA									
- *PGLS*	0.0137	2.104	0.08014	0.240498	0.009508	0.091203	0.049644	0.152039*	1363.007
- *OLS*	0.003867	1.309	0.2666	0.23016*	0.03162	0.05966	0.05909	0.07732	
ARANAE									
- *PGLS*	-0.00088	0.93	0.4467	10.88991**	-0.12848	-0.03234	-0.50753	0.150927	2645.568
- *OLS*	0.02837	3.321	0.01102*	10.88265**	0.14274	-0.49654	-0.50027	-0.07304	
ARANAE (EGGS)									
- *PGLS*	0.006996	1.56	0.1848	0.03117445**	-0.004	-0.00087	-0.00441	0.005462	-46.0342
- *OLS*	0.006996	1.56	0.1848	0.0311745**	-0.004	-0.00087	-0.00441	0.005462	
AVES									
- *PGLS*	0.000117	1.009	0.4027	0.1500964	0.015407	0.001356	-0.00558	-0.08067	1112.223
- *OLS*	0.007338	1.588	0.1773	0.0750516	0.020771	-0.00722	-0.00044	-0.09097	
BLATTODEA									
- *PGLS*	0.08371	8.263	2.39E-06**	6.17394**	-0.5469	-0.27825	-0.7962*	0.54407	2463.797
- *OLS*	0.105	10.33	7.22E-08**	6.4156**	-0.6646*	-0.3053	-0.7585*	0.3894	
CHELONIA									
- *PGLS*	0.007882	1.632	0.1661	0.111051	-0.03082	0.03555	0.036521	-0.06975*	812.1907
- *OLS*	0.007588	1.608	0.1721	0.06781	-0.02651	0.02718	0.0373	-0.07504*	
CHILOPODA									
- *PGLS*	0.01053	1.846	0.1198	1.37676**	-0.19783	-0.1128	0.1682	-0.13023	1848.414
- *OLS*	0.01215	1.978	0.09773	1.34681**	-0.19957*	-0.11901	0.17179	-0.14541	
COLLEMBOLA									
- *PGLS*	-0.00595	0.5296	0.7141	0.5185905	-0.03346	0.036409	0.004804	0.097132	1395.861
- *OLS*	0.001825	1.145	0.3352	0.46902**	-0.04664	0.01724	-0.06085	0.10008	
COLEOPTERA									
- *PGLS*	0.05063	5.24	0.000425**	9.82101**	0.873815**	0.101942	0.049895	-0.70463	2443.564

- *OLS*	0.09919	9.754	**1.90E-07****	**9.06195****	**1.11178****	0.37729	0.02596	-0.35959	
CRUSTACEA									
- *PGLS*	0.003532	1.282	0.277	0.1630307	**0.094866**	0.009069	**-0.09653**	0.126709	1301.505
- *OLS*	0.003532	1.282	0.277	0.16303	**0.094866**	0.009068	**-0.09653**	0.126708	
DERMAPTERA									
- *PGLS*	0.003668	1.293	0.2728	**0.621151****	-0.05059	0.015801	-0.08398	-0.0342	1490.794
- *OLS*	0.01227	1.988	0.09617	**0.62815****	-0.07326	0.02793	-0.08084	-0.02993	
DIPLOPODA									
- *PGLS*	0.03232	3.655	**0.006296***	1.237356	0.105302	**0.235413****	-0.13984	0.098062	1571.86
- *OLS*	0.05912	5.995	**0.000117****	**0.80923****	**0.15759***	**0.2051***	**-0.24646****	0.12714	
DIPLURA									
- *PGLS*	-0.00255	0.7982	0.5271	0.0029896	0.004129	0.00042	0.002031	0.002074	-524.811
- *OLS*	-0.00255	0.7982	0.5271	0.0029896	0.004129	0.00042	0.002031	0.002074	
DIPTERA									
- *PGLS*	0.0156	2.26	**0.06264**	2.461832	0.22867	**0.464444***	-0.16042	0.078837	2104.199
- *OLS*	0.04828	5.033	**0.000606****	**2.04338****	**0.45643***	**0.57702****	-0.09281	-0.02666	
EMBIOPTERA									
- *PGLS*	0.007511	1.602	0.1737	**0.088572***	0.024047	-0.01406	-0.01762	-0.05096	865.7303
- *OLS*	0.007511	1.602	0.1737	**0.088572***	-0.02405	-0.01406	-0.01762	-0.05096	
EPHEMEROPTERA									
- *PGLS*	0.000499	1.04	0.3868	0.011708	0.030255	0.01467	-0.01409	0.027303	578.9758
- *OLS*	0.001035	1.082	0.3652	0.03045	0.02334	0.02155	-0.01858	0.02674	
FORMICIDAE									
- *PGLS*	-0.00552	0.5636	0.6893	**6.82453**	0.34185	-0.39875	-0.37722	-0.48436	2649.579
- *OLS*	-0.00515	0.5929	0.668	**8.0999****	0.5689	-0.1069	-0.1566	0.165	
GASTROPODA									
- *PGLS*	0.04043	4.349	**0.001945***	0.69394	**0.1999****	**0.127311**	**-0.17552***	0.11171	1469.924
- *OLS*	0.0699	6.974	**2.17E-05****	**0.3354***	**0.24126****	**0.15617***	**-0.17194***	0.11252	

HEMIPTERA									
- *PGLS*	0.047	4.92	**0.000735***	**4.89632****	**0.8279****	-0.3437	**-1.0402****	**1.09602****	2316.213
- *OLS*	0.05657	5.767	**0.000172***	**5.1707***	**0.9015****	-0.298	**-1.0926****	**1.2189****	
HYMENOPTERA									
- *PGLS*	0.01934	2.568	**0.03816***	**2.77136***	0.15393	0.24681	0.11759	**-0.55802**	2127.497
- *OLS*	0.02246	2.827	**0.02499***	**2.89905***	0.24489	0.28948	0.06427	-0.35071	
HYRUDINEA									
- *PGLS*	-0.00427	0.6621	0.6188	3.16E-04	-1.07E-06	-1.44E-05	-5.80E-05	2.69E-04	-2470.32
- *OLS*	-0.00427	0.6621	0.6188	3.16E-04	-1.07E-06	-1.44E-05	-5.80E-05	2.69E-04	
INSECT (EGGS)									
- *PGLS*	0.01635	2.322	**0.05674**	**0.211165***	**-0.07294***	0.045432	**0.09988****	-0.0701	1143.373
- *OLS*	0.01853	2.501	**0.04251***	**0.22383****	**-0.07952***	0.04866	**0.10156****	-0.07014	
INSECT LARVAE									
- *PGLS*	0.01545	2.248	**0.06382**	**8.40612****	**-0.89211***	0.26652	0.20183	-0.12731	2595.99
- *OLS*	0.02354	2.916	**0.02157***	**9.207****	**-0.9479****	0.1655	0.2328	-0.3052	
INSECT PUPAE									
- *PGLS*	-0.01093	0.1403	0.9671	**0.11631783****	-0.00045	-0.00853	-0.00907	-0.00184	752.0684
- *OLS*	-0.01093	0.1403	0.9671	**0.11631783****	-0.00045	-0.00853	-0.00907	-0.00184	
ISOPODA									
- *PGLS*	0.01662	2.344	**0.05476**	**1.437102****	-0.23885	**0.341984***	0.020165	-0.39454	2338.469
- *OLS*	0.01733	2.402	**0.04989***	**1.4391****	-0.24453	**0.34267***	0.02062	-0.3978	
ISOPTERA									
- *PGLS*	0.0552	5.645	**0.000213***	**9.81619***	0.23363	**-1.87816***	**1.03187**	-0.67379	2798.099
- *OLS*	0.1315	13.04	**7.77E-10***	**9.1958****	0.2892	**-2.618**	1.0621	1.1354	
LEPIDOPTERA									
- *PGLS*	0.0149	2.203	**0.0685**	1.73191	**0.33281**	**0.29813**	-0.17215	0.24235	1989.99
- *OLS*	0.01096	1.881	0.1135	**2.1046****	**0.35104***	0.07549	**-0.35633**	0.13111	
MAMMALIA									

- *PGLS*	-0.00497	0.6067	0.6581	**2.46E-03****	-5.03E-06	-1.50E-03	6.48E-04	-2.14E-03	-705.67
- *OLS*	-0.00497	0.6067	0.6581	**2.46E-03****	-5.03E-06	-1.50E-03	6.48E-04	-2.14E-03	
MANTODEA									
- *PGLS*	0.01747	2.413	**0.04898***	**0.47595****	0.053287	**-0.12294***	-0.10013	0.158773	1498.24
- *OLS*	0.01747	2.413	**0.04898***	**0.47595****	0.053287	**-0.12294***	-0.10013	0.158773	
MOLLOPHAGA									
- *PGLS*	-0.01106	0.1303	0.9713	0.0271786	0.003665	0.004333	-0.00311	0.00328	301.4119
- *OLS*	-0.01106	0.1303	0.9713	0.0271786	0.003665	0.004333	-0.00311	0.00328	
MOLLUSCA									
- *PGLS*	0.04999	5.183	**0.000468****	**0.12781194****	**-0.02557**	0.000151	**-0.02849**	-0.02667	599.8272
- *OLS*	0.04999	5.183	**0.000468****	**0.12781194****	**-0.02557**	0.000151	**-0.02849**	-0.02667	
MYRIAPODA									
- *PGLS*	-0.00252	0.7999	0.526	**0.062799***	-0.01991	0.016495	**0.029342**	-0.0196	553.8461
- *OLS*	-0.00252	0.7999	0.526	**0.062799***	-0.01991	0.016495	**0.029342**	-0.0196	
NEUROPTERA									
- *PGLS*	-0.00341	0.7296	0.5723	**0.168284***	0.014297	-0.04746	-0.01627	0.05517	1354.13
- *OLS*	-0.00341	0.7296	0.5723	**0.168284***	0.014297	-0.04746	-0.01627	0.05517	
ODONATA									
- *PGLS*	0.009131	1.733	0.1425	0.255103	0.001118	**0.0606***	-0.0055	0.033981	789.5292
- *OLS*	0.02353	2.916	**0.02159***	**0.21677****	0.0318	0.03618	**-0.05658**	**0.08627***	
OLIGOCHAETA									
- *PGLS*	-0.00858	0.3235	0.8622	0.651144	0.069965	0.087971	-0.07175	0.077854	1793.128
- *OLS*	0.01065	1.856	0.118	0.56121	0.08683	0.134	**-0.28322**	-0.0465	
OPILIONES									
- *PGLS*	0.01807	2.463	**0.04519***	0.292356	0.013735	0.040207	**-0.05855**	0.060888	889.3882
- *OLS*	0.02463	3.007	**0.01856***	**0.2085****	0.04237	0.0316	**-0.07266***	0.0669	
ORTHOPTERA									
- *PGLS*	0.02963	3.427	**0.009233***	**13.506862****	-0.15224	-0.08203	**-0.91208**	**1.215889**	2796.865

- *OLS*	0.02963	3.427	**0.009233***	**13.506862****	-0.15224	-0.08203	**-0.91208**	**1.215889**	
PHASMATODEA									
- *PGLS*	0.00633	1.506	0.2001	**0.5007013***	0.053593	-0.0011	-0.16613	0.244612	1690.489
- *OLS*	0.00633	1.506	0.2001	**0.5007013***	0.053593	-0.0011	-0.16613	0.244612	
PLANT MATERIAL									
- *PGLS*	0.04127	4.422	**0.001719***	8.98985	**-1.04936***	**0.83164**	**2.00732****	-0.77233	1221.889
- *OLS*	0.0546	5.591	**0.000233****	**7.1244****	**-1.0971***	**1.4633****	**2.7292****	-0.4001	
PLECOPTERA									
- *PGLS*	0.01273	2.025	0.09073	**0.15300898**	-0.02319	-0.00056	-0.05419	**-0.10104**	1221.889
- *OLS*	0.01273	2.025	0.09073	**0.15300898**	-0.02319	-0.00056	-0.05419	**-0.10104**	
PSEUDOSCORPIONES									
- *PGLS*	0.003838	1.306	0.2675	**0.36139****	-0.07352	0.06379	**0.12355**	-0.0843	1332.221
- *OLS*	0.003838	1.306	0.2675	0.36139**	-0.07352	0.06379	**0.12355**	-0.0843	
PSOCOPTERA									
- *PGLS*	0.000188	1.015	0.3998	**0.0246196**	-0.00299	0.009092	-0.00273	-0.00116	150.5716
- *OLS*	0.000188	1.015	0.3998	**0.0246196**	-0.00299	0.009092	-0.00273	-0.00116	
REPTILE (EGGS)									
- *PGLS*	0.01681	2.359	**0.05341**	1.557304	-0.07433	**-0.16102**	0.001538	0.174289	1589.571
- *OLS*	0.002429	1.194	0.3136	**0.376462**	-0.00926	-0.1227	0.025201	0.209963	
RODENTIA									
- *PGLS*	-0.00514	0.5939	0.6673	4.28E-04	-2.56E-05	2.33E-04	1.28E-04	-3.83E-04	-1709.98
- *OLS*	-0.00514	0.5939	0.6673	4.28E-04	-2.56E-05	2.33E-04	1.28E-04	-3.83E-04	
SCORPIONIDA									
- *PGLS*	-0.00497	0.6072	0.6578	1.04505**	-0.11464	-0.10505	0.10566	-0.05438	1873.611
- *OLS*	-0.00497	0.6072	0.6578	1.04505**	-0.11464	-0.10505	0.10566	-0.05438	
SIPHONAPTERA									
- *PGLS*	0.006009	1.481	0.2078	0.00379887	0.002139	**-0.0073***	-0.0005	0.00073	27.09767
- *OLS*	0.006009	1.481	0.2078	0.00379887	0.002139	**-0.0073***	-0.0005	0.00073	

SOLIFUGA									
- *PGLS*	0.01137	1.915	0.1078	1.098349	-0.02536	0.015996	**0.085146***	0.018143	1050.741
- *OLS*	0.04605	4.838	**0.000846***	0.359552**	**-0.09529***	**0.12933****	**0.186437****	-0.00581	
SQUAMATA									
- *PGLS*	0.000186	1.015	0.3998	2.042	-0.10596	-0.34481	0.14252	-0.37862	2380.705
- *OLS*	0.01477	2.192	0.06973	1.30023*	-0.04229	**-0.46873**	0.18141	-0.5841	
THYSANURA									
- *PGLS*	0.02975	3.438	**0.009073***	0.252052**	**-0.06768**	-0.03455	**0.09029***	**-0.16097****	1248.117
- *OLS*	0.02975	3.438	**0.009073***	0.252052**	**-0.06768**	-0.03455	**0.09029***	**-0.16097****	
THYSANOPTERA									
- *PGLS*	0.01712	2.385	**0.05126**	0.029229	**0.036101****	-0.01233	**-0.02745***	**0.03216**	475.7116
- *OLS*	0.01712	2.385	**0.05126**	0.029229	**0.036101****	-0.01233	**-0.02745***	**0.03216**	
TRICHOPTERA									
- *PGLS*	0.0262	3.139	**0.01492***	0.0180908	0.011365	0.002549	**-0.01811**	**-0.02427**	206.0432
- *OLS*	0.0262	3.139	**0.01492***	0.0180908	0.011365	0.002549	**-0.01811**	**-0.02427**	
UROPYGI									
- *PGLS*	-0.00977	0.231	0.9209	4.19E-05	-8.19E-06	2.03E-06	9.67E-07	8.76E-06	-3759.62
- *OLS*	-0.00977	0.231	0.9209	4.19E-05	-8.19E-06	2.03E-06	9.67E-07	8.76E-06	
VERTEBRATA									
- *PGLS*	-0.00314	0.7516	0.5576	0.68301*	0.03959	-0.11714	0.02164	0.17116	1673.813
- *OLS*	-0.00314	0.7516	0.5576	0.68301*	0.03959	-0.11714	0.02164	0.17116	
ZYGOPTERA									
- *PGLS*	-0.00466	0.6314	0.6405	0.0199557	-0.00667	-0.00091	-0.00238	-0.00803	145.2847
- *OLS*	-0.00466	0.6314	0.6405	0.0199557	-0.00667	-0.00091	-0.00238	-0.00803	

Table 4: Results from phylogenetic regressions (PGLS) and ordinary regressions (OLS) from the relationship between dietary preferences and ecological traits for sampled lizard species around globe (N=323). Bold values presenting "*" are statistically significants, bold values presenting "**" are those with p-values <0.001 while bold only values represents marginal significance. [µ]: Estimated values of prey category ingestion based on the increasing of one unity on the body size.

CATEGORY	F	p	R^2	Est. [µ]	AIC	F	p	R^2	Est. [µ]
ACARI									
- Foraging mode	13.368	**<0.001****			931.504	0.423	0.516		
- Habitat	1.050	0.393			952.054	0.502	0.807		
- Distribution	0.025	0.876			947.418	0.019	0.890		
- Body size	0.053	0.819	-0.003	0.000	958.149	0.324	0.569	-0.002	-0.001
ARCHEOGNATHA									
- Foraging mode	0.096	0.756			-67.856	2.050	0.153		
- Habitat	0.256	0.957			-39.830	0.255	0.957		
- Distribution	3.417	**0.066**			-68.317	0.138	0.711		
- Body size	0.070	0.792	-0.003	0.000	-54.243	0.320	0.572	-0.002	0.000
AMBPLYPIGY									
- Foraging mode	0.000	0.993			-404.068	1.053	0.306		
- Habitat	0.677	0.669			-373.404	0.148	0.989		
- Distribution	0.540	0.463			-401.766	1.435	0.232		
- Body size	0.054	0.816	-0.003	0.000	-390.483	0.064	0.800	-0.003	0.000
AMPHIBIA									
- Foraging mode	0.199	0.656			-206.490	1.019	0.314		
- Habitat	3.598	**0.002***			-195.555	0.908	0.489		
- Distribution	0.149	0.699			-203.599	1.741	0.188		

- Body size	40.460	**<0.001****	0.109	0.001	-206.524	40.460	**<0.001****	0.109	0.001
AMPHIBIA (EGGS)									
- Foraging mode	0.199	0.656			53.819	1.019	0.314		
- Habitat	3.598	**0.002***			60.699	0.489	0.489		
- Distribution	0.149	0.699			56.710	1.741	0.188		
- Body size	40.460	**<0.001****	0.109	0.001	53.784	40.460	**<0.001****	0.109	0.001
AMPHIPODA									
- Foraging mode	0.003	0.958			139.043	1.007	0.316		
- Habitat	0.002	1.000			165.275	0.129	0.993		
- Distribution	0.044	0.835			141.844	1.729	0.189		
- Body size	0.012	0.913	-0.003	0.000	152.480	0.012	0.913	-0.003	0.000
ANURA									
- Foraging mode	0.003	0.955			1629.572	0.032	0.857		
- Habitat	3.104	**0.006***			1614.500	2.372	**0.030***		
- Distribution	0.317	0.574			1632.100	1.897	0.169		
- Body size	1.929	0.166	0.003	0.004	1641.081	2.113	0.147	0.003	0.003
ARACHNIDA									
- Foraging mode	0.054	0.817			1363.058	7.288	**0.007***		
- Habitat	1.538	0.165			1361.187	4.320	**<0.001****		
- Distribution	1.952	0.163			1364.007	12.560	**<0.001****		
- Body size	0.857	0.355	0.000	0.001	1375.205	0.167	0.684	-0.003	0.000
ARANAE									
- Foraging mode	0.160	0.689			2670.157	24.360	**<0.001****		
- Habitat	0.522	0.791			2654.008	1.961	**0.071**		
- Distribution	0.131	0.718			2673.027	5.664	**0.018***		
- Body size	6.297	**0.013***	0.016	-0.024		7.207	0.008	0.019	-0.024
ARANAE (EGGS)									
- Foraging mode	0.002	0.963			-84.606	0.758	0.385		

- Habitat	0.456	0.841			-57.606	0.302	0.936		
- Distribution	0.251	0.617			-82.014	3.825	**0.051**		
- Body size	0.082	0.774	-0.003	0.000	-71.793	0.082	0.774	-0.003	0.000
AVES									
- Foraging mode	0.162	0.687			1101.637	3.247	**0.073**		
- Habitat	2.167	**0.046***			1100.301	0.919	0.481		
- Distribution	1.320	0.251			1103.323	5.499	**0.020***		
- Body size	0.087	0.769	-0.003	0.000	1105.823	7.480	**0.007***	0.020	0.002
BLATTODEA									
- Foraging mode	0.055	0.815			2507.211	4.559	**0.034***		
- Habitat	0.526	0.788			2493.474	1.551	0.161		
- Distribution	4.243	**0.040***			2505.893	15.170	**<0.001****		
- Body size	2.803	0.095	0.006	-0.013	2520.116	4.384	**0.037***	0.010	-0.014
CHELONIA									
- Foraging mode	0.275	0.601			798.431	2.088	0.150		
- Habitat	3.616	**0.002***			793.687	0.675	0.670		
- Distribution	0.452	0.502			801.095	2.588	0.109		
- Body size	77.540	**<0.001****	0.192	0.004	756.796	77.540	**<0.001****	0.192	0.004
CHILOPODA									
- Foraging mode	0.001	0.978			1860.081	0.324	0.570		
- Habitat	0.320	0.926			1857.596	0.641	0.697		
- Distribution	4.209	**0.041***			1858.742	0.248	0.619		
- Body size	1.538	0.216	0.002	0.003	1872.297	0.697	0.404	-0.001	0.002
COLLEMBOLA									
- Foraging mode	0.003	0.960			1389.596	1.831	0.177		
- Habitat	0.927	0.476			1390.846	0.521	0.792		
- Distribution	1.174	0.279			1391.269	2.177	0.141		
- Body size	0.357	0.550	-0.002	-0.001	1402.828	3.415	**0.066***	0.007	-0.003

COLEOPTERA									
- Foraging mode	0.068	0.794			2474.559	1.453	0.229		
- Habitat	1.223	0.294			2457.234	1.743	0.111		
- Distribution	1.336	0.249			2476.135	11.050	**0.001***		
- Body size	0.134	0.715	-0.003	0.003	2488.185	0.062	0.804	-0.003	-0.002
CRUSTACEA									
- Foraging mode	0.060	0.806			1300.035	1.328	0.250		
- Habitat	8.199	**<0.001****			1262.528	4.862	**<0.001****		
- Distribution	8172770.000	0.094			1300.132	0.025	0.873		
- Body size	5.950	**0.015***	0.015	0.003	1310.306	5.950	**0.015***	0.015	0.003
DERMAPTERA									
- Foraging mode	0.006	0.940			1485.611	0.971	0.325		
- Habitat	1.976	**0.069**			1479.242	1.589	0.150		
- Distribution	0.045	0.833			1488.414	3.605	**0.059**		
- Body size	0.004	0.950	-0.003	0.000	1499.183	0.021	0.885	-0.003	0.000
DIPLOPODA									
- Foraging mode	0.282	0.596			1573.414	2.931	0.088		
- Habitat	1.382	0.221			1569.403	2.794	**0.012***		
- Distribution	0.184	0.668			1576.353	0.857	0.355		
- Body size	11.690	**0.001***	0.032	0.008	1579.162	15.010	**<0.001****	0.042	0.007
DIPLURA									
- Foraging mode	0.001	0.976			-555.052	0.317	0.574		
- Habitat	0.058	0.999			-518.347	0.092	0.997		
- Distribution	0.075	0.784			-552.284	0.879	0.349		
- Body size	0.134	0.714	-0.003	0.000	-541.474	0.134	0.714	-0.003	0.000
DIPTERA									
- Foraging mode	0.140	0.709			2122.034	0.107	0.744		
- Habitat	0.187	0.980			2116.402	0.697	0.653		

- Distribution	0.765	0.382			2124.252	4.373	0.037		
- Body size	0.760	0.384	-0.001	-0.005	2135.001	2.430	0.120	0.004	-0.008
EMBIOPTERA									
- Foraging mode	0.002	0.967			853.001	0.027	0.870		
- Habitat	9.658	**<0.001****			814.916	9.973	**<0.001****		
- Distribution	0.004	0.947			855.840	1.626	0.203		
- Body size	4.800	**0.029***	0.012	0.001	866.167	4.800	**0.029***	0.012	0.001
EPHEMEROPTERA									
- Foraging mode	0.018	0.893			556.816	1.490	0.223		
- Habitat	0.051	1.000			576.258	0.186	0.981		
- Distribution	0.000	0.993			559.676	0.211	0.647		
- Body size	0.151	0.698	-0.003	0.000	570.269	0.640	0.425	-0.001	0.000
FORMICIDAE									
- Foraging mode	0.120	0.729			2672.101	12.310	**0.001***		
- Habitat	0.429	0.859			2656.437	1.303	0.255		
- Distribution	0.788	0.375			2674.275	0.671	0.413		
- Body size	3.412	**0.066**	0.007	-0.022	2683.313	2.798	0.095	0.006	-0.018
GASTROPODA									
- Foraging mode	0.125	0.724			1494.628	1.746	0.187		
- Habitat	0.902	0.493			1494.506	2.515	**0.022***		
- Distribution	0.606	0.437			1496.989	2.703	0.101		
- Body size	3.994	**0.047***	0.009	0.004	1506.328	11.330	**0.001***	0.031	0.006
HEMIPTERA									
- Foraging mode	0.071	0.790			2346.035	1.995	0.159		
- Habitat	1.657	0.131			2328.175	1.609	0.144		
- Distribution	1.089	0.297			2347.860	0.157	0.692		
- Body size	10.700	**0.001***	0.029	-0.018	2354.609	11.840	**0.001***	0.033	-0.018
HYMENOPTERA									

- Foraging mode	0.276	0.599			2140.166	9.043	**0.003***		
- Habitat	2.021	**0.063**			2123.606	1.649	0.133		
- Distribution	7.978	**0.005***			2135.404	0.991	0.320		
- Body size	0.670	0.414	-0.001	-0.004	2153.861	0.322	0.571	-0.002	-0.003
HYRUDINEA									
- Foraging mode	0.003	0.959			-2563.183	1.019	0.314		
- Habitat	0.001	1.000			-2494.856	0.127	0.993		
- Distribution	0.642	0.424			-2560.980	0.575	0.449		
- Body size	0.043	0.835	-0.003	0.000	-2549.631	0.043	0.835	-0.003	0.000
INSECT EGG									
- Foraging mode	0.198	0.657			1163.242	5.154	**0.024***		
- Habitat	0.567	0.757			1170.340	1.901	0.080		
- Distribution	0.108	0.743			1166.173	0.164	0.686		
- Body size	0.161	0.689	-0.003	0.000	1176.983	0.207	0.649	-0.002	0.000
INSECT LARVAE									
- Foraging mode	0.027	0.870			2624.740	0.984	0.322		
- Habitat	1.511	0.174			2603.350	4.664	**<0.001****		
- Distribution	0.787	0.376			2626.822	4.105	**0.044***		
- Body size	2.299	0.130	0.004	-0.014	2638.335	5.471	**0.020***	0.014	-0.019
INSECT PUPAE									
- Foraging mode	0.361	0.548			764.224	3.253	**0.072**		
- Habitat	0.395	0.882			778.721	1.047	0.395		
- Distribution	0.326	0.568			767.101	0.232	0.631		
- Body size	0.000	0.982	-0.003	0.000	777.661	0.344	0.558	-0.002	0.000
ISOPODA									
- Foraging mode	0.014	0.906			2371.805	1.399	0.238		
- Habitat	0.090	0.997			2362.740	0.229	0.967		
- Distribution	0.067	0.795			2374.593	2.176	0.141		

- Body size	1.859	0.174	0.003	-0.006	2385.341	2.072	0.151	0.003	-0.006
ISOPTERA									
- Foraging mode	0.037	0.848			2829.103	0.033	0.856		
- Habitat	1.112	0.355			2806.874	2.518	**0.021***		
- Distribution	0.485	0.487			2831.497	29.670	**<0.001****		
- Body size	0.412	0.521	-0.002	-0.010	2842.723	4.567	**0.033***	0.011	-0.028
LEPIDOPTERA									
- Foraging mode	0.002	0.968			2006.381	2.943	0.087		
- Habitat	0.407	0.874			2001.100	0.356	0.906		
- Distribution	0.467	0.495			2008.757	0.082	0.775		
- Body size	0.492	0.484	-0.002	0.003	2019.730	0.949	0.331	0.000	-0.004
MAMMALIA									
- Foraging mode	0.057	0.812			-760.359	1.019	0.314		
- Habitat	0.782	0.584			-724.714	0.127	0.993		
- Distribution	0.326	0.568			-757.787	1.741	0.188		
- Body size	54.860	**<0.001****	0.143	0.000	-840.140	54.860	**<0.001****	0.143	0.000
MANTODEA									
- Foraging mode	0.019	0.891			1498.547	0.191	0.663		
- Habitat	0.386	0.888			1501.322	1.207	0.302		
- Distribution	1.820	0.178			1499.592	0.332	0.565		
- Body size	0.687	0.408	-0.001	-0.001	1511.707	0.687	0.408	-0.001	-0.001
MOLLOPHAGA									
- Foraging mode	0.008	0.928			269.837	1.865	0.173		
- Habitat	0.013	1.000			293.966	0.297	0.938		
- Distribution	0.579	0.447			272.108	0.014	0.905		
- Body size	0.014	0.904	-0.003	-0.003	283.431	0.014	0.904	-0.003	-0.003
MOLLUSCA									
- Foraging mode	0.000	1.000			582.650	0.596	0.441		

- Habitat	0.688	0.659			597.876	1.015	0.415		
- Distribution	0.172	0.679			585.319	5.505	**0.020***		
- Body size	0.446	0.505	-0.002	0.000	596.219	0.603	0.438	-0.001	0.000
MYRIAPODA									
- Foraging mode	0.000	0.991			536.887	0.020	0.886		
- Habitat	0.036	1.000			556.711	0.645	0.694		
- Distribution	0.036	0.850			539.693	0.000	0.983		
- Body size	1.244	0.266	0.001	0.000	548.197	1.244	0.266	0.001	0.000
NEUROPTERA									
- Foraging mode	0.011	0.916			1349.338	1.325	0.251		
- Habitat	2.027	**0.062**			1344.799	0.184	0.981		
- Distribution	0.004	0.947			1352.186	0.104	0.747		
- Body size	0.101	0.751	-0.003	0.000	1362.808	0.101	0.751	-0.003	0.000
ODONATA									
- Foraging mode	0.305	0.581			771.278	4.656	**0.032***		
- Habitat	2.308	**0.034***			774.416	2.820	**0.011***		
- Distribution	0.042	0.839			774.383	3.193	0.075		
- Body size	0.392	0.532	-0.002	0.000	784.491	0.998	0.319	0.000	0.001
OLIGOCHAETA									
- Foraging mode	0.051	0.821			1794.895	0.396	0.530		
- Habitat	0.065	0.999			1795.005	0.976	0.442		
- Distribution	0.483	0.488			1797.306	0.226	0.635		
- Body size	0.004	0.952	-0.003	0.000	1808.529	0.314	0.576	-0.002	0.002
OPILIONES									
- Foraging mode	0.036	0.850			876.397	0.060	0.807		
- Habitat	0.183	0.981			890.089	0.299	0.937		
- Distribution	0.658	0.418			878.617	0.402	0.526		
- Body size	0.598	0.440	-0.001	-0.001	889.597	1.456	0.228	0.001	-0.001

ORTHOPTERA									
- Foraging mode	0.110	0.740			2823.315	0.286	0.594		
- Habitat	3.263	**0.004***			2788.858	3.619	**0.002***		
- Distribution	7.199	**0.008***			2819.147	22.180	**<0.001****		
- Body size	2.244	0.135	0.004	-0.018	2835.538	1.462	0.228	0.001	-0.013
PHASMATODEA									
- Foraging mode	0.017	0.896			1693.943	2.505	0.114		
- Habitat	2.804	**0.011***			1679.588	1.686	0.124		
- Distribution	2.340	0.127			1694.469	2.132	0.145		
- Body size	1.371	0.243	0.001	0.003	1706.550	1.371	0.243	0.001	0.003
PLANT MATERIAL									
- Foraging mode	0.073	0.788			2661.402	1.301	0.255		
- Habitat	0.333	0.919			2646.430	1.755	0.108		
- Distribution	1.163	0.282			2663.155	0.220	0.639		
- Body size	15.220	**<0.001****	0.042	0.050	2663.621	43.510	**<0.001****	0.117	0.079
- Foraging mode	0.006	0.940			1215.050	0.898	0.344		
- Habitat	10.665	**<0.001****			1166.265	11.040	**<0.001****		
- Distribution	0.005	0.946			1217.893	0.370	0.544		
- Body size	4.892	**0.028***	0.002	0.012	1227.908	4.892	**0.028***	0.002	0.012
PSEUDOSCORPIONES									
- Foraging mode	0.433	0.511			1325.216	0.391	0.532		
- Habitat	1.749	0.109			1323.040	1.396	0.216		
- Distribution	0.338	0.561			1328.111	0.410	0.522		
- Body size	1.421	0.234	0.001	-0.001	1339.105	1.522	0.218	0.002	-0.001
PSOCOPTERA									
- Foraging mode	0.002	0.964			120.284	0.244	0.622		
- Habitat	0.197	0.978			145.638	2.299	**0.035***		
- Distribution	0.007	0.932			123.120	1.407	0.237		

- Body size	0.644	0.423	-0.001	0.000	133.843	0.644	0.423	-0.001	0.000
REPTILE (EGGS)									
- Foraging mode	4.790	0.029			1591.073	2.826	0.094		
- Habitat	0.934	0.470			1593.817	0.330	0.921		
- Distribution	13.992	**<0.001****			1584.973	0.332	0.565		
- Body size	30.520	**<0.001****	0.084	0.013	1582.564	44.430	**<0.001****	0.119	0.015
RODENTIA									
- Foraging mode	0.000	0.993			-1787.505	1.019	0.314		
- Habitat	0.052	0.999			-1731.568	0.127	0.993		
- Distribution	0.009	0.927			-1784.671	1.741	0.188		
- Body size	0.368	0.545	-0.002	0.000	-1774.208	0.368	0.545	-0.002	0.000
SCORPIONIDA									
- Foraging mode	0.000	0.985			1878.327	0.016	0.899		
- Habitat	0.977	0.441			1871.663	1.608	0.144		
- Distribution	0.118	0.732			1881.051	0.345	0.558		
- Body size	0.003	0.954	-0.003	0.000	1891.007	0.004	0.949	-0.003	0.004
SIPHONAPTERA									
- Foraging mode	0.000	0.985			-11.682	1.019	0.314		
- Habitat	0.000	1.000			16.904	0.127	0.993		
- Distribution	0.017	0.895			-8.857	1.741	0.188		
- Body size	0.132	0.717	-0.003	0.000	1.775	0.132	0.717	-0.003	0.000
SOLIFUGA									
- Foraging mode	5.742	**0.017***			1036.550	0.353	0.553		
- Habitat	1.838	0.091			1043.573	0.658	0.684		
- Distribution	1.268	0.261			1043.818	2.150	0.144		
- Body size	0.066	0.797	-0.003	0.000	1055.762	0.208	0.649	-0.002	0.000
SQUAMATA									
- Foraging mode	0.168	0.683			2397.230	4.396	**0.037***		

- Habitat	0.613	0.720			2384.799	0.392	0.884		
- Distribution	13.892	**<0.001****			2386.639	6.042	**0.015***		
- Body size	0.002	0.965	-0.003	0.000	2408.913	19.010	**<0.001****	0.053	0.025
THYSANURA									
- Foraging mode	0.000	0.988			1284.444	0.626	0.430		
- Habitat	0.719	0.635			1288.557	0.834	0.545		
- Distribution	3.827	**0.051**			1283.481	3.269	0.072		
- Body size	1.810	0.179	0.003	-0.001	1297.570	1.992	0.159	0.003	-0.001
THYSANOPTERA									
- Foraging mode	0.078	0.780			458.538	0.102	0.749		
- Habitat	0.656	0.685			475.962	0.532	0.784		
- Distribution	1.536	0.216			459.925	0.317	0.574		
- Body size	0.031	0.859	-0.003	0.000	472.199	0.031	0.859	-0.003	0.000
TRICHOPTERA									
- Foraging mode	0.001	0.974			176.856	0.310	0.578		
- Habitat	0.046	1.000			202.232	0.184	0.981		
- Distribution	0.094	0.759			179.605	1.112	0.292		
- Body size	0.239	0.626	-0.002	0.000	190.380	0.239	0.626	-0.002	0.000
UROPYGI									
- Foraging mode	0.008	0.931			-3881.895	1.019	0.314		
- Habitat	0.002	1.000			-3793.030	0.127	0.993		
- Distribution	0.175	0.676			-3879.222	0.575	0.449		
- Body size	1.579	0.210	0.002	0.000	-3871.309	1.579	0.210	0.002	0.000
VERTEBRATA									
- Foraging mode	2.037	0.155			1673.446	0.925	0.337		
- Habitat	0.590	0.738			1674.261	0.551	0.769		
- Distribution	0.372	0.542			1677.946	0.434	0.510		
- Body size	4.685	**0.031***	0.011	0.006	1685.120	20.720	**<0.001****	0.058	0.011

ZYGOPTERA									
- Foraging mode	0.001	0.969			112.823	1.019	0.314		
- Habitat	0.202	0.976			138.259	0.127	0.993		
- Distribution	0.466	0.496			115.200	0.575	0.449		
- Body size	0.353	0.553	-0.002	0.000	125.913	0.353	0.553	-0.002	0.000

Table 5: Mean and standard deviation values of prey ingestion (%) on each different habitat based on for significant values from the analysis on the relationship between dietary preferences and ecological traits for sampled lizard species around globe (N=323). Bold values presenting the highest ingestion value for a single prey category across habitat types.

CATEGORY	Arboreal	Bromelicolous	Fossorial	Saxicolous	Semi-aquatic	Semi-arboreal	Terrestrial
Amphibia	-	-	-	**0.05±0.38**	-	-	-
Amphibia (eggs)	-	-	-	**0.08±0.58**	-	-	-
Anura	0.15±0.81	**5.20±5.20**	-	0.04±0.22	4.15±5.35	-	0.52±3.85
Aves	**0.42±2.47**	-	-	0.05±0.38	-	-	0.04±0.43
Chelonia	-	-	-	**0.25±1.73**	-	-	0.03±0.35
Crustacea	-	-	-	0.17±1.22	**4.19±4.75**	-	0.22±1.98
Embioptera	0.05±0.38	-	-	0.01±0.06	**2.37±4.73**	-	0.04±0.34
Odonata	0.60±1.75	-	-	0.07±0.27	**0.75±0.94**	-	0.13±0.59
Orthoptera	13.67±13.21	**59.73±38.90**	8.79±23.55	11.83±14.84	7.64±6.66	14.24±13.82	12.65±14.05
Phasmatodea	**1.62±6.88**	0.30±0.30	-	0.24±0.84	0.43±0.81	0.73±1.26	0.19±1.16
Plecoptera	0.12±0.68	-	-	-	**4.40±8.80**	-	0.07±0.39
Number of species	62	2	18	50	5	4	182
Number of individuals	5079	131	1594	8160	242	237	22876

Table 6: Mean and standard deviation values of prey ingestion (%) on each different distribution pattern based on for significant values from the analysis on the relationship between dietary preferences and ecological traits for sampled lizard species around globe (N=323). Bold values presenting the highest ingestion value for a single prey category across habitat types.

CATEGORY	Tropical	Temperate
Blattodea	**7.09±12.10**	2.57±4.43
Chilopoda	**1.27±3.70**	1.07±2.94
Hymenoptera	**2.90±6.73**	3.67±6.41
Orthoptera	**15.71±17.47**	7.57±8.83
Reptile (eggs)	**0.43±4.03**	0.20±2.04
Squamata	0.57±2.88	**2.97±13.45**
Number of species	205	118
Number of individuals	25278	13041

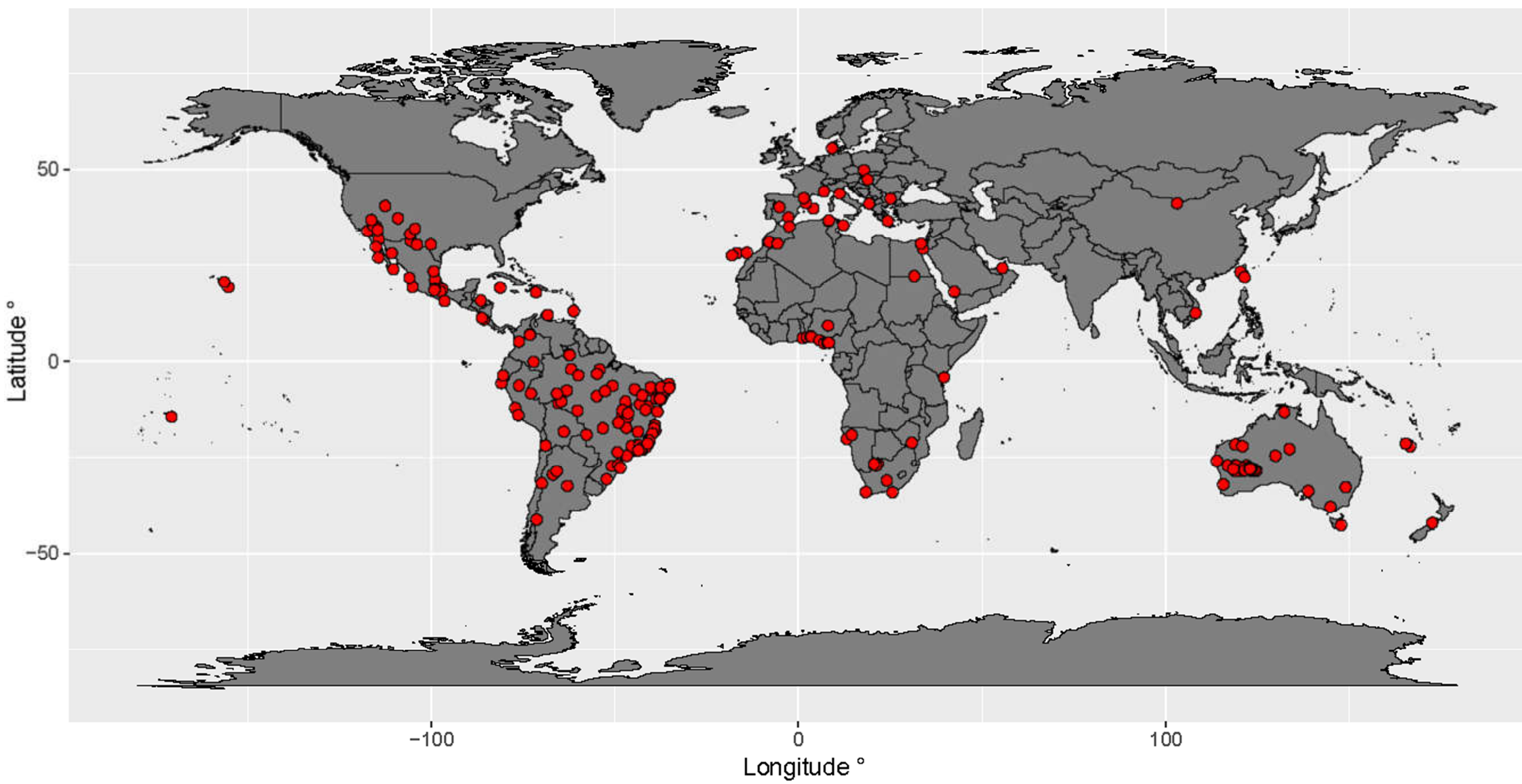
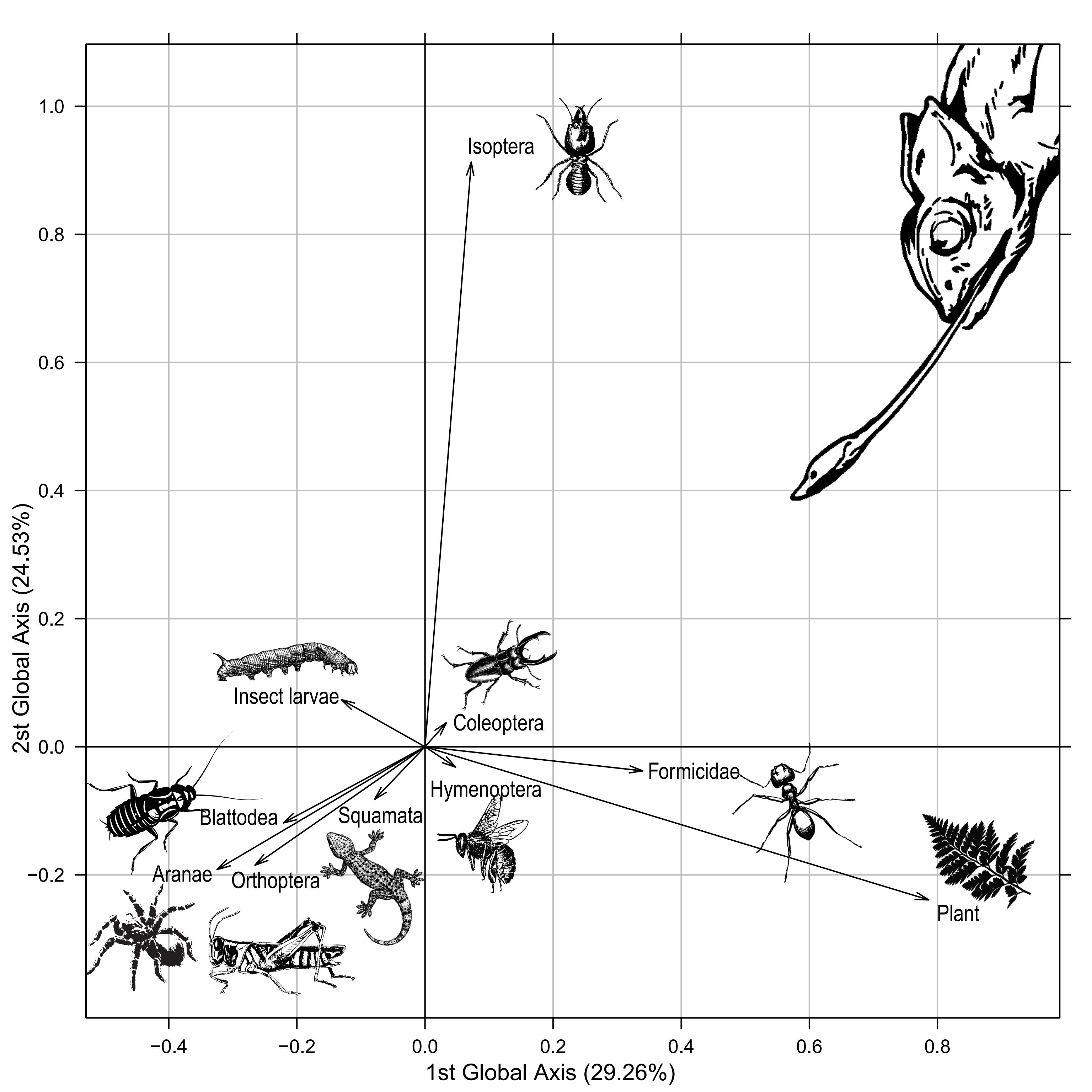


Figure 1: Sampling locations of all 323 lizard species from 722 populations from all globe, pooled for dietary database.

Figure 2- Phylogenetic tree of all sampled lizard species of our data (n=323), containing canonical eigenvalues for global principal components from pPCA analysis. White circles represent negative values on canonical axis while black circles represent positive values. Increasing on circle sizes represents higher association to a given axis from figure 3 (See 1st .pdf attached below). All images were collected from public domain repositories, see Photo Reference section on appendix 1 for links and authors.

Figure 3- Canonical axis based on the two global principal components from pPCA analysis from dietary aspects of sampled lizard species (n=323). Horizontal axis representes the first global component while the vertical axis represents the second global component (See 2st .pdf attached below)


Global axes species scores
IGUANIA
TOXICOFERA
ANGUIMORPHA
EPISQUAMATA
LACERTOIDEA
SCINCOIDEA
GEKKOTA
Dactyloidae
Corytophanidae
Liolaemidae
Polychrotidae
Phrynosomatidae
Crotaphytidae
Iguanidae
Tropiduridae
Agamidae
Chamaeleonidae
Varanidae
Anguidae
Helodermatidae
Xenosauridae
Lacertidae
Amphisbaenidae
Bipedidae
Gymnophthalmidae
Teiidae
Scincidae
Cordylidae
Gerrhosauridae
Xantusiidae
Gekkonidae
Phylodactylidae
Sphaerodactylidae
Eublepharidae
Diplodactylidae
Carphodactylidae
Global axis 1
Global axis 2
Global axis 1 score
Global axis 2 score
Prey Category
Prey Categories Scores
Aranae
Blattodea
Coleoptera
Formicidae
Hymenoptera
Insect larvae
Isoptera
Orthoptera
Plant
Squamata
- 0 +
* See figure 3 for further information



Isoptera
Insect larvae
Coleoptera
Formicidae
Hymenoptera
Blattodea
Squamata
Aranae
Orthoptera
Plant
1st Global Axis (29.26%)
2st Global Axis (24.53%)
−0.4
−0.2
0.0
0.2
0.4
0.6
0.8
1.0
−0.2

MYRMECOPHAGY IN LIZARDS:

EVOLUTIONARY AND ECOLOGICAL IMPLICATIONS

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Abstract

Myrmecophagy (ant feeding) is well known among many vertebrates. We study evolutionary and ecological aspects of ant ingestion in lizards in a global perspective. Using a worldwide database of lizard diets, we were able to sample 722 populations from 323 species. We tested the influence of phylogeny on myrmecophagy and its relationship with climate, foraging mode, habitat and body size. We also performed a reconstruction of ancestor states to understand how myrmecophagy evolved during the evolutionary history of lizards. We found that myrmecophagy in lizards is strictly related to evolutionary history; ant ingestion is restricted to specific clades (mostly within the Iguania). No relationship was found between myrmecophagy and climate, foraging mode, habitat, or body size. We suggests that morphological (lingual prehension, stocky bodies) and physiological (venom resistance) adaptations within many iguanian clades permit these lizards to exploit ants as an important food source. The absence of iguanian clades in some regions could have allowed other non-Iguania clades to have higher rates of ant ingestion (such as European lacertids). The absence of a relationship between myrmecophagy and climate variables likely reflects a combination of the high availability of ants in most climate regimes and the nearly global distribution of myrmecophagous lizards. The lack of relationship between foraging mode and habitat on myrmecophagy suggests that the mode of prey discrimination is more important than foraging strategy or ant diversification across all habitat types. Absence of a relationship of myrmecophagy to lizard body size likely has two nonexclusive causes. First, the smallest lizards may eat very few ants because ant defensive behaviors should have a relatively greater effect on them. Larger lizards likely don’t eat ants because the energy they would gain would be less than the energy used to search for and capture ants. Finally, our findings are consistent with recent proposals for myrmecophagy on lizards, based upon new phylogenies. Thus, we highlight the importance of specific studies regarding prey selection and noxious resistance to clarify some of the hypotheses that we propose.

Keywords

Formicidae, lizards, Squamata, phylogenetic comparative methods, reconstruction of ancestor states, diet

Introduction

Dietary preferences are a keystone for understanding ecological niches. It is possible to correlate diet to many aspects of species ecology, including foraging behavior, habitat preferences, activity period, reproduction and even morphology. Numerous studies reveal that feeding habits of individual species (and even clades) can be influenced by environment characteristics, competition, food availability, and climatic factors (recent approach) (Pianka 1973; Lenihan *et al.* 2011) and also determined by evolutionary history and community formation (historical approach) (Losos 1996; Webb 2000). For example, many cichlid fish species have a plastic dietary niche, switching from carnivorous and herbivorous behaviors depending on food availability (Stauffer & van Snick Gray 2004). Nevertheless, most typhlopid snakes have similar diets (they primarily prey on insects, especially ant brood and termites), regardless of the environments they live in or the continents they live on. This has been interpreted as dietary niche conservatism (Webb & Shine 1993; Webb *et al.* 2001). Lizards (the non-Serpentes squamates) have proven to be ideal models for studies of diets and their correlates. Nevertheless, few studies combine ecological and historical approaches (but see Vitt and Pianka, 2005; Vitt et al., 2003), and most groups/species are yet to have their diets described.

Myrmecophagy is feeding on ants (Hymenoptera; Formicidae) and is one of the most common kinds of stenophagy. Ants are widely distributed among all continents and terrestrial habitats (except polar ones), and, excluding humans and most cattle, they account for the highest biomass in terrestrial environments (near 30%) (Hölldobler & Wilson 1990, 1994). The conspicuousness of myrmecophagy should be expected.

Myrmecophagy is widespread among non-aquatic vertebrates and invertebrates, including other ant species (Briese 1984; Kelt *et al.* 1996; Swenson *et al.* 1999; Cushing 2012), and adaptations to this behavior are common. Almost all ant species are social, so they create aggregations (foraging trails and nests), which could favor individuals of predatory species that find and feed on ants (Hölldobler & Wilson 1990, 1994). Ants have a number of morphological, physiological, and behavioral traits designed to avoid predation (i.e.: soldier casts, nest complexity, chemical defenses). Nevertheless, many myrmecophagous species have evolved adaptations protecting them from ant defenses. The giant anteater (*Myrmecophaga* sp.) is an extreme example. It has a complex morphology (especially cranial) strictly adapted to feed on ants and other social insects (Naples 1999). Other terrestrial vertebrates have been able to sequester some of the chemicals produced by ants to use in their own chemical defense. These include frogs (e.g., poison dart frogs; Dendrobatidae, Darst *et al.* 2005). Dendrobatid frogs are the most poisonous frogs in the world, and the level of skin toxicity and their aposematic color is strictly associated with ingestion of ants, from which they incorporate alkaloids from ants on their skin, increasing poison toxicity (Caldwell 1996; Mebs *et al.* 2010).

Among lizards, myrmecophagy is well documented, and lizards within almost all major clades eat some ants (Pianka & Vitt 2003). Nevertheless, studies suggests that dietary preference for ants within lizards is strongly influenced by phylogeny (Vitt & Pianka 2005). Iguanian lizards tend to eat more ants than non-iguanians lizards, which is often associated with the sit-and-wait foraging mode and a lack of chemical discrimination of prey. Although many lizard clades have well developed vomeronasal systems for discriminating prey, iguanians have a poorly developed vomeronasal system for chemical discrimination. As a consequence, they often feed on insects with chemical defenses (i.e: alkaloids from ants, other hymenopterans and beetles). The sit-and-wait foraging mode also contributes to ant ingestion, as ants are a highly mobile prey and sit-and-wait lizards detect them visually (Vitt *et al.* 2003; Vitt & Pianka 2005). Moreover, some iguanian lizards tend to specialize on ants, for example *Moloch horridus*, the Australian agamid thorny devil lizard (Pianka & Pianka 1970). An individual can eat approximately 750 ants per day under natural conditions (Withers & Dickman 1995). Phrynosomatid lizards in the genus *Phrynosoma* are another example. They are primarily myrmecophagous and some species (i.e.: *Phrynosoma cornutum*) have a compound in their blood plasma that detoxifies harvester ants (*Pogonomyrmex*) venom, allowing them to withstand a lethal dose approximately 5.5 times higher than phrynosomatid lizards in the genus *Sceloporus* (Schmidt *et al.* 1989). In addition, species of *Phrynosoma* sequester some of the ant chemicals into their circulatory system providing some defense against canid (Sherbrooke *et al.* 2004) and cat (Sherbrooke *et al.* 2012) predators. It seems clear that specialization on ants by a wide diversity of tetrapod vertebrates has had a significant effect on their evolutionary history (Sites Jr *et al.* 2011).

Although these are the most obvious examples of myrmecophagy, many other lizards ingest large numbers of ants. Yet, they do not appear to have obvious morphological, behavioral, or physiological adaptations associated with specialization on ants. Vitt et al. (2003), suggest that the inability of most lizards using the sit-and-wait foraging mode to find hidden and low mobility prey results from their reliance on visual cues to detect prey. Recent changes in squamate phylogenetic relationships suggest that iguanians are a recent clade rather than ancestral as previous phylogenetic hypothesis had suggested (Pyron *et al.* 2013). Based on this and other recent phylogenetic hypotheses, ant ingestion may also be correlated with the time of diversification. Iguanian lizards and ants diversified at approximately the same time evolutionarily, which likely set the stage for myrmecophagy by these lizards . Ant ingestion by lizards may also be influenced by relatively recent ecological influences. However, no studies correlate recent ecological variables as predictors of ant ingestion by lizards even though empirical observations on lizard diets suggest that myrmecophagous lizards tend to occur more often in arid areas such as deserts (author's data). The relationship between termite diversity and lizard diversity in the Australian deserts is well established (Morton & James 1988). These findings suggest that social insects in arid areas may impact diversification of lizards in these areas, but the degree to which recent ecological factors influence ant eating by lizards remains poorly explored.

In this study, we test the following hypotheses: (1) myrmecophagy does not occur randomly across the Squamata phylogeny. Prediction: species in iguanian clades ingest more ants than species in other clades (2) myrmecophagy is highly conserved in the Iguania and arose early in their diversification. Prediction: the iguanian ancestor probably had a degree of ant ingestion, (3) myrmecophagy is correlated to climatic variables. Prediction: ant ingestion is higher in seasonal and dry areas, and (4) myrmecophagy is correlated to foraging mode, habitat and body size. Prediction: ant ingestion is higher in sit-and-wait/terrestrial/smaller lizards.

Materials and Methods

Dietary database and data collecting

We compiled data from a total of 722 populations of 323 lizard species, sampling 29 families from all continents except Antarctica (Figure 1, Table S1). Dietary data were obtained from two major sources. (1) Bibliographic searches of online scientific databases from Google Scholar™ and Zoological Record™. We used the keyword "lizard" together with the following keywords: "diet, feeding habits, feeding ecology, dietary aspects," within the year range of 1900 to 2015 and (2) data collected by all authors during the last four decades.

We used data from direct observation of stomach contents, fecal analysis and even observations. In each observed population, four variables were calculated: occurrence (number of individuals ingesting a given prey category), number, volume and mass of prey. Whenever data were separated into ontogenetic and/or sexual categories (e.g.: juvenile/adults, males/females), we calculated weighted averages for each prey category using sample sizes as weights. We also recalculated percentages to remove unidentified prey or to combine prey categories in order to standardize our data set. With respect to data that we collected, diet analysis was performed by direct observation of prey items in lizard stomachs. We dissected all specimens and removed their stomachs for analysis under a stereomicroscope. We identified and categorized each prey item. For each prey category, we calculated absolute and relative occurrence, number and volume (mm^3). To calculate volume, we measured width and length from each intact prey using an electronic calliper (0.01 mm) and then applied the following ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right) \times \left(\frac{w}{2}\right)^2,$$

where *l* is the prey length and *w* is the prey width. After collecting data, we performed weighted averages for each prey category to combine populations from a given species using sample sizes of each population as weights. Finally, we estimated volumetric values for populations where volume data was missing, using linear equations based on the relationship between occurrence and volume from species containing both kinds of data. We choose occurrence as an estimator of prey volume because this variable is less influenced by the relationship of prey numbers to volumes in lizard diets (lizard diets often contain many very small prey and a few larger ones, the latter providing the greatest amount of energy). Finally, we used volumetric percentages of ant ingestion to test the hypotheses that we present.

Ecological and climatic variables

We assembled a data set for the following variables for each population that we sampled: Latitude and Longitude (on decimal degrees), foraging mode (active or sit-and-wait), maximum SVL (in mm), and habitat (arboreal, semi-arboreal, bromelicolous, terrestrial, fossorial, semi-aquatic and saxicolous). Data for these same variables were extracted from bibliographic sources that included dietary data or supplemented by database papers and/or species description papers. Climatic predictors were generated for 19 climatic variables from *Worldclim* (Hijmans *et al.* 2005). We performed a principal components analysis (PCA), using the canonical axis that accounted most of the total variation. We extracted the first two canonical axes from temperature and precipitation variables. Temperature principal components together explained 99% of data total variation. TEMP1 was positively correlated with seasonality and negatively correlated to high temperatures, representing a gradient of stable warm climates to colder seasonal ones. TEMP2 was positively correlated with isothermality and negatively correlated to high temperatures, representing a gradient of warm seasonal climates to stable colder ones. Precipitation principal components explained together 96% of all variation. PREC1 is positively correlated to precipitation seasonality while negatively correlated with total precipitation, representing a gradient of wet and stable climates versus dry seasonal ones. PREC2 is positively correlated to precipitation seasonality during wet months, thus demonstrating a gradient of wet stable climates to seasonal climates but with high precipitation values during rainy season. We then used these four climatic variables for conducing the analysis describe below .

Statistical Analysis

To test for phylogenetic signal on myrmecophagy, we used K statistics from the *phytools* package for R (Revell 2012). We used a phylogenetic tree of sampled species containing branch lengths and a matrix containing ant ingestion percentages for each sampled species. Values near zero for K indicate phylogenetic independence of data while values near 1 indicate that a given character follows a Brownian Motion (BM) evolutionary model (Freckleton *et al.* 2002; Blomberg *et al.* 2003; Losos 2008). $K>1$ indicates that closely related taxa are more similar than expected in a BM model. Posteriorly, we tested for significance on phylogenetic signal (null hypothesis $K = 0$) based on randomizations of species names in the phylogeny using likelihood relationships tests (Blomberg *et al.* 2003). The phylogeny used for this test was extracted from Pyron *et al.* (2013).

To test for the influence of climatic variables and ecological traits on myrmecophagy, we built ordinary least squares models (OLS). We also built phylogenetic regression models using phylogenetic generalized least squares models (PGLS) (Grafen 1989). To implement PGLS models, we created covariance matrices based on Brownian Motion expectations from a phylogenetic tree of sampled species extracted from Pyron *et al.* (2013). These models remove the effect of evolutionary history thus providing data independency. Phylogenetic regressions were performed with the *ape* package for R (Paradis *et al.* 2004).

To identify were myrmecophagy arose during the evolutionary history of lizards, we reconstructed ancestral states. We used a BM evolutionary model based on ant ingestion values from sampled species using a maximum likelihood approach (Felsenstein 1981; Schluter *et al.* 1997). We performed reconstruction of ancestor states with *phytools* package for R.

We conducted all statistical analyses using R version 3.4.3 (R Development Core Team 2017) with a significance level of 5% to reject null hypotheses.

Results

From all 323 species we sampled, 70% (226 species across 18 families) presented some degree of ant ingestion. Ant ingestion weighted (sample size) average was 10.17% (Figure 2).

Phylogenetical influences on myrmecophagy

Blomberg's K test detected a significant phylogenetic signal for ant ingestion in lizards ($K = 0.3200$, $p = 0.001$), demonstrating that ant ingestion did not evolve randomly in lizard evolutionary history.

Reconstruction of ancestor states revealed that myrmecophagy in lizards evolved at least five times among major clades on Iguania, with most ant-eating species in just three families; Tropiduridae, Phrynosomatidae, and Agamidae, and lesser in Dactyloidae and Liolaemidae (Figure 2). It appears that the last common iguanian ancestor already included ants in its diet. Although myrmecophagy also evolved in Lacertoidea, it is still very rare/absent in the other subclades of the Lacertoidea, such as Gymnophthalmidae and Teiidae.

Relationship between myrmecophagy vs. climatic variables

Phylogenetic regressions found no relationship between ant ingestion and climatic variables (df=3, F= 0.563, p = 0.686), and similar results were obtained with simple ordinary least squares test (df=3, F= 0.592, p = 0.668). These results suggest that there is no relationship between climatic characteristics and ant ingestion in lizards, or that ant eating is not influenced by climatic environmental variables.

Relationship between myrmecophagy vs. foraging mode, habitat and body size

Myrmecophagy vs. foraging mode PGLS was not significant (df = 1, F = 0.703, p = 0.40), although OLS was highly significant (df = 1, F = 12.297, p < 0.001). Neither PGLS nor OLS produced significant results for ant eating and habitat relationships (gl = 6, F = 0.4627, p = 0.8357; df = 6, F = 1.2939, p = 0.2595, respectively). Finally, PGLS and OLS models produced non-significant relationships between body size and myrmecophagy (df = 1, F = 3.412, p = 0.0657; df = 6, F = 2.798 p = 0.0954, respectively) . These results suggest a lack of association between ant eating and ecological variables among lizard species.

Discussion

Phylogenetic influences on myrmecophagy

Myrmecophagy has evolved independently a number of times across lizard evolutionary history and is not related to present day climate or standard ecological variables. This result is expected, considering previous studies on lizard diets at a global scale (Vitt *et al.* 2003; Vitt & Pianka 2005). These studies, combined with ours, indicate that ant specialization evolved a number of times independently in lizards. Although iguanians are a relatively recent clade among squamates, ant specialization in this clade appears to date back to the most recent common ancestor of the Iguania, but this had not been tested. Vitt and Pianka (2005) performed an analysis to determine whether history explained dietary preferences of lizards, and approximately 27.6% of the variation in lizard diets could be traced to the Iguania and Scleroglossa dichotomy. This analysis used a morphology-based phylogenetic hypothesis (see Estes and Camp, 1988). The high ingestion of prey containing noxious chemicals for defense, especially ants (but also beetles and other hymenopterans) by Iguania largely explained this dichotomy. Using an ancestor reconstruction, we corroborate these results, as Iguania is the clade with highest ant ingestion, and the last common ancestor of Iguania most likely had already some degree of ant use. For example, among families in the Iguania, those with > 40% of their diet being ants are few (e.g., Tropiduridae, Phrynosomatidae, Agamidae).

We propose that most of the preference for ants by lizard species in the Iguania is explained by the sit-and-wait foraging mode, visual prey discrimination, and a suite of associated derived traits (Vitt *et al.* 2003; Vitt & Pianka 2005). The morphology-based phylogeny would suggest that scleroglossans (especially autarchoglossans) switched from an ambush sit-and-wait foraging mode to an active one, and that they had both chemical and visual prey discrimination historically (Schwenk 1993, 2000; Schwenk & Wagner 2001). As a consequence, they should access prey that were not available to iguanians (sit-and-wait ambushers, with visual discrimination) and could avoid eating prey with chemical defenses (Cooper Jr 1994, 1995), such as ants. Because most iguanians cannot detect hidden prey as the result of their lack of well developed vomeronasal sysytems, they have high ingestion rates of mobile prey including many noxious insects (beetles and hymenopterans) (Vitt & Pianka 2005). Our results, combined with more recent phylogenies (Sites Jr *et al.* 2011) provide other insights. First, Iguania is considered to be a derived clade in the most recent Squamata phylogenetic hypothesis (using molecular data) (Pyron *et al.* 2013). So, when compared to former scleroglossans, all ecological traits that were considered plesiomorphic are now considered as a derived state. In this context, we can hypothesize that the iguanian ancestor had biological traits that pre-adapted iguanians for myrmecophagy. In addition to sit-and-wait foraging mode and visual discrimination of prey, lingual prehension of prey (Cooper 1995), robust and relatively impermeable bodies covered with scales (to avoid physical injuries from aggressive ants) (Pianka & Vitt 2003), territorial behavior (to protect ant nest areas from possible competitors) (Huey & Pianka 1981) and physiological resistance to noxious ant chemicals by some strictly myrmecophagous genera (e.g.: *Phrynosoma*, Schmidt *et al.* 1989). Cause and effect remain unknown, but repeated evolutionary shifts to myrmecophagy and the suite of associated morphological and physiological traits (e.g.: eating apparatus, mimic behavior, venom assimilation) (Caldwell 1996; Naples 1999; Cushing 2012) among ant-eating iguanians suggest that the abundance and diversity of ants played a major role in the evolution of these traits in iguanian lizards and possibly many other taxa. A recent study hypothesized that ant preferences in the Iguania might be associated with the concurrent diversification of ants and species within the Iguania during the Cretaceous rather than the inability to detect different prey like lizard clades in which the vomeronasal system is well developed (Sites Jr *et al.* 2011). Our analysis supports this hypothesis and also suggests that many of the often extreme (e.g., *Moloch*) adaptations in ant specialists are relatively recent in origin.

Curiously, another finding of our work is that some species of Lacertidae (a former autarchoglossan family) had relatively high values of ant ingestion, yet lizards in this family are typically active foragers with streamlined bodies and a well-developed vomeronasal system for prey discrimination. Whether these species have diverged from their ancestors and other extant lizards in the Lacertoidea in terms of morphology, physiology, and behavior remains undetermined. Other lizards in the Lacertoidea, such as New World teiids, rarely eat ants (e.g.: Vitt *et al.* 1999; Rocha & Rodrigues 2005; Mesquita *et al.* 2006). In addition, it also seems that Lacertidae ancestor had also a degree of ant ingestion. Interesting, lacertids diversification occurred on regions (basically on Europe) where iguanian lizards are almost absent (with only few agamids) (Estes *et al.* 1988). If iguanians are in fact the most suitable anteaters than other lizard clades, then the absence of strong competitors for ants could have driven an ecological shift on lacertids trophic niche during their evolutionary history, promoting ants as an important component of their diet. Although this may seem speculative, no other "scleroglossan fauna" besides lacertids presents significant values of myrmecophagy across many genera we sampled. It was also expected previously that ants ingested by lacertids did not contain as many noxious chemicals as other ants from other sites (Vitt & Pianka 2004). Anyway, the lack of experimental studies concerning these aspects of iguanians plus further investigation on ant's toxicity and the relationship to ant ingestion on lizards makes difficult to assure more clear conclusions on the phylogenetic basis of myrmecophagy. In general, we can assume that phylogenetic history is probably the most important predictor for myrmecophagy on lizards, were Iguania (and secondly Lacertidae) have a high degree of ant ingestion when compared to others lizard, probably due to adaptations to access these insects as resource.

Relationship between myrmecophagy vs. climatic variables

We found no relationship between myrmercophagy in lizards and climatic variables. It is well known that ants are a common element of most environments around the world (Hölldobler & Wilson 1990; Dunn *et al.* 2007). Even in harsh environmental regimes, such as deserts and other arid areas, ants are diverse and abundant (Davidson 1977; Andersen 2007), largely the result of adaptations that help reduce water loss and the ability to survive with a hydric deficit (e.g.: underground nests, moisture control behavior, broad and fat-coated cuticles) (Lighton & Feener Jr 1989; Johnson 2000; Bollazzi & Roces 2010). Moreover, ant diversity and abundance in desert habitats usually plays key roles in maintaining community structure (both animal and vegetal, e.g.: Brown & Davidson 1977; Marone *et al.* 2000) and total biomass. Consequently, one might expect ant ingestion in lizards to be correlated with climatic variables, especially in environmental regimes were other prey for lizards might be more difficult to detect/access. Nevertheless, we found no correlation between ant ingestion and climate. We provide two possible nonexclusive explanations: (1) overall ant ingestion might be very similar among biomes and (2) some ant-eating lizard clades occur across all biomes (corroborated by phylogenetic signal). The first makes the assumption that because ants are both abundant and globally distributed in terrestrial habitats (Folgarait 1998; Dunn *et al.* 2007), they should be found in lizards diets globally independent of climatic regimes. So, if ants are equally frequent in lizard diets, no correlations would be found when accounting for differences in ant ingestion between climatic variables. The second explanation is based on the assumption that every biome/climatic regime in the world is inhabited by ant-eating lizard clades. In the tropics, ant-eating species are found in the Tropiduridae (Neotropical) and Agamidae (Paleotropical). In more temperate regions (mostly on deserts and shrublands), ant-eating species are found in the Agamidae (Old World, southern hemisphere) Liolemidae (New World southern hemisphere) and Phrynosomatidae (New World northern hemisphere). Additionally, ants as an abundant and seasonally available prey category may contribute to structuring of many if not all lizard communities (e.g.: Pianka 1973; Vitt *et al.* 1999; Vitt *et al.* 2003). The presence of these ant-eating taxa all around the globe may explain the absence of a relationship between climate and mymercophagy. Although both of the above explanations are plausible, we found the second one more plausible. If clade history plays a significant role in the evolution of myrmecophagy in lizards (which we have shown), we would expect a lack of a climatic effect, which we have also shown.

Relationship between myrmecophagy vs. foraging mode, habitat and body size

With the exception of the OLS for foraging mode versus ant-eating, we found no evidence for relationships between ant ingestion and the ecological variables. Foraging mode and its correlates to dietary preferences (especially in lizards) have been studied for decades (Huey & Pianka 1981; Cooper Jr 1994, 1995). Sit-and-wait predators typically feed on highly mobile prey, a result of their reliance on visual prey discrimination. Ants spend much of their time moving (e.g.: foraging/harvesting, Carroll & Janzen 1973; Traniello 1989), especially when compared to prey items eaten by many lizards (e.g., Orthoptera, Aranae, etc.). The expectation is that ant ingestion should be higher for sit-and-wait ambushers than active foragers. Nevertheless, our data shows a lack of association between these variables. First of all, foraging mode on lizards is directly associated to evolutionary history, especially on the major clades (Cooper Jr 1995). Plus, we found significant association between myrmecophagy and foraging mode on traditional OLS. These differences on results show how we can mislead interpretations while avoiding phylogenetic comparative methods. Considering this, we suggest that myrmecophagy on lizards is probably more associated to visual discrimination than to foraging mode itself. Another evidence for this proposition is that nocturnal lizards such as gekkotans (mostly sit-and-wait ambushers) have very low rates of ant ingestion. Many ant species have nocturnal habits and/or possess adaptations to nocturnality (Menzi 1987; Narendra *et al.* 2017). Nevertheless, geckos primary uses olfactory discrimination of preys instead of visual, so they probably tend to avoid feeding on ants (as these insects often contains noxious chemicals, plus other preys with better energetic intakes are active at night, such as spiders). It is also important to highlight that though foraging mode dichotomy is very known from literature, it has also been criticized, where other studies suggests a continuum instead of a dichotomy (Cooper 2005; Cooper 2007). So, maybe the available data we have to perform this study was not sufficient to define a common pattern. Unfortunately, mostly data on lizards foraging mode is based on the classical dichotomy active foraging vs. sit-and-wait ambusher.

The lack of association between habitat variables. We can also attribute this absence of relationship due to the high level of diversification on ants. Like lizards, ants occupies many different microhabitats, since from litter to tree canopies although it may present different abundance patterns (Longino & Nadkarni 1990; Yanoviak & Kaspari 2000). Indeed, ants can be an available resource in both vertical (arboreal, saxicolous) and terrestrial habitats, so availability and ingestion rate can be similar among all these habitat types. Nevertheless, previous studies on Australian deserts suggests that reptiles (specially lizards) that are ant brood specialists (which eats larvae, pupae and eggs) have a tendency to fossorial behavior (Abensperg-Traun & Steven 1997). Whether the relationship of habitat and myrmecophagy can vary between macro and microscale, from communities to biomes, remains unknown. As our focus was to search for global patterns on lizard ant ingestion and how it is related to habitat, we concluded that in general, there is no association between lizard ant ingestion and habitat preferences, probably due to high ant availability among all habitat types.

Associations between diet and body size are well known for many species, especially vertebrates (e.g.: Vézina 1985; Costa *et al.* 2008; Owen-Smith & Mills 2008). Increased body size generally results in an increase in prey size (Barnes *et al.* 2010). For most lizards that feed on arthropods or vertebrates, larger bodies and heads are positively correlated to larger prey, suggesting that energetic intake from few larger prey is more efficient eating many smaller prey (Costa *et al.* 2008). Ants are typically very small (especially worker casts, which are the most abundant) relative to lizards, when compared to other insects (they range from approximately 1-20mm) (Hölldobler & Wilson 1990, 1994). Within these, we hypothesized that smaller lizards prey on ants more often than larger lizards. However, the relationship between body size and ant ingestion was not ($p = 0.06$). Maybe sample size, although it may seem large, was not enough for a significant result concerning this relationship. Furthermore, most ant-eating lizards are medium sized lizards (e.g.: *Phrynosoma*, *Tropidurus*, *Plica*, *Moloch*, *Ctenophorus*, figure 3), while smaller lizards (even among iguanians) do not feed on ants as much as these other genera. Besides the relatively small size of ants, these animals are mainly clustered and can be aggressive when disturbed (Whitehouse & Jaffe 1996; Sakata & Katayama 2001). Some species can even easily kill a small lizard (there are even species of army ants that prey upon small vertebrates. e.g.: Eciton, Sazima 2017) Within these, it is also possible that body size is not a good predictor of ant ingestion, as although they can be considered a small prey when compared to other preys, their ecological aspects and aggressive behavior characteristics can make their ingestion difficult to smaller lizards.

Conclusion

We found that myrmecophagy in lizards is mostly explained based on phylogenetic history. Major Iguania clades appear to have adaptations that can at least facilitate the ingestion of ants. These include: lingual prehension of prey, visual cues for prey detection, and lack of a well-developed vomeronasal system among others. These adaptations could have made them suitable competitors for ants on many lizard communities, where some species have developed a diet strictly composed by ants. Moreover, the presence of ant-eating lizards on Lacertidae family may be related to the absence of iguanian lizards compounding mostly of European lizard communities, thus lowering competition for ants. Although this may seem speculative, we open new insights on the relationship between ant-eating and lizard evolutionary history. The next steps to elucidate many of the questions that arose on this work lies on the performing of comparative studies on ant aggressiveness/ toxin resistance, ant eating efficiency, for instance. Also, myrmecophagy is apparently not correlated to any other climatic or ecological variable (foraging mode, habitat and body size). Most of this lack of relationship between ant ingestion and climate and habitat can be due to the high diversity and abundance of ants and ant eating clades across all habitats and biomes, resulting in a similar ingestion rate across all habitats and environmental regimes. Foraging mode seems not to be an important predictor of ant ingestions, which seems to be more related to prey discrimination process. Finally, body size also did not predict ant ingestion rates, and we hypothesized that larger lizards would not eat ants because of the low energetic efficiency on ant feeding; while really small lizards can suffer from ant aggressive behavior more drastically during predation than medium sized lizards. These last explanations are also gates for further studies such as ontogenetic variation researches specifically regarding ant ingestions as well as comparative studies on ant ingestion within myrmecophagous genera. These kinds of researches can help elucidate predator-prey size relationships between lizards and ants for a better clarification of some suggested hypotheses on this present work.

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Figures

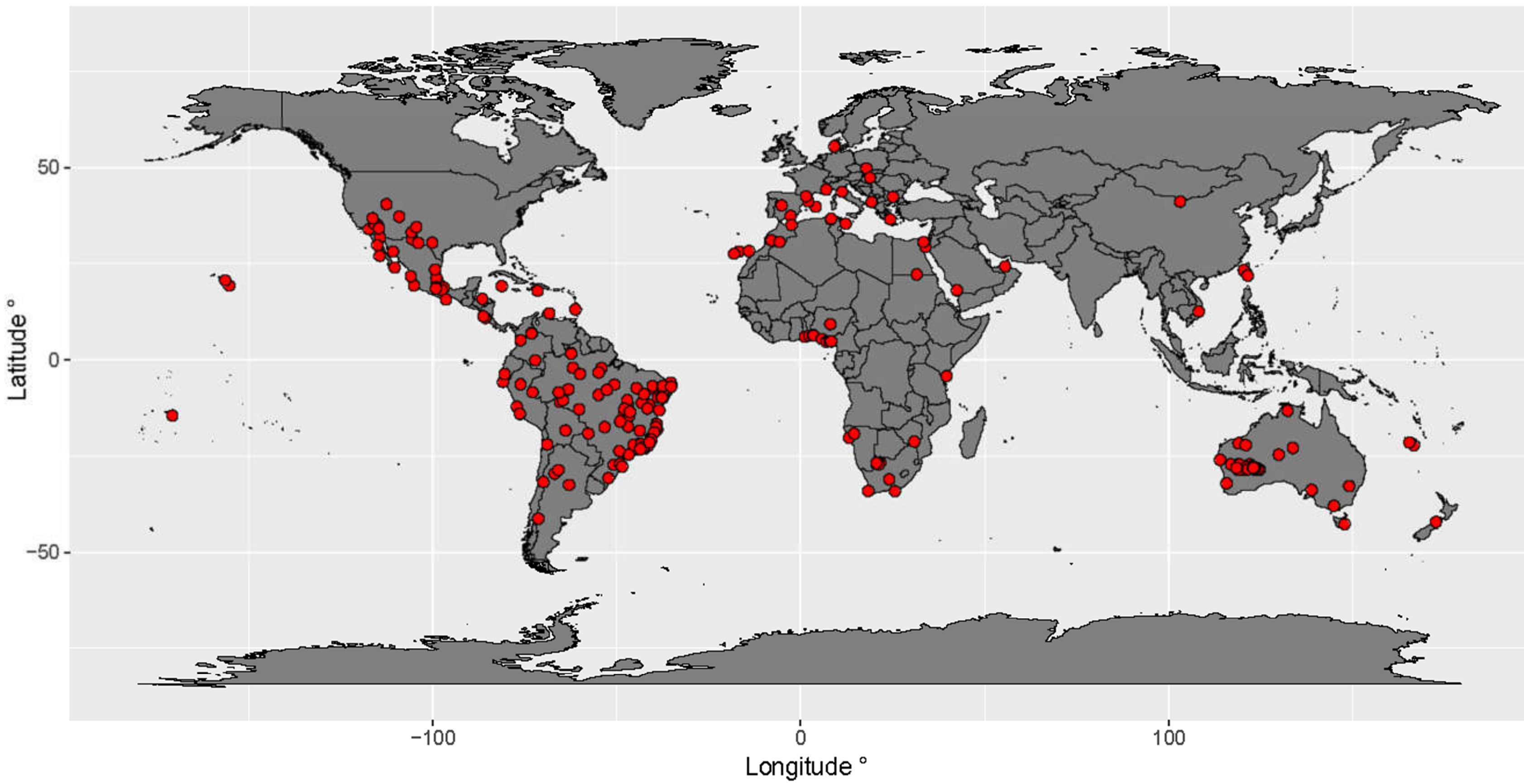

Figure1: Sampling locations of all 323 lizard species from 722 populations from all globe, pooled for dietary database.

Figure 2: Reconstruction of ancestor state based on maximum likelihood of Formicidae ingestion on lizards phylogeny (N = 323). Warmer colors represent low ant ingestion while colder colors represents high ant ingestion rate. (See 1st .pdf attached below)

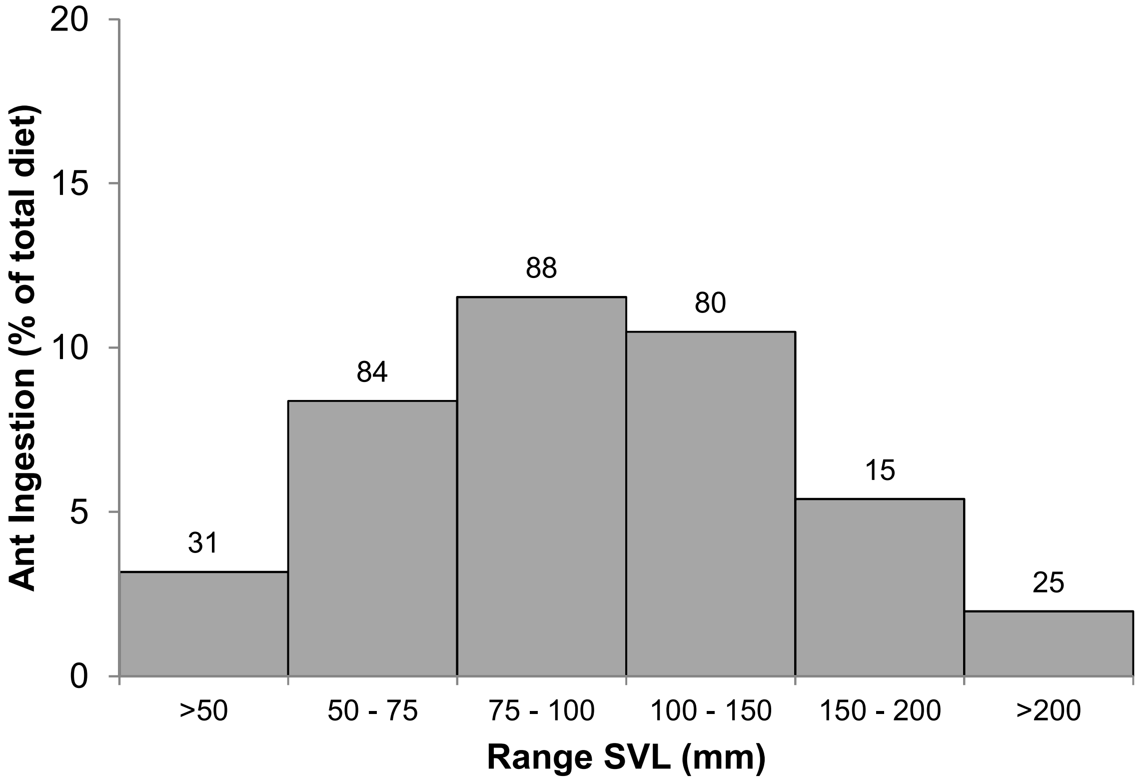

Figure 3: Lizard average ant ingestion by maximum snout-vent length (SVL) range. Values on bar tops are the total number of species from each SVL range.

Iguania
Toxicofera
Anguimorpha
Episquamata
Lacertoidea
Scincoidea
Gekkota
Dactyloidae
Corytophanidae
Liolaemidae
Polychrotidae
Phrynosomatidae
Crotaphytidae
Iguanidae
Tropiduridae
Agamidae
Chamaeleonidae
Varanidae
Anguidae
Helodermatidae
Xenosauridae
Lacertidae
Amphisbaenidae
Bipedidae
Gymnophthalmidae
Teiidae
Scincidae
Cordylidae
Gerrhosauridae
Xantusiidae
Gekkonidae
Phylodactylidae
Sphaerodactylidae
Eublepharidae
Diplodactylidae
Carphodactylidae
0
25
50
75
100
Ant ingestion on total diet (%)
Legend
Weigthed mean of ant ingestion (10.71%)
Clade above mean ant ingestion
Clade above 40% of ant ingestion