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MICHELE DE OLIVEIRA

PADRÕES DE VARIAÇÃO MORFOLÓGICA EM *Ophiodes fragilis* (SQUAMATA, DIPLOGLOSSIDAE) RELACIONADOS A ASPECTOS ABIÓTICOS E BIÓTICOS

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Regional Integrada do Alto Uruguai e das Missões como parte dos requisitos para obtenção do Título de Mestre em Ecologia (Ecologia e Conservação da Biodiversidade).

Ecologia e Conservação da Biodiversidade
Prof. Dr. Rodrigo Fornel
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"E quando a tempestade tiver passado, mal te lembrarás de ter conseguido atravessá-la, de ter conseguido sobreviver. Nem sequer terás a certeza de a tormenta ter realmente chegado ao fim. Mas uma coisa é certa. Quando saíres da tempestade já não serás a mesma pessoa. Só assim as tempestades fazem sentido".

Haruki Murakami – Kafka à beira mar

“Talvez nos faça bem ter uma queda de vez em quando. Desde que não nos quebre”.

J. M. Coetzee – Desonra

"A felicidade pode ser encontrada nas horas mais sombrias, se a pessoa se lembrar de acender a luz".

J. K. Rolwing – Harry Potter e o Prisioneiro de Azkaban

Padrões de variação morfológica em *Ophiodes fragilis* (Squamata, Diploglossidae) relacionados a aspectos abióticos e bióticos

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09 de agosto de 2017

Resumo: O gênero *Ophiodes* é endêmico da região Neotropical e inclui lagartos ápodos de hábitos terrícolas, que apresentam capacidade de autotomia caudal. A espécie *Ophiodes fragilis* possui ampla distribuição, associada predominantemente com formações florestais com diferentes características. O presente trabalho analisou os padrões morfológicos das escamas cefálicas de *Ophiodes fragilis*, buscando testar a existência de uma relação entre estes padrões e os diferentes ambientes de ocorrência da espécie, bem como a presença de variação geográfica resultante de isolamento pela distância. Buscou também investigar a influência de fatores abióticos (ambientais) e bióticos (dieta) sobre a variação morfológica dos organismos. Para tanto, foram utilizadas técnicas de morfometria geométrica, modelagem de nicho, análise de dieta e análises estatísticas uni e multivariadas. A hipótese da variação geográfica por isolamento pela distância não foi corroborada. A variação morfológica existente é explicada pela diferença ambiental entre os habitats e pelo tipo de dieta dos organismos. A temperatura é o principal fator que influencia tanto a distribuição da espécie quanto em sua variação morfológica, pois determina a disponibilidade de artrópodes, que são o recurso alimentar mais relevante para estes lagartos.

Palavras-chave: morfometria geométrica, modelagem de nicho, região Neotropical.

Patterns of morphological variation in *Ophiodes fragilis* (Squamata, Diploglossidae) related to abiotic and biotic aspects

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Abstract: The genus *Ophiodes* (Wagler, 1828) is endemic to the Neotropical region and includes limbless lizard of fossorial habits that have a caudal autotomy capacity. The species *Ophiodes fragilis* (Raddi, 1820) has a wide distribution, associated predominantly with forest formations with different characteristics. The present work analyzed the morphological patterns of cephalic scales of *Ophiodes fragilis*, searching to test the existence of a relationship between these patterns and the different environments of occurrence of the species, as well as the presence of geographic variation resulting from isolation by distance. It also sought to investigate the influence of abiotic (environmental) and biotic (diet) factors on the morphological variation of organisms. For that, we used geometric morphometrics procedures, niche modeling, dietary analysis and univariate and multivariate statistical analyzes. The hypothesis of geographic variation resulting from isolation by distance was not corroborated. The existing morphological variation is explained by the environmental difference between the habitats and the type of diet of the organisms. The temperature is the main factor that influences both the distribution of the species and its morphological variation, since it determines the availability of arthropods, which are the most relevant food resource for these lizards.

Keywords: geometric morphometrics, niche modeling, ecoregions.

APRESENTAÇÃO DA DISSERTAÇÃO

A presente dissertação está organizada em uma introdução geral, dois capítulos no formato de artigos científicos, já formatados nas normas de publicação dos periódicos aos quais pretendemos submetê-los, e uma conclusão geral. Na introdução geral é apresentada a problemática da pesquisa. No primeiro capítulo, abordamos as questões referentes à variação morfológica em *Ophiodes fragilis*, analisando a hipótese de que essa variação é decorrente do tipo de ambiente no qual os organismos se encontram, em função dos diferentes recursos oferecidos. Pretende-se submeter este artigo ao periódico *Ecology* (Qualis A1 na área da Biodiversidade). Tendo constatado neste primeiro trabalho que a morfologia muda em função do ambiente no qual o organismo se encontra, investigamos no segundo capítulo quais são os fatores ambientais que influenciam a variação morfológica. Este artigo será submetido ao periódico *Journal of Zoology* (Qualis A2 na área da Biodiversidade).

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SUMÁRIO

INTRODUÇÃO GERAL

Em 1858, Charles Darwin e Alfred Russel Wallace propuseram a teoria da descendência com modificações e sobrevivência diferencial por meio da seleção natural (DARWIN e WALLACE, 1858). Essa teoria teve um impacto profundo no pensamento científico, unificando todos os campos da biologia e culminando com a elaboração da síntese evolutiva moderna na primeira metade do século XX, cujas principais afirmações são os fundamentos da biologia evolutiva (FUTUYMA, 2009). A teoria sintética moderna considera a diversidade e a adaptação do mundo orgânico como resultado da produção contínua de variação e dos efeitos seletivos do ambiente (MAYR, 1977).

O ponto central da biologia evolutiva consiste em descrever e analisar a história, as causas e os mecanismos da evolução (FUTUYMA, 2009), sendo que esta pode ser entendida como a mudança na forma e no comportamento dos organismos ao longo das gerações (RIDLEY, 2006). Dentro da biologia evolutiva, a morfologia é a área que tem por objetivo a compreensão da biologia dos organismos com base em sua aparência estrutural, considerando qualquer aspecto que determine a formação e mudança das estruturas morfológicas dos organismos (BETZ, 2006). No entanto, poucos estudos foram capazes de quantificar a relação entre morfologia e capacidade de performance dentro das espécies (LOSOS, 1990). Os trabalhos de Grant (1986) e Wainright (1988, 1996) estão entre os raros exemplos que possuem estudos acoplados a experimentos de campo para investigar a hipótese de que diferenças na morfologia se traduzem em diferenças na capacidade de performance.

Indivíduos pertencentes a um mesmo táxon tendem a ter planos corporais similares, devido a mecanismos genéticos e de desenvolvimento que mantêm um padrão macroevolutivo mais ou menos estável de expressão fenotípica (CARROLL, 2005). Entretanto, as condições ambientais podem influenciar o fenótipo, causando respostas plásticas nos organismos (RONGLING et al., 2003). Ao longo de sua distribuição, membros da mesma espécie podem habitar ambientes com características diversas. As condições físicas, tais como complexidade do habitat, tipo de substrato e temperatura, bem como as condições ecológicas, como interações de competição, pressão de predação e hábitos alimentares, podem diferir entre ambientes (IDASZKIN et al., 2013), levando à diferenciação morfológica nos organismos que os habitam.

A existência de diferenças qualitativas e quantitativas em traços morfológicos, fisiológicos, comportamentais e até mesmo moleculares e cromossômicos entre populações espacialmente segregadas é chamada de variação geográfica. Essa variação apresenta, em última instância, base genética e pode ser adaptativa ou não (MAYR, 1977). Eventualmente, resulta em processos de formação de raças geográficas ou mesmo em novas espécies e pode ser resultado da ação da seleção natural. Processos de especiação ocorrem mesmo em presença de fluxo gênico, como documentado para os lagartos do gênero *Anolis*, para os quais a especiação se deu em função da especialização para ocupação de estratos diferentes de um mesmo ambiente (LOSOS et al., 2006).

O modelo de isolamento pela distância afirma que a divergência genética e a diminuição do fluxo gênico acentuam-se com a distância geográfica entre as populações (WRIGHT, 1943). Pode-se considerar que o mesmo ocorre com a morfologia. Assim, quanto mais distantes os grupos estiverem, mais distintos morfologicamente eles serão entre si. Da mesma forma, populações de uma mesma espécie vivendo em habitats heterogêneos podem responder de maneiras diferentes às características destes ambientes, levando a uma diferenciação morfológica em função das diferentes condições às quais estão submetidos (CASAS, 2011).

A estrutura do habitat é de fundamental importância para a organização das comunidades faunísticas. O habitat pode ser complexo e heterogêneo, sendo que a complexidade se refere à estruturação vertical de seus elementos, enquanto que a heterogeneidade se refere à estruturação horizontal (AUGUST, 1983). Uma maior heterogeneidade de habitats oferece maiores possibilidades de nichos (MAGURRAN, 1988).

A composição das espécies animais presentes neste habitat e de suas abundâncias dependem, em última análise, do componente da estrutura da vegetação (CASAS, 2011). Desta forma, alterações na estrutura da vegetação exercem uma grande influência nas distribuições e adaptações dos organismos (WIENS, 2005), já que resultam em uma gama diferenciada de condições e recursos disponíveis. Consequentemente, para entender o papel ecológico que uma espécie desempenha, torna-se necessária a realização de estudos que envolvam questões sobre uso do habitat, ecologia trófica e ecologia reprodutiva.

A dieta de uma espécie resulta da ecologia local da população e da história evolutiva do táxon (CARVALHO et al., 2007), fornecendo informações a respeito dos itens consumidos, da importância relativa de cada item, das estratégias de forrageamento e dos modos de detecção de presas (BELVER e ÁVILA, 2001;

CAPPELLARI et al. 2007; HUEY e PIANKA, 1981). A exploração de itens alimentares abundantes no ambiente é o principal fator de sucesso na utilização de diferentes habitats (ZAMPROGNO e TEIXEIRA, 1998).

Neste sentido, a ecomorfologia compreende a inter-relação entre a morfologia e o ambiente natural no qual ela se encontra, buscando possibilitar o entendimento da contribuição mútua de ambos os aspectos (MOTTA e KOTRSCHAL, 1992). Dedica-se, então, ao estudo da relação entre os caracteres morfológicos dos organismos e sua função no habitat em que vivem (LOSOS, 1990) e se utiliza da variação morfológica dos indivíduos para estudar a adaptação dentro das populações (BARRETO-LIMA, 2012). Fundamenta-se na ideia de que as formas dos organismos e seus modos de vida correlacionam-se, de maneira que o ambiente age sobre o fenótipo por meio de pressões seletivas e seleciona os organismos de acordo com os recursos disponíveis (NORTON et al., 1995; TEIXEIRA e BENNEMANN, 2007). As variações na morfologia das espécies constituem, portanto, um reflexo parcial do uso diferenciado de recursos (PIANKA, 2000).

Na região Neotropical, a herpetofauna ocupa zonas climáticas diferentes, num gradiente norte-sul que vai desde regiões tropicais a subtropicais, temperadas e frias (LEMA, 2002). Além das diferenças climáticas, as regiões habitadas por estes organismos apresentam diferentes tipos de solo e vegetação, resultando em uma grande heterogeneidade de habitats (RAMBO, 1956; RIZINNI, 1997), formando diferentes ecorregiões, que incluem a Floresta com Araucária (Araucaria Moist Forest), o Pampa (Uruguayan Savanna) e as Florestas Costeiras da Serra do Mar (Serra do Mar Coastal Forests). Portanto, a herpetofauna representa um excelente objeto de estudo para explorar aspectos ecomorfológicos.

A ordem Squamata consiste em um grupo monofilético de répteis escamados formado por 4900 espécies de lagartos, 3070 espécies de serpentes e 200 espécies de Amphisbaenia (HEDGES e VIDAL, 2009) e engloba uma diversidade considerável de organismos de forma e tamanho variáveis. O termo "lagarto" é usualmente utilizado para se referir a todos os Squamata que não são serpentes ou Amphisbaenia, incluindo organismos profundamente diferentes em termos de morfologia e ecologia (VITT e CALDWELL, 2014).

Estudos moleculares recentes, por meio da análise de DNA nuclear e mitocondrial, sugerem que boa parte da filogenia clássica de Squamata, baseada em certos caracteres morfológicos, está incorreta. Uma nova divisão separa Dibamidae dos demais, como o grupo mais basal da ordem. Os outros membros da ordem seriam agrupados em Gekkota, Scinciformata, Toxicofera e Laterata. Dentro de Toxicofera, o grupo Anguimorpha incluí três famílias que possuem gêneros de lagartos ápodos: Anguidae, Aniellidae e Diploglossidae (SITES et al., 2011).

A sistemática filogenética clássica considera Diploglossinae como uma subfamília de Anguidae (BORGES-MARTINS, 1998; POUGH, 2008). Todavia, estudos moleculares indicam que este grupo apresenta um nível de divergência com Anguidae muito semelhante ao da família Anniellidae (MACEY et al., 1999; TOWNSEND et al., 2004; WIENS et al., 2006). Desta forma, Anguidae inclui apenas as subfamílias Anguinae e Gerrhonotinae, enquanto que Diploglossidae constitui uma família distinta (VIDAL e HEDGES, 2009).

A família Diploglossidae surgiu no final do período Cretáceo (VITT e CALDWELL, 2014) e inclui três gêneros. O gênero *Celestus* Gray, 1839 possui 29 espécies e ocorre nas Índias Ocidentais. O gênero *Diploglossus* Wiegmann, 1834 é formado por 18 espécies encontradas na América Central. O gênero *Ophiodes* Wagler, 1828 é endêmico da América do Sul e sua taxonomia ainda não está completamente esclarecida. Os diploglossídeos são lagartos de corpo alongado que geralmente possuem membros pequenos e uma longa cauda longa. Os membros são bastante reduzidos em alguns táxons que podem, inclusive, apresentar ausência de membros anteriores e membros posteriores vestigiais (VITT e CALDWELL, 2014).

O gênero *Ophiodes* é formado por lagartos de corpo cilíndrico e alongado, com tamanho máximo de 50 centímetros, ausência de membros anteriores e membros posteriores vestigiais. Estes lagartos apresentam hábitos terrícolas ou fossoriais, são vivíparos e se alimentam principalmente de artrópodes (BERNARDO e PIRES, 2006; MARQUES e SAZIMA, 2004; MONTECHIARO et al., 2011; PIZZATTO, 2005). A capacidade de autotomia caudal é uma característica típica deste gênero, que faz com que seus integrantes sejam conhecidos como cobras-de-vidro (BERNARDE, 2012).

A taxonomia do gênero *Ophiodes* é bastante controversa. Atualmente, há cinco espécies reconhecidas: *O. fragilis* (Raddi, 1826), *O. vertebralis* (Bocourt, 1881), *O. striatus* (Spix, 1824), *O. intermedius* (Boulenger, 1894) e *O. luciae* (Caacciali & Scott, 2015), além de três espécies ainda não descritas identificadas por Borges-Martins (1998). Uma sexta espécie, *O. yacupoi* (Gallardo, 1966), é considerada por alguns autores para a Bolívia e Argentina (GENISE, 1983; MONTANELLI e CHEBEZ, 1997), embora haja evidências de que se trata de uma variação de *O. fragilis* (BORGES-MARTINS, 1998).

Os lagartos deste gênero são forrageadores ativos e alimentam-se principalmente de artrópodes, sendo observadas práticas de canibalismo entre machos e juvenis. Montechiaro et al. (2011) concluíram que os itens mais importantes na dieta de *O.* cf *striatus* no sul do Brasil são Araneae e Orthoptera. Este mesmo estudo concluiu que a dieta das fêmeas é mais similar à dos juvenis do que à dos machos adultos. Entretanto, os autores apontam que a variação morfológica observada por eles entre machos e fêmeas não parece estar relacionada ao comportamento alimentar, mas sim ao comportamento reprodutivo da espécie. As fêmeas de *O. fragilis* apresentam tamanho corporal maior, enquanto que os machos apresentam os membros posteriores vestigiais ligeiramente maiores (PIZATTO, 2005).

Os estudos relativos ao gênero são escassos e concentram-se principalmente na biologia reprodutiva e na ecologia alimentar (BRUNER et al., 2005; MONTECHIARO, 2011). A morfologia e os padrões de diferenciação das espécies ainda são pouco conhecidos. Assim, seu estudo utilizando técnicas que quantifiquem a forma como ferramenta para compreender a diferenciação regional torna-se extremamente importante. Nesse sentido, o objetivo geral do presente trabalho foi verificar a existência de variações morfológicas em *O. fragilis*, relacionadas à dieta e às variações ambientais.

O primeiro capítulo teve por objetivo analisar a ocorrência de padrões morfológicos para a espécie, determinados pelo tipo de ambiente no qual ela se encontra inserida. A hipótese investigada foi a de que diferentes substratos oferecem diferentes recursos alimentares, resultando numa diferenciação nas entre as escamas dos indivíduos, já que estas estão relacionadas aos centros de ossificação do crânio, cujas características também dependem do tipo e tamanho do alimento ingerido.

O segundo capítulo buscou identificar quais as variáveis ambientais relacionadas com a distribuição potencial da espécie e a variação morfológica observada. Fatores com a temperatura e a precipitação estão relacionadas com a abundância de artrópodes, uma das principais fontes alimentares de *Ophiodes*. Portanto, esperamos que estas variáveis sejam determinantes tanto para a distribuição potencial da espécie quanto para os padrões morfológicos observados.

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CAPÍTULO 1 – BREAKING THE HABITAT: CHANGES IN FEEDING MODIFY MORPHOLOGY OF GLASS LIZARD *Ophiodes fragilis* (SQUAMATA, DIPLOGLOSSIDAE)

ABSTRACT

Although Squamata's cephalic scales function is well known, the functional meaning and the factors involved in morphological variation have not been sufficiently elucidated. Populations of the same species inserted in different habitats may show variations in response to local conditions. Thus, we aimed to verify the existence of morphological variation on cephalic scales of *Ophiodes fragilis* using geometric morphometrics techniques. And to relate this variation to the isolation by distance, environmental variation or dietary differences. We not verify significant geographic variation through isolation by distance ($p > 0.05$). However, there was significant morphological variation ($p < 0.05$) among ecoregions. This variation can be attributed to differences in feeding habits, caused by the influence of environmental variables, mainly the rainfall and the seasonality of temperature on the life cycle of arthropods, the primary food source of these organisms. In this way, the variation found is explained by the type of environment in which the organisms are inserted and not by the geographical distance between them.

Keywords: geometric morphometrics, cephalic scales, ecoregions, dietary analysis, isolation by distance.

INTRODUCTION

Evolution explains how the form and function of organisms are determined by the characteristics of their environments, including physical conditions, food resources and biotic interactions. Through it, the attributes of individuals in populations are continuously adjusted over generations to the changes in the environment. Its results cannot be understood without considering the environment, so ecology establishes a context for evolution (Ricklefs 2012).

Morphological variation of species is therefore an inevitable consequence of environmental variation, each of which must be well adapted to the habitat requirements of any part of its range. To understand how the adaptations of organisms reflect their environment, it is necessary to elucidate the selective factors and mechanisms of evolutionary response involved (Mayr 1977; Ricklefs 1990).

At the morphological level, individuals from natural populations show variation for practically all measurable characteristics (Ridley 2006). The existence of geographic variation in characters related to morphology and ecology was documented in several groups of organisms (Futuyma 2009; Moraes 2008), including some Squamata species with a wide distribution (Daltry et al. 1997; Vitt et al. 1997).

Squamata are one of the most diverse groups among vertebrates, including about 4900 species of lizards described (Hedges & Vidal 2009), which are organisms of great importance for evolutionary and ecological studies (Pyron 2013). The Diploglossidae family has approximately 51 species, most of which are terrestrial and forage in the litter (Vitt & Caldwell 2014).

The genus *Ophiodes* Wagler, 1828 occurs exclusively in the Neotropical region, in the east of the Andes, distributing to the center, east and southeast of South America (Pizatto, 2005). This genus has predominantly cryptozoic habits, and its members have a long cylindrical body, absence of anterior limbs, vestigial posterior limbs and caudal autotomy capacity, which makes them popularly known as glass snakes (Montechiaro et al. 2011). This genus encompasses five species, among them *Ophiodes fragilis* (Raddi, 1820).

Studies with other genera of lizards indicate that differences in diet, ecology and patterns of bone growth can be reflected in morphology, including in the formation of cephalic scales (Bruner et al. 2005; Costantini et al. 2010, Hughe et al. 2009). However, there are no studies on the morphology of the cephalic scales for any species of the genus *Ophiodes*. Thus, the implementation of works in this area becomes fundamental for the better understanding of these organisms and the influence of the environmental conditions on their morphology.

In this meaning, we tested the existence of morphological patterns for the cephalic scales of *O. fragilis* by means of geometric morphometrics techniques and dietary analysis. For that, the shape and size variations of these scales were analyzed in specimens belonging to different ecoregions (two types of forests and a type of savanna vegetation) and groups by geographic proximity. Our hypothesis was that the individuals of *O. fragilis* present different morphological patterns in the cephalic scales. Since these are organisms of terrestrial habits, therefore highly dependent and influenced by the substrate in which they are, we hope that each ecoregion has selected a different morphological pattern. Since the cephalic scales are related to the centers of ossification of the skull, whose characteristics also depend on the type and size of the ingested food, we expect a morphological differentiation between the scales of the individuals, once different substrates offer different alimentary resources.

MATERIAL AND METHODS

Sample and morphological analysis

For analysis of the morphology of the cephalic scales, we examined 200 individuals of *O. fragilis* from the southern region of Brazil, preserved in liquid medium in the follow collections: Museu de História Natural Capão da Imbuia (MHNCI), Museu de Ciências Naturais (MCN) of the Fundação Zoobotânica do Rio Grande do Sul, Museu Zoobotânico Augusto Ruschi (Muzar) of the Universidade de Passo Fundo and Museu Regional do Alto Uruguai e das Missões (MuRAU) of the Universidade Regional Integrada do Alto Uruguai e das Missões (S1 Appendix). The specimens were grouped by geographic proximity and according to the ecoregion (Olson et al. 2001) in which they were captured (Fig. 1), being: 97 of Araucaria Moist Forest (AMF), 31 of Serra do Mar Coastal Forest (SMCF) and 72 of Uruguayan Savanna (US). It was not possible to obtain information about the sex of most specimens, so this criterion was not considered in the analyzes.

Each specimen had the cephalic region photographed in dorsal view with a 5.0 megapixel resolution digital camera, with macro function, without flash, at a standard focal length of ten centimeters. The photographs were brought together with the tpsUtil 1.55 (Rohlf 2012). Subsequently, 25 two-dimensional anatomic landmarks (Fig. 2) were digitalized by the same person (MO) for the cephalic scales of the specimens, using tpsDig 2.17 (Rohlf 2013). The coordinates of landmarks were superimposed with a Generalized Procrustes Analysis (Dryden & Mardia 1998; Rohlf & Slice 1990), which removes non-form differences such as scale, position and orientation (Adams, Rohlf & Slice 2004; Zelditch 2004).

The size of the cephalic scales of the specimens was estimated from the log-transformed centroid size. The centroid size is defined as the square root of the sum of the squares of the distance from each landmark to the centroid of the shape of the landmark configuration (Bookstein 1991). The size variation between ecoregions and geographic groups was explored using a Variance Analysis (ANOVA), with Tukey's test for multiple comparisons. For this analysis, we used R, in version 2.14.1 (R Development Core Team 2011), with the Rmorph package (Baylac 2008).

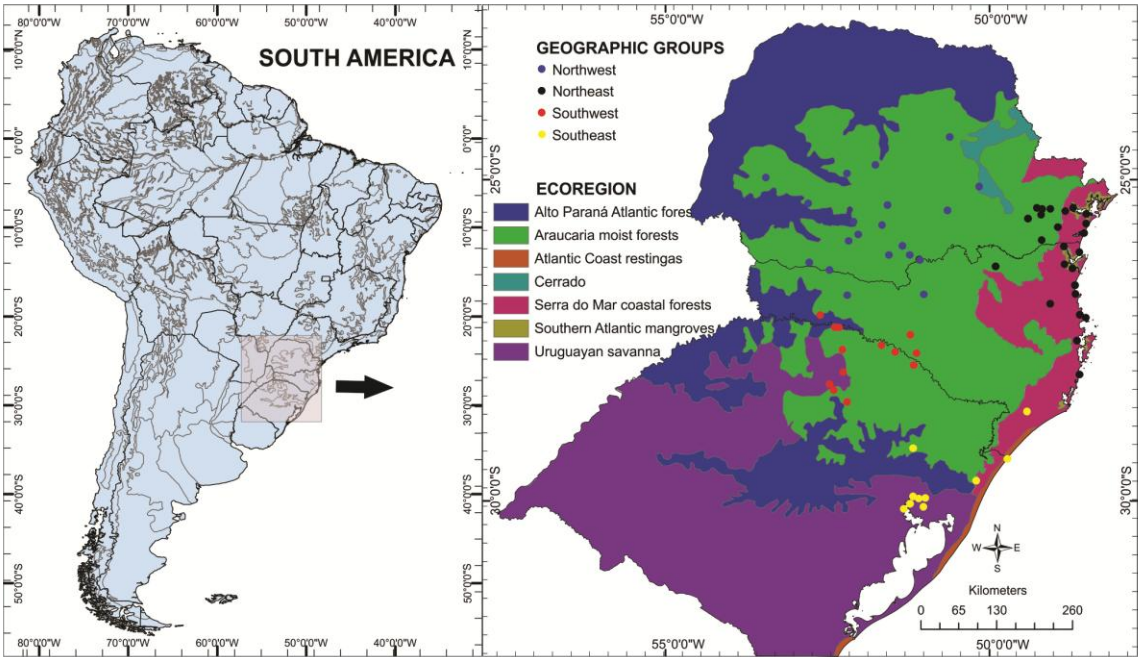

Figure 1. Map of South America indicating the geographical distribution of specimens for *O. fragilis*, according to ecoregion. Points of different colors represent the geographic groups.

The presence of allometry was examined by a multivariate regression of the shape by size (Monteiro 1999), the first being represented by the coordinates of Procrustes and the second by the size of the centroid. This procedure, performed with MorphoJ (Klingenberg 2011), removes the allometry effect from the data set, and the regression residuals represent a size independent variable (Klingenberg 2016). As the presence of allometry (6.4% of the shape explained by the size, $p < 0.001$) was verified, we used the residuals of the regression in the later analyzes referring to the variation of the shape.

The variation in shape of the cephalic scales in the specimens of the geographic groups and ecoregions was explored through a Canonical Variate Analysis (CVA). The difference in shape was tested by a Multivariate Analysis of Variance (MANOVA) with subsequent correction of Bonferroni. For the analysis of shape variation, we used MorphoJ (Klingenberg 2011), except for MANOVA, for which we used R, in version 2.14.1 (R Development Core Team 2011), with the Rmorph package (Baylac 2008).

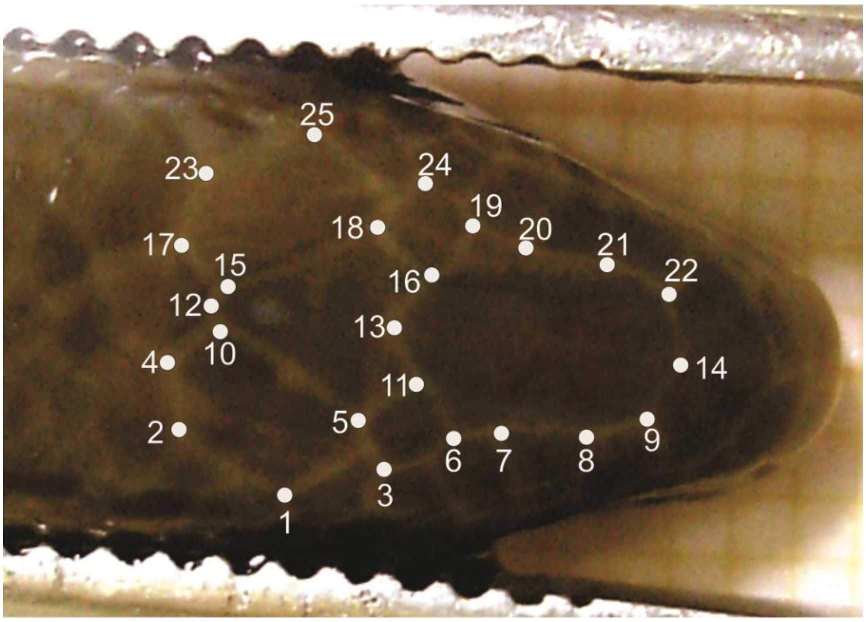

Figure 2. Disposition of 25 landmarks in the cephalic scales of *O. fragilis*. 1, 2, 4, 10: outline of the right parietal scale; 15, 17, 23, 25: outline of the left parietal scale; 7, 8, 9, 20, 21, 22: outline of frontal scale; 12, 13, 14 midline, passing through the interparietal and frontal scales.

Geographic variation

The information about the specimens gathering sites (taken in the visited collections) was used as a basis to generate a geographic distance matrix using Geographic Distance Matrix Generator (Ersts 2009). To do so, the gathering sites were grouped by geographic proximity, using the mean point of the coordinates of each of the four groups for the generation of the matrix. For the morphological variation, a Mahalanobis distances matrix was generated (Fornel et al. 2010). To test the occurrence of isolation by geographic distance, both matrices, geographic and morphological, had their similarities tested using the Mantel's Test, using 10,000 random permutations. For this analysis, we used the ade4 package in R (R Development Core Team 2011).

Dietary analysis

For the analysis related to the diet, we used the data referring to 60 specimens preserved in a liquid medium in the Museu de Ciência e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (MCP), in the Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul (MCN) and in the Museu de História Natural Capão da Imbuia (MHNCI) (S2 Appendix). These specimens are a subsample for the ecoregions analyzed here. As the isolation by distance hypothesis was not corroborated, we did not perform the dietary analysis for the geographic groups. Data on the diet of these specimens were collected, analyzed and published in full by

Montechiaro et al. (2011) which dissected, analyzed and identified the stomach contents of the specimens.

The individual prey volume (in mm^3) was estimated by the ellipsoid formula according to Lima et al. (2010), where L is the largest prey length and W is the largest prey width. The total volume of all prey was calculated as the sum of the volume of all its prey items:

$$V = 4/3\pi\ (L/2)(\mathrm{W}/2)^2$$

We evaluated the superimposition of diet in numerical and volumetric proportions of category of prey between the ecoregions by the similarity index Ojk (Pianka 1973), according to Cappellari et al. (2007). In this index, *pij* and *pik* represents the proportion of prey items in each category in the *j* and k groups. Values range from 0 (no similarity) to 1 (complete similarity):

$$Ojk = \frac{\sum PijPik}{\sqrt{\sum Pij^2 \sum Pik^2}}$$

To estimate the importance of each prey category consumed, we calculated the index of importance value (IV) of Gadsden & Palacios-Orona (1997) as:

$$IV = V'ij + N'ij + F'ij$$

Were, V'ij = Vij / ΣNij; N'ij = Nij / ΣNij; F'ij = Fij / ΣNij; being Vij the volume of prey category i in predator j; ΣVij the total volume of stomach content, Nij the number of items of prey category i in predator j, ΣNij the total number of items in the sample, Fij the number of stomachs of predator j in which prey category i was found; Nj the total number of stomachs of predator j.

RESULTS

Size and shape variation

When grouped according to geographic proximity, the organisms presented a difference in size for the cephalic scales ($F_{3,\ 196} = 8.21$, $p < 0.001$), and the southeast group had individuals smaller than the other three groups ($p < 0.01$) (Fig. 3). The results for the shape variation followed the same trend: the southeast group differed from the others (southwest: $F_{3,\ 196} = 12.42$; $p < 0.001$; northwest: $F_{3,\ 196} = 6.89$; $p < 0.01$; northeast: $F_{3,\ 196} = 4.65$, $p < 0.01$). The first axis of the CVA (Fig. 4) explained 50.51% of the shape variation and placed the southeast specimens in the negative scores, with a more compact and robust shape, and the specimens of the other three groups in the positive scores, with a more elongated and graceful shape.

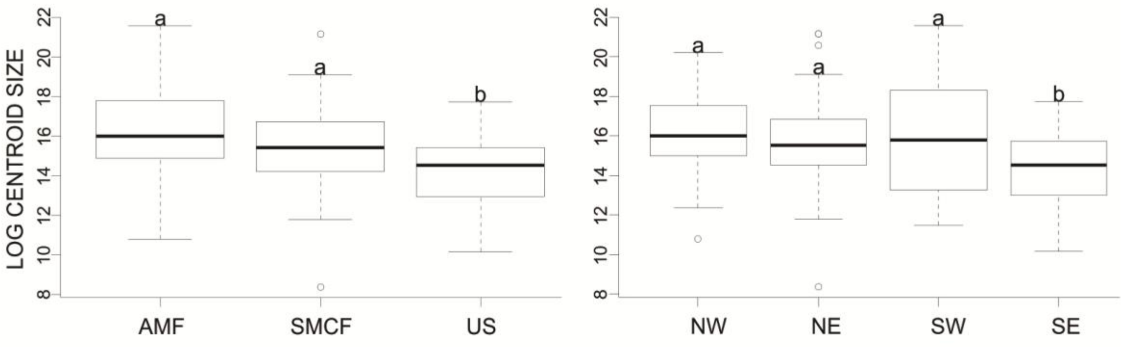

Figure 3. Box plot with standardized deviation of the centroid size across ecoregions and geographic groups. Different letters represent significative difference in Tukey's test. AMF: Araucaria Moist Forests; SMCF: Serra do Mar Coastal Forests; US: Uruguayan Savanna; NW: northwest; NE: northeast; SW: southwest; SE: southeast.

When grouped in the ecoregions, the specimens also presented size variation ($F_{2, 197} = 14.76$, $p < 0.0001$) (Fig. 3). Those belonging to Uruguayan Savanna were smaller than those of Araucaria Moist Forests (p < 0.0001) and Serra do Mar Coastal Forests ($p = 0.04$). There was no difference in size between the specimens of the two forest formations ($p = 0.22$) (Fig. 3).

We also verified the existence of shape variation between the specimens belonging to Uruguayan Savanna and Araucaria Moist Forests ($F_{2, 197} = 11.56$, $p < 0.001$) and Uruguayan Savanna and Serra do Mar Coastal Forests ($F_{1, 101} = 7.83$; $p < 0.001$). The specimens of the two forest formations did not differ in shape ($F_{1, 126} = 0.13$, $p = 0.96$).

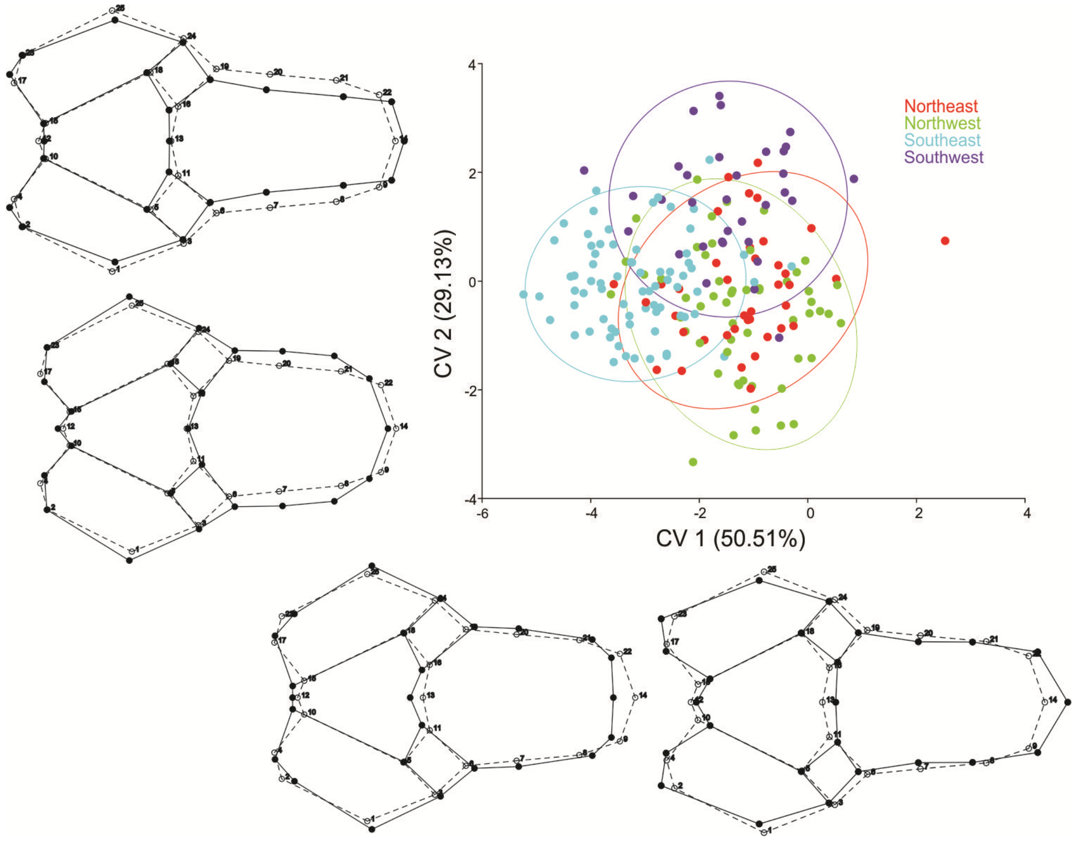

Figure 4. Canonical Variate axes (CV) depicting the shape variation among individuals from different geographic groups of *O. fragilis*. The scatter plot of CV1 versus CV2 is shown with the shape transformations along the extremes of the discriminant scores. Dotted lines indicate the consensus shape of each axis and the solid lines the positive and negative extreme shapes for each axis. Ellipses show 90% confidence intervals.

The shape variation along the first axis of the CVA (Fig. 5) placed the specimens of the forest formations predominantly on the negative scores, with a more elongated frontal scale ending at acute angle, with a sharper shape. Uruguayan Savanna specimens were predominantly placed on the positive scores, with a broader frontal scale, ending at a right angle, and a more robust shape. The second axis showed a tendency to separate forest groups, with Araucaria Moist Forests being more concentrated in negative scores, with a narrower front scale and a wider interparietal scale, and Serra do Mar Coastal Forests more concentrated in the positive scores, with a wider frontal scale and a narrower interparietal scale.

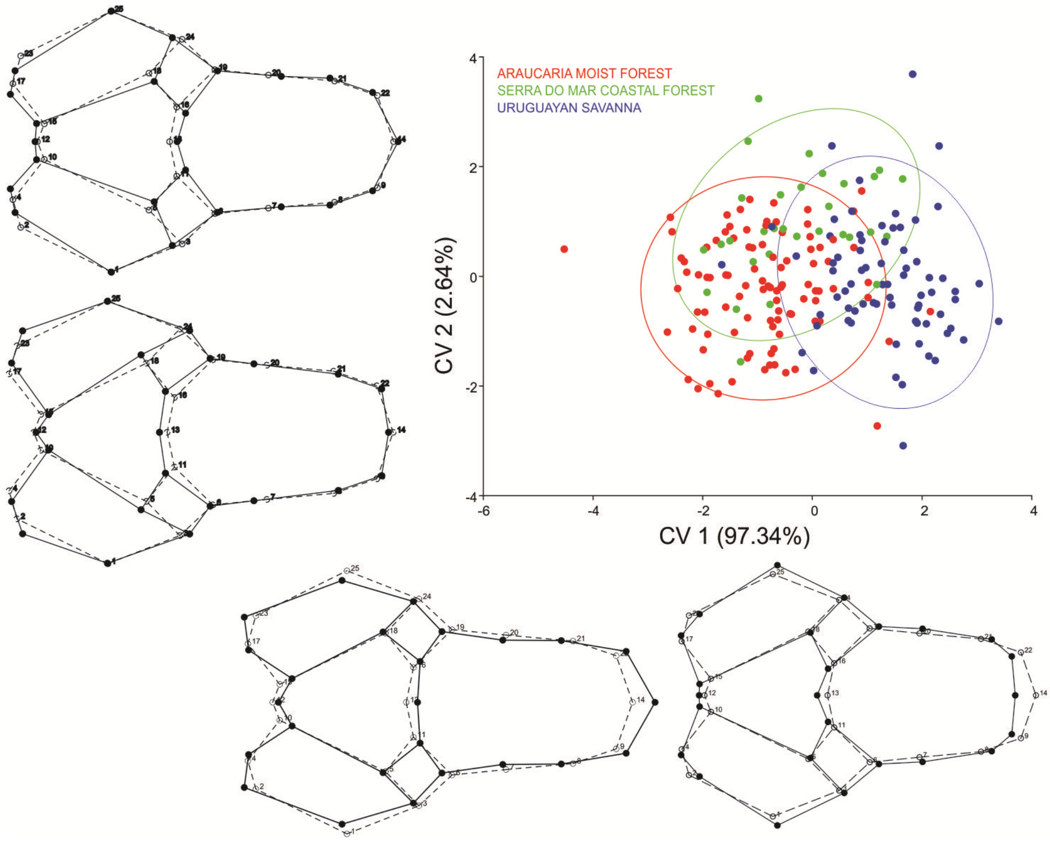

Figure 5. Canonical Variate axes (CV) depicting the shape variation among individuals from different ecoregions of *O. fragilis*. The scatter plot of CV1 versus CV2 is shown with the shape transformations along the extremes of the discriminant scores. Dotted lines indicate the consensus shape of each axis and the solid lines the positive and negative extreme shapes for each axis. Ellipses show 90% confidence intervals.

Geographic variation

The Mantel's test between the matrices of morphological variation and geographic distance was not significant ($p > 0.05$), indicating that there was no geographic structuring in the form of the cephalic scales. Morphological changes, therefore, are results of other factors and not of the occurrence of geographic variation. The differences in the shape and size of the specimens from the southeast group can be explained by the ecoregion in which they are found, since this group is formed predominantly by Uruguayan Savanna specimens.

Dietary analysis

The food similarity, based on the numerical proportions of prey categories, was higher among the two forest formations (Ojk = 0.87) than between Uruguayan Savanna and Araucaria Moist Forests (Ojk = 0.43) and between Uruguayan Savanna and Serra do Mar Coastal Forests (Ojk = 0.42). Considering the volumetric proportions, food similarity was also higher among forest formations (Ojk = 0.77) than between Uruguayan Savanna and Araucaria Moist Forests (Ojk = 0.41) and Uruguayan Savanna and Serra do Mar Coastal Forests (Ojk = 0.23).

The Importance Value Index of the preyed items indicates that Orthoptera (IV = 1.04), Araneae (IV = 0.93) and Opiliones (IV = 0.31) were the most important categories for the Araucaria Moist Forests specimens. The first two categories were also the most important for Serra do Mar Coastal Forests specimens (Orthopera IV = 1.04, Araneae IV = 0.71), followed by *O. fragilis* (IV = 0.47) and Blattaria (IV = 0.36). For the Uruguayan Savanna specimens, the most important categories were Isopoda (IV = 1.01), Lepidoptera larvae (IV = 0.85) and Araneae (IV = 0.69) (Table 1). The total volume of prey was higher in Araucaria Moist Forests specimens (123142.69 mm^3), followed by Serra do Mar Coastal Forests specimens (65595.75 mm^3) and Uruguayan Savanna specimens (34419.68 mm^3). More information about number, volume and frequency of occurrence of each prey category in the specimens of each ecoregion, see S3 Appendix.

In this study, the organisms belonging to forest formations presented larger prey (Orthoptera and Araneae) and higher total volume in their stomach contents, whereas those belonging to the savanna showed smaller and cylindrical prey (Isopoda and Lepidoptera larvae) and lower total volume. These food preferences were reflected in the morphology, with the organisms of the forest formations being larger and with graceful forms and those of the savanna formation smaller and more robust.

Table 1. Importance of each category of prey in the diet of *O. fragilis* in Neotropical region according to the Gadsden & Palacios-Orona (1997) Importance Value Index (IV) for the specimens of each of the ecoregions. AMF: Araucaria Moist Forests; SMCF: Serra do Mar Coastal Forests; US: Uruguayan Savanna.

Item	AMF	SMCF	US	All specimens
Acari	0.00	0.00	0.09	0.09
Araneae	0.93	0.71	0.69	2.33
Blattaria	0.18	0.36	0.18	0.73
Coleoptera (larvae)	0.07	0.00	0.15	0.22
Diptera	0.00	0.00	0.07	0.07
Hemiptera	0.00	0.00	0.07	0.07
Isopoda	0.16	0.19	1.11	1.46
Lepidoptera (larvae)	0.12	0.14	0.84	1.12
Insect miscellanea	0.13	0.16	0.13	0.43
Opiliones	0.31	0.00	0.00	0.31
Orthoptera	1.04	1.04	0.09	2.18
O.fragilis	0.23	0.47	0.00	0.71
Stylommatophora	0.05	0.00	0.00	0.05

DISCUSSION

Squamata scales are considered key pre-adaptations for the adaptive radiation that resulted in the terrestrial environment, since they provide protection against abrasion and loss of water (Alibardi 2003; Walker & Liem 1994). Although the function of these scales is well understood, the functional significance of variation in their size and shape is not yet known (Arnold & Peterson 2002; Burstein et al. 1974; Oufieiro et al 2011). The interaction of genetic characteristics with the specific conditions of each environment leads individuals to develop differences in morphological and ecological characteristics mediated by natural selection and by the phenotypic plasticity of the species (Aubret et al. 2004; Herrel et al. 2008).

The cephalic scales present a wide variation in lizards. Morphological differences between and within species reflect differences in diet, ecology, and patterns of bone growth (Niehoff et al. 2004). How morphological differences evolved can provide useful information about morphological and genetic patterns and selective pressures acting on these organisms. Several studies with lizard communities suggest that these animals differ in what they eat (Pianka 1974; Vitt 2004), where and how they forage (Colli & Paiva 1997; Vitt & Pianka 2005) and the temporal period of activity (Vitt et al. 2003).

Our results demonstrated that the morphological variation in *O. fragilis* is due to environmental factors and not to geographic variation. The savanna specimens, which are mostly in the southeast group, differed from the others in both shape and size. The analysis of dietary habits showed that this variation is a result of the diet of these organisms. The *O. fragilis* that inhabit the savanna consume a smaller amount of food and preys of smaller size, which results in organisms more robust and smaller. The values of trophic diversity indicate that the variety of prey is also smaller in the savanna formation.

The two forest environments analyzed showed greater similarity in size and shape, which resulted from the similarity of diet among the organisms that inhabit them. These organisms consume a larger volume of prey, resulting in larger and more elongated forms. The trophic diversity was higher in these ecoregions and the prey consumed were larger. We highlight the occurrence of cannibalism among Serra do Mar Coastal Forests populations, which may be the result of greater competition pressure between adult and juvenile males, since this ecosystem is one of the most fragmented and impacted by human activities (SOS Mata Atlântica 1998).

The species of snakelike lizards of superficial morphotype present a tendency to explore the surface of the soil and make frequent use of the herbaceous vegetation. This is what happens with the genus *Ophiodes* (Wiens et al. 2006), which feeds mainly on arthropods present in the substrate in which they are inserted (Montechiaro 2011). The distribution and abundance of food resources may result not only from the availability but also from the ecological conditions exhibited in a given environment (Oliveira 2011).

The composition of the substrate is influenced both by the type of soil and the type of vegetation of a given location. The litter of forest environments is quite distinct from the vegetation of grasses that covers the savanna areas. In view of this, it is possible to infer that the change in the type of substrate and the food resources it provides may be leading to the morphological differences observed in this study.

The Uruguayan Savanna is composed mainly of medium-sized, perennial and annual grasses (WWF, 2017). In this way, the substrate in which these organisms move is more malleable than the litter of the forest environmental, allowing more robust forms to develop. In forests, dense litter, consisting of dead leaves, bark and tree branches, may be offering greater resistance to displacement locomotion, resulting in more graceful shapes.

These same factors can justify the absence of isolation by geographic distance. Geographically distant individuals were morphologically similar because they are living in similar habitats. It is not the geographic distance that is determining the morphology, but the specificity developed in relation to the environment and the resources available to it.

In Australia, species of the limbless lizards *Aprasia* of the family Pygopodidae have a fragmented distribution, in which each species occupies a different area in the temperate region of the south and west of the continent. Speciation of this genus is attributed to changes in the climate, which consequently caused changes in the environment over geological time (Ehmann 1992; Jennings et al. 2003; Smith & Henry 1999). Likewise, the ecoregions of the study area share a peculiar geoclimatic history, including oceanic transgressions and regressions, profound changes on climate and water availability, and even geological and soil composition (Klein 1975; Leite & Klein 1990; Marchiori 2002; Marchiori 2004; Rambo 1956). These factors may have contributed to the speciation of the genus *Ophiodes* and even to the morphological differences we observe.

As a result of the heterogeneity of the environment, notable phenotypic variations can occur among individuals of the same genotype at different locations (Sánches et al., 2011). These morphological variations between species reflect, even partially, the differentiated use of diverse resources and ecologies. In this way, there is a parallel between morphological and ecological similarity (Pianka 2000), and a set of morphological characteristics may point to an adjustment to a certain dimension of the ecological niche (Teixeia & Bennemann 2007). In summary, the environment selects the characteristics that best fit the organism in developing its way of life and achieving reproductive success (Stearns & Hoekstra 2003).

However, not all characteristics of an organism and not all uses of a characteristic by an organism constitute an adaptation (Freeman & Herron 2009). This ability to express alternative patterns of morphology, physiology, and behavior in response to environmental pressures may also be a result of the phenotypic plasticity of the organism (Schlichting 1986). Some responses may be natural consequences of biological, physical, chemical, and ancestral processes that may have occurred, regardless of how evolution has adapted a particular population to the conditions it is currently on (Stearns & Hoekstra 2000). A careful investigation of the factors involved is necessary to assert that a plastic response is an adaptation and not a product of other processes.

The results obtained so far do not corroborate the hypothesis of morphological differentiation by geographic isolation. Therefore, the morphological variation is not a result of the genetic drift caused by distance isolation. It is due to local environmental factors, which determine the type of substrate and food resources available to the organisms.

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SUPPORTING INFORMATION

S1 Appendix. List of the museum collection numbers of specimens used in the geometric morphometric procedures, their geographic coordinates, ecoregions and geographic groups. Abbreviation of museum names: Museu de História Natural Capão da Imbuia (MHNCI), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Museu Zoobotânico Augusto Ruschi da Universidade de Passo Fundo (MUZAR), Museu Regional do Alto Uruguai da Universidade Regional Integrada do Alto Uruguai e das Missões (MuRAU). Abbreviation of geographic goups: Northwest (NW), Northeast (NE), Southwest (SW), Southeast (SE).

Museum nº	Latitude	Longitude	Ecoregion	Group
MHNCI808	-25.5258	-48.3429	Serra do mar coastal forests	NE
MHNCI849	-25.3205	-49.1223	Araucaria moist forests	NE
MHNCI1699	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI2075	-24.9558	-53.4553	Araucaria moist forests	NW
MHNCI2076	-24.9558	-53.4553	Araucaria moist forests	NW
MHNCI2106	-25.9281	-49.1989	Araucaria moist forests	NE
MHNCI5166	-26.1614	-51.5525	Araucaria moist forests	NW
MHNCI5177	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5178	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5180	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5181	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5182	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5184	-25.9411	-52.1756	Araucaria moist forests	NW
MHNCI5186	-25.9411	-52.1756	Araucaria moist forests	NW
MHNCI5187	-25.9411	-52.1756	Araucaria moist forests	NW
MHNCI5189	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5190	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5192	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5193	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5195	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI519	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5197	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5198	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5199	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5200	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI5359	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI6630	-26.2381	-51.0783	Araucaria moist forests	NW
MHNCI6933	-24.5200	-48.1081	Serra do mar coastal forests	NE
MHNCI6983	-26.3044	-48.8456	Serra do mar coastal forests	NE
MHNCI6984	-26.2300	-51.0864	Araucaria moist forests	NW
MHNCI7073	-26.7673	-48.6770	Serra do mar coastal forests	NE
MHNCI7119	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI7227	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI7442	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI7513	-22.9194	-42.8186	Serra do mar coastal forests	NE
MHNCI7699	-26.1169	-48.6161	Serra do mar coastal forests	NE
MHNCI8086	-24.8931	-52.2028	Araucaria moist forests	NW
MHNCI8159	-25.6956	-51.6597	Araucaria moist forests	NW
MHNCI8994	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI9026	-25.4417	-49.0633	Serra do mar coastal forests	NE
MHNCI9164	-25.4278	-49.2731	Araucaria moist forests	NE

MHNCI9397	-26.3364	-49.9064	Araucaria moist forests	NE
MHNCI9398	-26.3364	-49.9064	Araucaria moist forests	NE
MHNCI9641	-25.4278	-49.2731	Araucaria moist forest	NE
MHNCI9662	-25.7263	-48.9479	Serra do mar coastal forests	NE
MHNCI9667	-25.8175	-48.5428	Serra do mar coastal forests	NE
MHNCI9668	-25.8175	-48.5428	Serra do mar coastal forests	NE
MHNCI9742	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI9744	-25.8389	-52.0281	Araucaria moist forests	NW
MHNCI9746	-25.9411	-52.1756	Araucaria moist forests	NW
MHNCI10067	-26.2300	-51.0864	Araucaria moist forests	NW
MHNCI10091	-26.2769	-52.7839	Araucaria moist forests	NW
MHNCI10107	-26.3958	-52.4708	Araucaria moist forests	NW
MHNCI10123	-26.3958	-52.4708	Araucaria moist forests	NW
MHNCI10267	-25.5931	-49.4103	Araucaria moist forests	NE
MHNCI10456	-25.9281	-49.1989	Araucaria moist forests	NE
MHNCI10532	-25.8175	-48.5428	Serra do mar coastal forests	NE
MHNCI10608	-28.5978	-49.4244	Serra do mar coastal forests	NE
MHNCI10667	-25.5200	-48.5092	Serra do mar coastal forests	NE
MHNCI10712	-26.9194	-49.0661	Araucaria moist forests	NE
MHNCI10757	-25.6417	-52.1028	Araucaria moist forests	NW
MHNCI10997	-27.4942	-48.6556	Serra do mar coastal forests	NE
MHNCI11224	-26.1169	-48.6161	Serra do mar coastal forests	NE
MHNCI11400	-23.6203	-45.4131	Serra do mar coastal forests	NE
MHNCI11663	-25.4278	-49.2731	Araucaria moist forests	NE
MHNCI11922	-26.1614	-51.5525	Araucaria moist forests	NW
MHNCI12042	-25.7263	-48.9479	Serra do mar coastal forests	NE
MHNCI12068	-26.0267	-48.8550	Serra do mar coastal forests	NE
MHNCI12290	-30.0331	-51.2300	Uruguayan savanna	SE
MHNCI12291	-30.0331	-51.2300	Uruguayan savanna	SE
MHNCI12392	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12460	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12461	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12462	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12602	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12603	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI12604	-25.4452	-51.9360	Araucaria moist forests	NW
MHNCI13779	-28.5978	-49.4244	Araucaria moist forests	NW
MHNCI13815	-26.3044	-48.8456	Serra do mar coastal forests	NE
MHNCI13917	-26.3044	-48.8456	Serra do mar coastal forests	NE
MHNCI15836	-25.5200	-48.5092	Serra do mar coastal forests	NE
MuRAU004	-27.6342	-52.2739	Araucaria moist forests	SW
MUZAR106	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR22	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR52	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR53	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR54	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR55	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR58	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR62	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR63	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR64	-28.1702	-52.4711	Araucaria moist forests	SW

MUZAR67	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR71	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR83	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR86	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR88	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR90	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR96	-28.1702	-52.4711	Araucaria moist forests	SW
MUZAR106	-28.1702	-52.4711	Araucaria moist forests	SW
MuRAU106	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU123	-27.6342	-52.2739	Araucaria moist forests	SW
MUZAR132	-27.0964	-52.6183	Araucaria moist forests	SW
MUZAR133	-28.4492	-52.2000	Araucaria moist forests	SW
MUZAR134	-27.9797	-52.2597	Uruguayan savanna	SW
MuRAU152	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU154	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU165	-27.6342	-52.2739	Araucaria moist forests	SW
MuRAU167	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU274	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU281	-27.0903	-48.6114	Serra do Mar costal forests	NW
MuRAU369	-27.6342	-52.2739	Araucaria moist forests	SW
MCN521	-29.1681	-51.1794	Araucaria moist forests	SE
MCN523	-30.0811	-51.0233	Uruguayan savanna	SE
MCN769	-30.0811	-51.0233	Uruguayan savanna	SE
MCN778	-30.0811	-51.0233	Uruguayan savanna	SE
MCN779	-30.0811	-51.0233	Uruguayan savanna	SE
MCN879	-30.0331	-51.2300	Uruguayan savanna	SE
MCN880	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1052	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1053	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1054	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1055	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1056	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1058	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1059	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1061	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1155	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1163	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1164	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1165	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1166	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1168	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1392	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1393	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1442	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1550	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1600	-30.0811	-51.0233	Uruguayan savanna	SE
MCN1784	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1864	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1944	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1956	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1957	-30.0331	-51.2300	Uruguayan savanna	SE

MCN1958	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1960	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1961	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1962	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1966	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1967	-30.0331	-51.2300	Uruguayan savanna	SE
MCN1968	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2080	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2415	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2428	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2429	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2430	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2612	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2634	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2694	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2725	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2896	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2897	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2902	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2903	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2904	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2906	-29.9511	-51.0939	Uruguayan savanna	SE
MCN2907	-29.9444	-50.9919	Uruguayan savanna	SE
MCN2932	-30.0331	-51.2300	Uruguayan savanna	SE
MCN2933	-30.0331	-51.2300	Uruguayan savanna	SE
MCN3004	-29.9444	-50.9919	Uruguayan savanna	SE
MCN3125	-30.0331	-51.2300	Uruguayan savanna	SE
MCN3127	-30.0331	-51.2300	Uruguayan savanna	SE
MCN3238	-30.0331	-51.2300	Uruguayan savanna	SE
MCN3556	-30.0331	-51.2300	Uruguayan savanna	SE
MCN3702	-29.9178	-51.1836	Uruguayan savanna	SE
MCN3800	-30.0331	-51.2300	Uruguayan savanna	SE
MCN4071	-29.9444	-50.9919	Uruguayan savanna	SE
MCN4098	-28.0233	-48.6133	Serra do Mar costal forests	NE
MCN6067	-30.0331	-51.2300	Uruguayan savanna	NE
MCN6638	-28.5978	-49.4244	Serra do Mar costal forests	SE
MCN6640	-28.5978	-49.4244	Serra do Mar costal forests	NE
MCN8029	-30.0331	-51.2300	Uruguayan savanna	SE
MCN8122	-30.0331	-51.2300	Uruguayan savanna	SE
MCN8646	-29.6750	-50.2072	Serra do Mar costal forests	SE
MCN9094	-30.0331	-51.2300	Uruguayan savanna	SE
MCN9529	-30.0331	-51.2300	Uruguayan savanna	SE
MCN12802	-30.0331	-51.2300	Uruguayan savanna	SE
MCN15565	-27.8750	-51.1722	Araucaria moist forests	SW
MCN15566	-26.7597	-52.1911	Araucaria moist forests	NW
MCN15567	-26.7597	-52.1911	Araucaria moist forests	NW
MCN15568	-26.7597	-52.1911	Araucaria moist forests	NW
MCN15569	-26.7597	-52.1911	Araucaria moist forests	NW
MCN15570	-27.8750	-51.1722	Araucaria moist forests	SW
MCN15572	-26.7597	-52.1911	Araucaria moist forests	NW
MCN15574	-26.7597	-52.1911	Araucaria moist forests	NW

MCN15614	-27.8750	-51.1722	Araucaria moist forests	SW
MCN15615	-27.6892	-51.1300	Araucaria moist forests	SW
MCN15623	-27.6892	-51.1300	Araucaria moist forests	SW
MCN15801	-27.8750	-51.1722	Araucaria moist forests	SW
MCN16336	-27.4017	-51.2250	Araucaria moist forests	SW
MuZARsn	-27.6342	-52.2739	Araucaria moist forests	SW

S2 Appendix. List of the museum collection numbers of specimens used in the dietary analysis, their geographic coordinates and ecoregions. Abbreviation of museum names: Museu de História Natural Capão da Imbuia (MHNCI), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Museu de Ciências e Tecnologia – PUCRS (MCP).

Museum nº	Latitude	Longitude	Ecoregion
MCN1063	-26.2769	-52.7839	Uruguayan Savanna
MCN1956	-30.0331	-51.23	Uruguayan Savanna
MCN1957	-30.0331	-51.23	Uruguayan Savanna
MCN1961	-30.0331	-51.23	Uruguayan Savanna
MCN1962	-30.0331	-51.23	Uruguayan Savanna
MCN1967	-30.0331	-51.23	Uruguayan Savanna
MCN2080	-30.0331	-51.23	Uruguayan Savanna
MCN2414	-30.0331	-51.23	Uruguayan Savanna
MCN2416	-30.0331	-51.23	Uruguayan Savanna
MCN2694	-30.0331	-51.23	Uruguayan Savanna
MCN3520	-30.0331	-51.23	Uruguayan Savanna
MCN3556	-30.0331	-51.23	Uruguayan Savanna
MCN3578	-30.0331	-51.23	Uruguayan Savanna
MCN4098	-28.0233	-48.6133	Serra do Mar Coastal Forests
MCN7019	-30.0331	-51.23	Uruguayan Savanna
MCN15565	-27.875	-51.1722	Araucaria Moist Forests
MCN15566	-26.7597	-52.191097	Araucaria Moist Forests
MCN15567	-26.7597	-52.191097	Araucaria Moist Forests
MCN15568	-26.7597	-52.191097	Araucaria Moist Forests
MCN15573	-26.7597	-52.191097	Araucaria Moist Forests
MCN15574	-26.7597	-52.191097	Araucaria Moist Forests
MCN15614	-27.875	-51.1722	Araucaria Moist Forests
MCN15623	-27.6892	-51.13	Araucaria Moist Forests
MCP0295	-30.0603	-51.1738	Uruguayan Savanna
MCP2259	-28.4667	-49.0069	Serra do Mar Coastal Forests
MCP3796	-29.3694	-49.8497	Serra do Mar Coastal Forests
MCP3820	-29.3694	-49.8497	Serra do Mar Coastal Forests
MCP3823	-29.3694	-49.8497	Serra do Mar Coastal Forests
MCP4639	-30.03	-51.2286	Uruguayan Savanna
MCP5403	-25.4858	-49.2193	Araucaria Moist Forests
MCP 5987	-29.3819	-50.8088	Araucaria Moist Forests
MCP6169	-26.4861	-49.0677	Serra do Mar Coastal Forests
MCP6211	-30.03	-51.2286	Uruguayan Savanna
MCP6359	-30.0379	-52.8825	Araucaria Moist Forests
MCP7216	-25.6948	-51.654	Araucaria Moist Forests
MCP7841	-26.7698	-48.6767	Serra do Mar Coastal Forests
MCP7844	-26.7698	-48.6767	Serra do Mar Coastal Forests
MCP7846	-26.7698	-48.6767	Serra do Mar Coastal Forests
MCP7848	-26.7698	-48.6767	Serra do Mar Coastal Forests

MCP10484	-27.3902	-53.4303	Araucaria Moist Forests
MCP10485	-27.3592	-53.3944	Araucaria Moist Forests
MCP10486	-27.3592	-53.3944	Araucaria Moist Forests
MCP10516	-26.9078	-48.6619	Serra do Mar Coastal Forests
MCP12119	-26.7753	-51.015	Araucaria Moist Forests
MCP12368	-29.537	-50.0923	Serra do Mar Coastal Forests
MCP12578	-29.1681	-51.1794	Araucaria Moist Forests
MCP12764	-29.9433	-51.7181	Uruguayan Savanna
MCP13136	-29.1627	-51.1524	Araucaria Moist Forests
MCP14289	-28.7353	-51.7021	Araucaria Moist Forests
MCP14342	-30.0547	-51.1823	Uruguayan Savanna
MCP17667	-26.2381	-51.0783	Araucaria Moist Forests
MCP17671	-26.2381	-51.0783	Araucaria Moist Forests
MHNCI7391	-25.4278	-49.2731	Araucaria Moist Forests
MHNCI9232	-26.23	-51.0864	Araucaria Moist Forests
MHNCI9742	-25.7675	-49.7174	Araucaria Moist Forests
MHNCI9743	-25.8389	-52.0281	Araucaria Moist Forests
MHNCI9744	-25.8389	-52.0281	Araucaria Moist Forests
MHNCI9745	-25.8389	-52.0281	Araucaria Moist Forests
MHNCI9746	-25.8389	-52.0281	Araucaria Moist Forests
MHNCI11662	-25.9411	-52.1756	Araucaria Moist Forests

S3 Appendix. Number (N), volume (V), and frequency of occurrence (F) of each prey category in the diet of Araucaria Moist Forests (AMF), Serra do Mar Coastal Forests (SMCF), Uruguayan Savvana (US) an total os specimens of *O. fragilis* in Neotropical region.

	AMF			**SMCF**			**US**			**Total**		
Item	N (%N)	V (%V)	F (%F)	N (%N)	V (%V)	F (%F)	N (%N)	V (%V)	F (%F)	N (%N)	V (%V)	F (%F)
Reptilia												
Squamata undet.		0 (0)	0 (0)		0 (0)	0 (0)					747.39 (0.29)	1 (1.38)
O. fragilis	4 (6.90)	16055.21 (13.04)	1 (3.45)	1 (5.55)	21763.97 (33.18)	1 (8.33)	0 (0)	0 (0)	0 (0)	5 (3.26)	37819.18 (14.88)	2 (2.77)
Gastropoda												
Stylommatophora	1 (1.72)	181.05 (0.15)	1 (3.45)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.65)	181.05 (0.07)	1 (1.38)
Crustacea												
Isopoda	7 (12.07)	1010.24 (0.82)	1 (3.45)	2 (11.11)	315.21 (0.48)	1 (8.33)	27 (47.36)	8315.01 (24.14)	7 (38.88)	42 (27.45)	11056.02 (4.35)	12 (16.66)
Arachnida												
Acari	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (3.50)	0.23 (0.00)	1 (5.55)	2 (1.30)	0.23 (0.00)	1 (1.38)
Araneae	12 (20.69)	38922.19 (61.61)	12 (41.38)	7 (38.88)	4401.64 (6.71)	3 (25)	7 (12.28)	8248.53 (23.96)	6 (33.33)	31 (20.26)	53650.67 (21.12)	25 (34.72)
Opiliones	9 (15.52)	2909.26 (2.36)	4 (13.79)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	9 (5.88)	2909.26 (1.14)	4 (5.55)
Insecta												
Blattaria	3 (5.17)	3549.20 (2.88)	3 (10.34)	2 (11.11)	5994.10 (9.14)	2 (16.66)	1 (1.75)	3811.86 (11.07)	1 (5.55)	9 (5.88)	21995.41 (8.65)	7 (9.72)
Coleoptera (larvae)	1 (1.72)	2380.43 (1.93)	1 (3.45)	0 (0)	0 (0)	0 (0)	2 (3.50)	212.13 (0.61)	2 (11.11)	3 (1.96)	2592.56 (1.02)	3 (4.16)
Diptera	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.75)	10.25 (0.02)	1 (5.55)	2 (1.30)	434.77 (0.17)	2 (2.77)
Hemiptera	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.75)	11.53 (0.03)	1 (5.55)	1 (0.65)	11.53 (0.00)	1 (1.38)
Lepidoptera (larvae)	3 (5.17)	771.80 (0.63)	2 (6.90)	1 (5.55)	658.82 (1.00)	1 (8.33)	15 (26.31)	8593.38 (24.96)	6 (33.33)	20 (13.07)	11168.31 (4.39)	11 (15.27)
Orthoptera	18 (31.03)	48262.98 (39.19)	10 (34.48)	5 (27.77)	22870.92 (34.87)	5 (41.66)	1 (1.75)	908.41 (2.63)	1 (5.55)	28 (18.30)	77792.11 (30.62)	19 (26.38)
Insect miscellanea		3740.89 (3.04)	3 (10.34)		111.34 (0.17)	2 (16.66)		881.63 (2.56)	2 (11.11)		9511.03 (3.74)	8 (11.11)
Non-identified arthropods		5359.44 (4.35)			9479.75 (14.45)			3426.72 (9.95)			24123.89 (9.49)	
Total	58	123142.69	38	18	65595.75	15	57	34419.68	28	153	253993.4	97

CAPÍTULO 2 – SUN DOES SHINE AND RAIN DOES FALL: THE INFLUENCE OF CLIMATE IN THE MORPHOLOGY OF *Ophiodes fragilis* (SQUAMATA, DIPLOGLOSSIDAE)

ABSTRACT

The morphological variation of organisms is influenced mainly by climate and habitat conditions. In the Neotropical region, *Ophiodes fragilis* presents characteristic morphological patterns in different ecoregions. This study sought to investigate the environmental variables that are influencing these patterns. To do so, we generated a niche model and compared the environmental characteristics of the occurrence sites of the species with the variation of shape and size of the cephalic scales of the organisms. Our analyzes showed that variables related to temperature and precipitation are the main determinants for the occurrence of *O. fragilis*. Seasonality of temperature and precipitation rates affect the life cycle of arthropods, thus determining the availability of food resources, and the metabolism of lizards, influencing foragin, leading to observed morphological variation.

Keywords: geometric morphometrics, niche modeling, ecomorphology, Neotropical region.

INTRODUCTION

One of the objectives of ecomorphology is to find adaptive explanations for specific forms, considering external environments as the evolutionary cause for the observed morphology (Betz 2006). Considering adaptation as a form of response to the environment, the main factors that exert selective effects on the morphological variation of organisms are climate and habitat characteristics (Ridley 2006; Mayr 1977). Therefore, evolutionary events that lead to species diversification are generally related to the landscape physiognomy and alteration of the ecosystems in which organisms are inserted (Burbrink et al. 2008).

The global temperature and precipitation patterns are among the most important environmental abiotic factors, exerting great influence on the geographic distribution of the species (Futuyma 2009). Climate variables, such as temperature and precipitation, have an influence on thermoregulatory mechanisms (Ashton et al. 2000; Martinez et al. 2013) and on the availability of food in the environment (Cardini et al., 2007). The morphological variation resulting from these patterns may reflect both evolutionary adaptation and the phenotypic plasticity of the species (Caceres et al. 2014, Jaffe et al. 2016, Meloro et al. 2014).

In South America, the herpetological fauna occupies different climatic zones, in a north-south gradient that ranges from tropical to subtropical regions (Lema, 2002). In addition to the climatic differences, the regions inhabited by these organisms present different types of soil and vegetation, resulting in a great heterogeneity of habitats (Rambo, 1956; Rizinni, 1997), forming different ecosystems.

The morphological variation in *Ophiodes fragilis* (Raddi, 1826) was still little explored. Recent studies point to a correlation between morphological variation and the environment, with forest and grasses formations presenting differentiated patterns of cephalic scales for these organisms (Oliveira et al. – in preparation). In this sense, the present study sought to investigate the influence of environmental variables on the potential distribution of the species and its morphology, seeking to identify which are the variables responsible for the variation in the shape and size of the cephalic scales of these organisms.

MATERIAL AND METHODS

Geometric morphometrics procedures

Our sample consisted of photographs of cephalic scales of 200 specimens of *O. fragilis* from southern of Neotropical region, preserved in a liquid medium, belonging to the collections of the following museums: Museu de História Natural Capão da Imbuia (MHNCI), Museu de Ciências Naturais (MCN) of the Fundação Zoobotânica do Rio Grande do Sul, Museu Zoobotânico Augusto Ruschi (Muzar) of the Universidade de Passo Fundo and Museu Regional do Alto Uruguai e das Missões (MuRAU) of the Universidade Regional Integrada do Alto Uruguai e das Missões (Fig. 1) (S1 Appendix). The photographs were taken at a standard distance of 10 centimeters, aiming to minimize lens distortions (Meloro et al. 2008). The cephalic scales were chosen because they generally reflect the patterns of bone growth (Costantini et al. 2010).

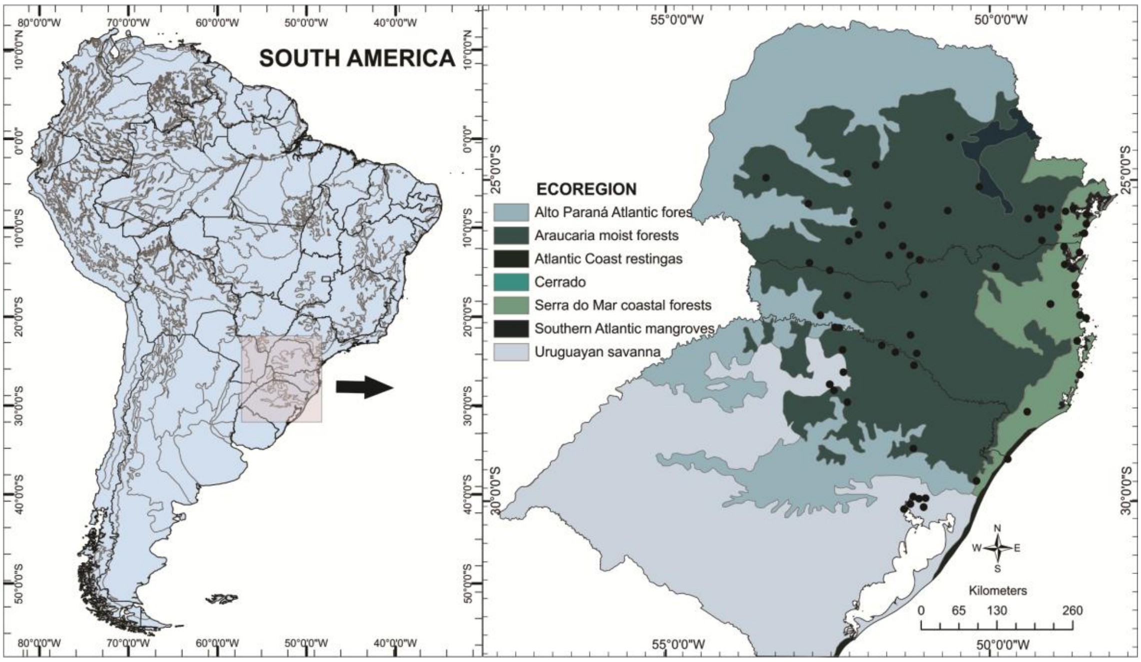

Figure 1. Map of South America showing the geographical distribution of specimens for *O. fragilis* analyzed in this study, according to the ecoregions which belong.

In each of the photographs, we digitalized 25 anatomical landmarks (Fig. 2) using the software tpsDig2, in version 2.17 (Rophlf 2013). This procedure was done by the same person (MO) to minimize errors resulting from the perception of different observers (Bubadué et al., 2016). After this, the coordinates of the landmarks were overlaid by the Generalized Analysis of Procrustes (Rohlf and Slice 1990), which removes the non-form-related effects, creating a matrix exclusively of shape coordinates (Adams, Rohlf & Slice 2004; Maestri et al. 2015). From this matrix, we extract the measure of the Procrustes distance, which can be understood as a measure of how the form varies in relation to the consensus. The size of the specimens was estimated by log-transformed centroid size, which is the square root of the sum of the squares of the distances of each landmark relative to the centroid of the configuration (Bookstein 1991).

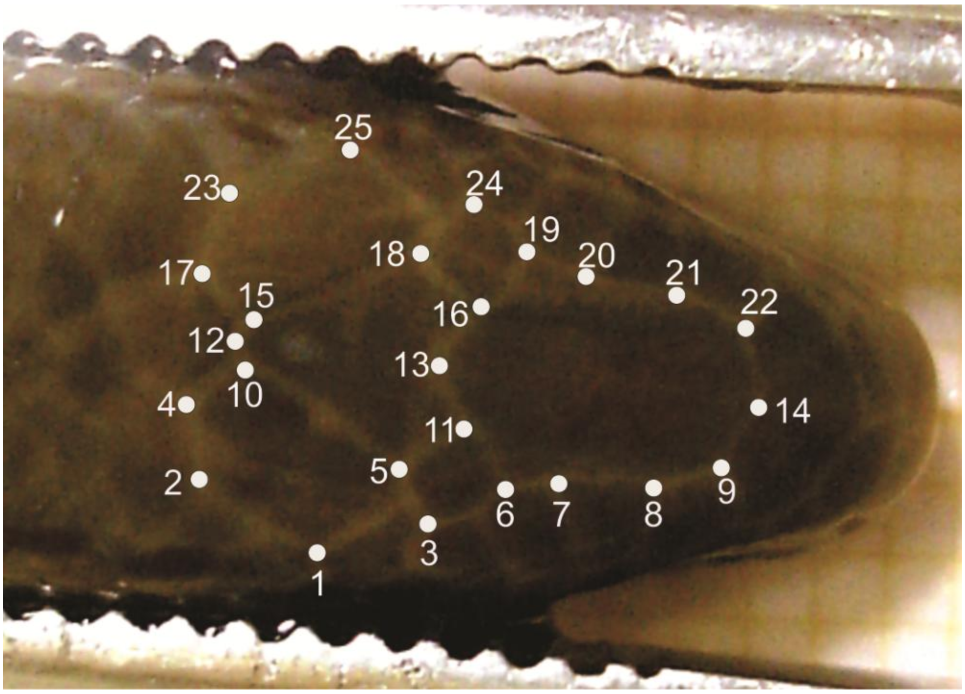

Figure 2. Disposition of 25 landmarks in the cephalic scales of O. fragilis. 1, 2, 4, 10: outline of the right parietal scale; 15, 17, 23, 25: outline of the left parietal scale; 7, 8, 9, 20, 21, 22: outline of frontal scale; 12, 13, 14 midline, passing through the interparietal and frontal scales.

Species distribution modeling and extraction of environmental variables

The potential distribution for *O. fragilis* in southern Neotropical region was generated by means of the maximum entropy algorithm, using Maxent version 3.3.3k (Phillips et al. 2006; Phillips & Dudik 2008). Maxent estimates the probability of occurrence of a species, finding the probability of maximum entropy distribution, subject to a set of environmental constraints that represent incomplete information about the target distribution (Phillips et al. 2006).

The model was generated using only presence data (N = 200) (S1 Appendix, Fig. 1) and environmental layers with spatial resolution of 0.0083 degrees decimal (~ 1km2). We used 19 bioclimatic layers (World-Clim, available at http://www.worldclim.org/) obtained with interpolated data derived from precipitation and temperature, an altitude layer (World-Clim, available at http://www.worldclim.org/) and a land cover map (based on UN Land Cover Classification System, available at http://due.esrin.esa.int/globcover/). All layers were processed using ArcMap v.10.2.2, being converted in raster with the same level of resolution as the bioclimatic and clipped for the limits of the southern region of Brazil.

We extracted a matrix with the values of each layer used for the study area and performed a Principal Component Analysis (PCA) to identify correlations between the variables of this matrix, selecting the axes that explained 95% of the correlation structure. This procedure was run in R v.2.14.1 (R Development Core Team 2012), and resulted in the selection of 14 layers for the species analyzed (S2 Appendix). Presence data were obtained from the records of the specimens of the visited collections. All runs were set with a convergence threshold of $1.0E^{-5}$ with 500 interactions and 10,000 background points. The analysis of the importance of variables was measured by jack-knife, response curves and random seed.

The spatial distribution model was generated by bootstrapping methods, with substitutions using 70% of the points of presence for training and 30% for test models (Pearson 2007). The potential distribution map of the species was produced using the logistic output format (Phillips & Dudik 2008), seeking to ensure a more accurate approximation of the estimated probability of the species being present in a given environment (Elith et al. 2011). The validation of the model was done by the calculation of the area under the curve (AUC) from a receiver operating characteristic curve (ROC).

Statistical analysis

We used the Procrustes distance and the centroid size for the analyzed specimens as response variables and the environmental data at the points of occurrence of each of them as explanatory variables. The values of the environmental variables were extracted using ArcMap 10.2.2, in a local scale of $1km^2$, corresponding to the cell in which the specimen was present. We performed multiple regressions between morphological and environmental variables. For this analysis, we used R v.2.14.1 (R Development Core Team 2011).

RESULTS

According to the model of maximum entropy, the distribution of *O. fragilis* in southern Neotropical region (Figure 3) is influenced mainly by three variables: precipitation of driest month (bio14, 34.8%), seasonality of temperature (bio04, 28.4%) and altitude (alt, 22.3%). The other variables used had an influence lower than 4.5% in the distribution of the species. The model performance, defined by the area under the curve (AUC), was highly discriminative for the species (AUC = 0.933).

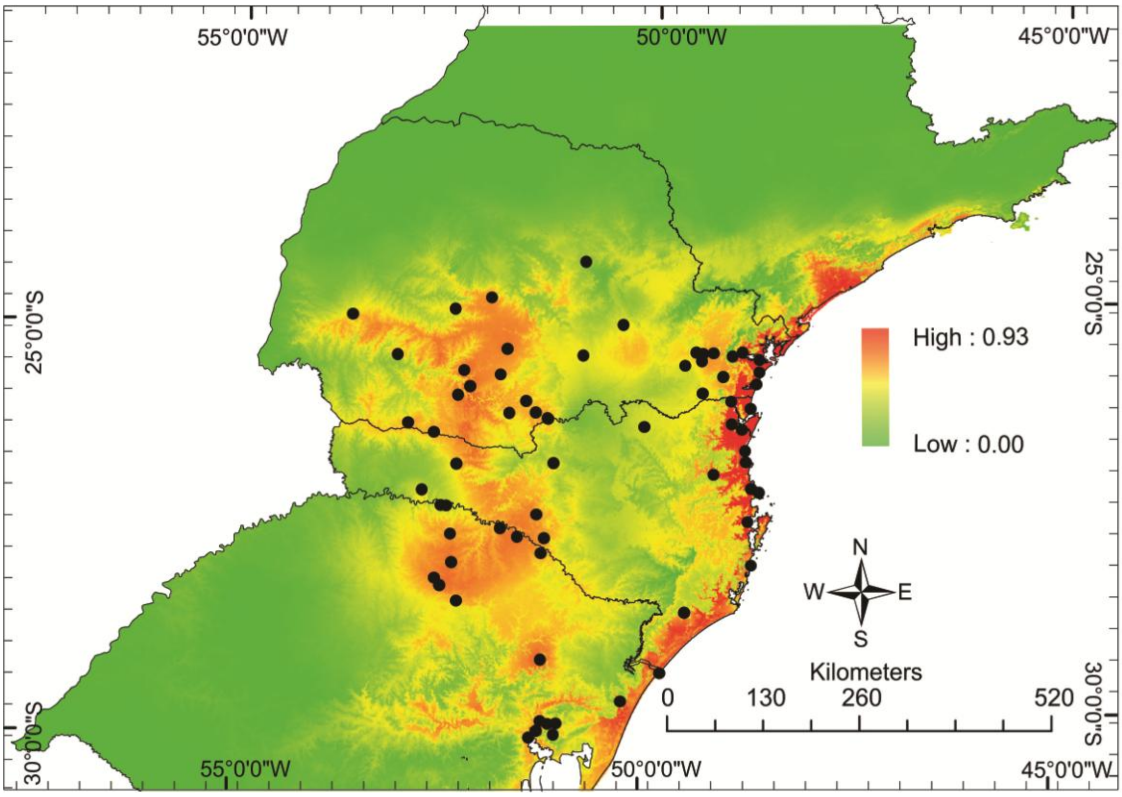

Figure 3. Map of potential distribution for *O. fragilis* in south of Neotropical region. High values represent the most probable places of occurrence of species.

The multiple regression showed the influence of environmental variables on size ($F_{14, 185} = 2.63$; $R^2 = 0.10$; $p < 0.001$) and the shape ($F_{14, 185} = 2.89$; $R^2 = 0.11$; $p < 0.001$) of the cephalic scales of *O. fragilis*. The size was influenced by temperature seasonality (bio4; $p = 0.02$), mean temperature of warmest quarter (bio10, $p = 0.02$), precipitation of warmest quarter (bio18; $p = 0.001$) and land cover (globcover, $p = 0.001$). The shape was influenced by the by the annual average temperature (bio1, $p = 0.04$), temperature seasonality (bio4, $p = 0.02$), precipitation of warmest quarter (bio18, $p = 0.01$) and land cover (globcover, $p = 0.002$) (Fig. 4).

Temperature seasonality and precipitation in the warmer quarter caused changes in both the shape and size of organisms. Those living in open areas have a greater amplitude in size variation, and are smaller than those inhabiting forests. Forest organisms tend to be larger and have a smaller amplitude in size variation.

The organisms that live in places with an average temperature in the 30ºC range presented greater amplitude in the shape variation, while those living in the extremes of higher and lower temperatures had smaller deviations than the consensus form. The same was observed for the size, which varied more between organisms in this temperature range. The organisms that inhabit places where the precipitation of warmest quarter ranges from 400 to 600 mm presented a greater amplitude of variation in relation to the consensus form. Again, the size followed the same pattern, varying further at sites within this precipitation range (Fig. 4).

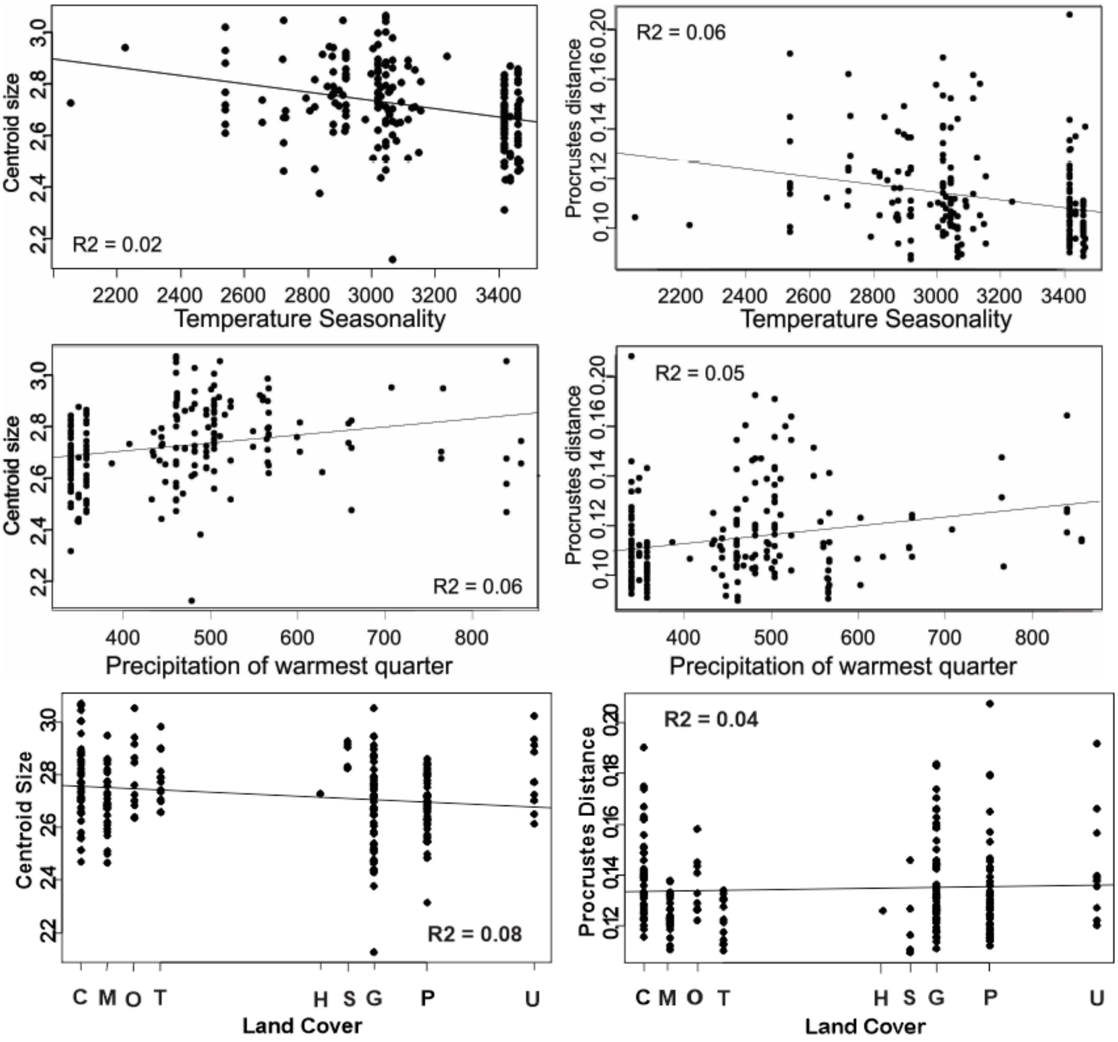

Figure 4. The relationship between size and shape variation and temperature sazonality (above), precipitation in the warmest quarter (center), and land cover (bellow). The value of the coefficient of determination is shown. For land cover: C: cropland; M: mosaic cropland and natural vegetation; T: tree vegetation; H: mosaic herbaceous cover; S: shrubland; G: grassland; P: sparse vegetation; U: urban areas.

DISCUSSION

One of the most relevant aspects of the spatial dimension of the ecological niche is the physical structure of the environment (Schoener & Adler 1991), which determines the conditions and availability of foraging sites, thermoregulation and shelter against predators (Rand & Humphrey 1968), and gives rise to non-random patterns in lizard communities distribution (Ricklefs & Lovette 1999; Shenbrot et al., 1991; Vitt & Zani, 1996). The potential distribution of *O. fragilis* was determined by the precipitation of the driest month, by temperature seasonality and by altitude.

Variables related to precipitation and temperature also determined the morphological variation of the cephalic scales, as temperature seasonality and precipitation of warmest quarter, leading to changes in both shape and size of these organisms. Precipitation and temperature are effective indicators of productivity in ecosystems, varying as a function of latitudinal gradients and other factors such as altitude (Ricklefs 2012), which had a considerable weight in determining the potential distribution of the species. These variables change the structure of the habitat that in turn change the trophic niche of the populations and the consequence of these are the different patterns in the morphology that we observed.

Ouriero et al. (2011) point out that climate is one of the main factors affecting the physiological traits and life history of lizards. The temperature of the ectothermal body is increased by external sources of heat. The conservation of thermal energy is obtained by a smaller area of body surface, which is also limited for the absorption of heat. Therefore, smaller body size may be a necessity to avoid overheating in warmer habitats and conserve thermal energy in cooler habitats (Aho et al. 2011), which would explain the smaller size of the organisms in the extremes of temperatures.

The influence of precipitation is related to the availability of food resources. Foraging and breeding activities of arthropods are determined by the seasonality of climatic conditions, especially precipitation indices (Shakir & Ahmed 2015; Whitford 1996; Wolda 1988). The abundance of these organisms is usually higher in wetter seasons (Tanaka & Tanaka 1982). Arthropods, including insects of the order Orthoptera, are the main food source of *O. fragilis* in southern of Neotropical region (Montechiaro et al. 2011) and a relationship between the morphological variation of cephalic scales of this species and dietary habits, including the number of prey ingested, has already been confirmed (Oliveira et al. – in preparation). In forest environments, the organisms consume a larger volume of prey and present a larger cephalic configuration, whereas in savanna formations the volume of prey consumed is lower, which results in smaller organisms.

On this study, we found that organisms in open areas are smaller and vary more in size than forest organisms. This may be related to the type of substrate in which they are inserted. When considering the points of occurrence of the species, we can see that these organisms inhabit areas dominated by Uruguayan Savanna.

This less dense substrate may be offering less friction on the displacement, allowing the selection of more robust and smaller forms. On the other hand, the litter of forest formations, formed by dead leaves, branches and bark of trees, is denser and may be creating greater difficulties of locomotion, selecting more slender and elongated forms. In addition, as the grasslands presents a more heterogeneous substrate, where pastures, plantations and herbaceous and shrub vegetation form a complete mosaic, the shape varies more than in forest formations, where the litter is more homogeneous.

The relationship between form and locomotion was observed by Pianka (1969), who points out the association of long-legged lizards with open areas and short legs with closed areas of dense vegetation. North American iguanids inhabiting open areas are smaller and have shorter legs than those on densely vegetated habitats (Scheibe 1987). Lizards of the genus *Aprasia* are also selected by the environment, presenting morphological differences depending on the type of climate and vegetation in which they are inserted (Jennings et al. 2003). An association between morphology and habitat was also found by Irschick & Losos (1999) in lizards of the genus *Anolis*, in which body diameter, sprint sensitivity and type of environment are closely related.

In this way, we can infer that the occurrence of *O. fragilis* results from specific conditions of precipitation and temperature, which determine habitat structure and the availability of the necessary resources for the survival and reproduction of these individuals. Environmental variation leads to a differentiated range of available resources, which results in morphological variation. This inference has profound implications for the conservation of this species, as global changes will result in increased temperatures, leading to significant habitat changes that may affect the availability of resources and the metabolic activity of organisms.

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SUPPORTING INFORMATION

S1 Appendix. List of the museum collection numbers of specimens used in this study and their geographic coordinates. Abbreviation of museum names: Museu de História Natural Capão da Imbuia (MHNCI), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Museu Zoobotânico Augusto Ruschi da Universidade de Passo Fundo (MUZAR), Museu Regional do Alto Uruguai da Universidade Regional Integrada do Alto Uruguai e das Missões (MuRAU).

Museum nº	Latitude	Longitude	Museun nº	Latitude	Longitude
MHNCI808	-27.0903	-48.6114	MuRAU106	-25.5258	-48.3429
MHNCI849	-27.6342	-52.2739	MuRAU123	-25.3205	-49.1223
MHNCI1699	-27.0964	-52.6183	MUZAR132	-25.4278	-49.2731
MHNCI2075	-28.4492	-52.2000	MUZAR133	-24.9558	-53.4553
MHNCI2076	-27.9797	-52.2597	MUZAR134	-24.9558	-53.4553
MHNCI2106	-27.0903	-48.6114	MuRAU152	-25.9281	-49.1989
MHNCI5166	-27.0903	-48.6114	MuRAU154	-26.1614	-51.5525
MHNCI5177	-27.6342	-52.2739	MuRAU165	-25.8389	-52.0281
MHNCI5178	-27.0903	-48.6114	MuRAU167	-25.8389	-52.0281

MHNCI5180	-27.0903	-48.6114	MuRAU274	-25.8389	-52.0281
MHNCI5181	-27.0903	-48.6114	MuRAU281	-25.8389	-52.0281
MHNCI5182	-27.6342	-52.2739	MuRAU369	-25.8389	-52.0281
MHNCI5184	-29.1681	-51.1794	MCN521	-25.9411	-52.1756
MHNCI5186	-30.0811	-51.0233	MCN523	-25.9411	-52.1756
MHNCI5187	-30.0811	-51.0233	MCN769	-25.9411	-52.1756
MHNCI5189	-30.0811	-51.0233	MCN778	-25.8389	-52.0281
MHNCI5190	-30.0811	-51.0233	MCN779	-25.8389	-52.0281
MHNCI5192	-30.0331	-51.2300	MCN879	-25.8389	-52.0281
MHNCI5193	-30.0331	-51.2300	MCN880	-25.8389	-52.0281
MHNCI5195	-30.0811	-51.0233	MCN1052	-25.8389	-52.0281
MHNCI519	-30.0811	-51.0233	MCN1053	-25.8389	-52.0281
MHNCI5197	-30.0811	-51.0233	MCN1054	-25.8389	-52.0281
MHNCI5198	-30.0811	-51.0233	MCN1055	-25.8389	-52.0281
MHNCI5199	-30.0811	-51.0233	MCN1056	-25.8389	-52.0281
MHNCI5200	-30.0811	-51.0233	MCN1058	-25.8389	-52.0281
MHNCI5359	-30.0811	-51.0233	MCN1059	-25.8389	-52.0281
MHNCI6630	-30.0811	-51.0233	MCN1061	-26.2381	-51.0783
MHNCI6933	-30.0811	-51.0233	MCN1155	-24.5200	-48.1081
MHNCI6983	-30.0811	-51.0233	MCN1163	-26.3044	-48.8456
MHNCI6984	-30.0811	-51.0233	MCN1164	-26.2300	-51.0864
MHNCI7073	-30.0811	-51.0233	MCN1165	-26.7673	-48.6770
MHNCI7119	-30.0811	-51.0233	MCN1166	-25.4278	-49.2731
MHNCI7227	-30.0811	-51.0233	MCN1168	-25.4278	-49.2731
MHNCI7442	-30.0811	-51.0233	MCN1392	-25.4278	-49.2731
MHNCI7513	-30.0811	-51.0233	MCN1393	-22.9194	-42.8186
MHNCI7699	-30.0331	-51.2300	MCN1442	-26.1169	-48.6161
MHNCI8086	-30.0331	-51.2300	MCN1550	-24.8931	-52.2028
MHNCI8159	-30.0811	-51.0233	MCN1600	-25.6956	-51.6597
MHNCI8994	-30.0331	-51.2300	MCN1784	-25.4278	-49.2731
MHNCI9026	-30.0331	-51.2300	MCN1864	-25.4417	-49.0633
MHNCI9164	-30.0331	-51.2300	MCN1944	-25.4278	-49.2731
MHNCI9397	-30.0331	-51.2300	MCN1956	-26.3364	-49.9064
MHNCI9398	-30.0331	-51.2300	MCN1957	-26.3364	-49.9064
MHNCI9641	-30.0331	-51.2300	MCN1958	-25.4278	-49.2731
MHNCI9662	-30.0331	-51.2300	MCN1960	-25.7263	-48.9479
MHNCI9667	-30.0331	-51.2300	MCN1961	-25.8175	-48.5428
MHNCI9668	-30.0331	-51.2300	MCN1962	-25.8175	-48.5428
MHNCI9742	-30.0331	-51.2300	MCN1966	-25.8389	-52.0281
MHNCI9744	-30.0331	-51.2300	MCN1967	-25.8389	-52.0281
MHNCI9746	-30.0331	-51.2300	MCN1968	-25.9411	-52.1756
MHNCI10067	-30.0331	-51.2300	MCN2080	-26.2300	-51.0864
MHNCI10091	-30.0331	-51.2300	MCN2415	-26.2769	-52.7839
MHNCI10107	-30.0331	-51.2300	MCN2428	-26.3958	-52.4708
MHNCI10123	-30.0331	-51.2300	MCN2429	-26.3958	-52.4708
MHNCI10267	-30.0331	-51.2300	MCN2430	-25.5931	-49.4103
MHNCI10456	-30.0331	-51.2300	MCN2612	-25.9281	-49.1989
MHNCI10532	-30.0331	-51.2300	MCN2634	-25.8175	-48.5428
MHNCI10608	-30.0331	-51.2300	MCN2694	-28.5978	-49.4244
MHNCI10667	-30.0331	-51.2300	MCN2725	-25.5200	-48.5092

MHNCI10712	-29.9511	-51.0939	MCN2896	-26.9194	-49.0661
MHNCI10757	-29.9511	-51.0939	MCN2897	-25.6417	-52.1028
MHNCI10997	-29.9511	-51.0939	MCN2902	-27.4942	-48.6556
MHNCI11224	-29.9511	-51.0939	MCN2903	-26.1169	-48.6161
MHNCI11400	-29.9511	-51.0939	MCN2904	-23.6203	-45.4131
MHNCI11663	-29.9511	-51.0939	MCN2906	-25.4278	-49.2731
MHNCI11922	-29.9444	-50.9919	MCN2907	-26.1614	-51.5525
MHNCI12042	-30.0331	-51.2300	MCN2932	-25.7263	-48.9479
MHNCI12068	-30.0331	-51.2300	MCN2933	-26.0267	-48.8550
MHNCI12290	-29.9444	-50.9919	MCN3004	-30.0331	-51.2300
MHNCI12291	-30.0331	-51.2300	MCN3125	-30.0331	-51.2300
MHNCI12392	-30.0331	-51.2300	MCN3127	-25.4452	-51.9360
MHNCI12460	-30.0331	-51.2300	MCN3238	-25.4452	-51.9360
MHNCI12461	-30.0331	-51.2300	MCN3556	-25.4452	-51.9360
MHNCI12462	-29.9178	-51.1836	MCN3702	-25.4452	-51.9360
MHNCI12602	-30.0331	-51.2300	MCN3800	-25.4452	-51.9360
MHNCI12603	-29.9444	-50.9919	MCN4071	-25.4452	-51.9360
MHNCI12604	-28.0233	-48.6133	MCN4098	-25.4452	-51.9360
MHNCI13779	-30.0331	-51.2300	MCN6067	-28.5978	-49.4244
MHNCI13815	-28.5978	-49.4244	MCN6638	-26.3044	-48.8456
MHNCI13917	-28.5978	-49.4244	MCN6640	-26.3044	-48.8456
MHNCI15836	-30.0331	-51.2300	MCN8029	-25.5200	-48.5092
MuRAU004	-30.0331	-51.2300	MCN8122	-27.6342	-52.2739
MUZAR106	-29.6750	-50.2072	MCN8646	-28.1702	-52.4711
MUZAR22	-30.0331	-51.2300	MCN9094	-28.1702	-52.4711
MUZAR52	-30.0331	-51.2300	MCN9529	-28.1702	-52.4711
MUZAR53	-30.0331	-51.2300	MCN12802	-28.1702	-52.4711
MUZAR54	-27.8750	-51.1722	MCN15565	-28.1702	-52.4711
MUZAR55	-26.7597	-52.1911	MCN15566	-28.1702	-52.4711
MUZAR58	-26.7597	-52.1911	MCN15567	-28.1702	-52.4711
MUZAR62	-26.7597	-52.1911	MCN15568	-28.1702	-52.4711
MUZAR63	-26.7597	-52.1911	MCN15569	-28.1702	-52.4711
MUZAR64	-27.8750	-51.1722	MCN15570	-28.1702	-52.4711
MUZAR67	-26.7597	-52.1911	MCN15572	-28.1702	-52.4711
MUZAR71	-26.7597	-52.1911	MCN15574	-28.1702	-52.4711
MUZAR83	-27.8750	-51.1722	MCN15614	-28.1702	-52.4711
MUZAR86	-27.6892	-51.1300	MCN15615	-28.1702	-52.4711
MUZAR88	-27.6892	-51.1300	MCN15623	-28.1702	-52.4711
MUZAR90	-27.8750	-51.1722	MCN15801	-28.1702	-52.4711
MUZAR96	-27.4017	-51.2250	MCN16336	-28.1702	-52.4711
MUZAR106	-27.6342	-52.2739	MuZARSN	-28.1702	-52.4711
MHNCI808	-27.0903	-48.6114	MuRAU106	-25.5258	-48.3429
MHNCI849	-27.6342	-52.2739	MuRAU123	-25.3205	-49.1223
MHNCI1699	-27.0964	-52.6183	MUZAR132	-25.4278	-49.2731
MHNCI2075	-28.4492	-52.2000	MUZAR133	-24.9558	-53.4553
MHNCI2076	-27.9797	-52.2597	MUZAR134	-24.9558	-53.4553
MHNCI2106	-27.0903	-48.6114	MuRAU152	-25.9281	-49.1989
MHNCI5166	-27.0903	-48.6114	MuRAU154	-26.1614	-51.5525
MHNCI5177	-27.6342	-52.2739	MuRAU165	-25.8389	-52.0281
MHNCI5178	-27.0903	-48.6114	MuRAU167	-25.8389	-52.0281

MHNCI5180	-27.0903	-48.6114	MuRAU274	-25.8389	-52.0281
MHNCI5181	-27.0903	-48.6114	MuRAU281	-25.8389	-52.0281
MHNCI5182	-27.6342	-52.2739	MuRAU369	-25.8389	-52.0281
MHNCI5184	-29.1681	-51.1794	MCN521	-25.9411	-52.1756
MHNCI5186	-30.0811	-51.0233	MCN523	-25.9411	-52.1756
MHNCI5187	-30.0811	-51.0233	MCN769	-25.9411	-52.1756
MHNCI5189	-30.0811	-51.0233	MCN778	-25.8389	-52.0281
MHNCI5190	-30.0811	-51.0233	MCN779	-25.8389	-52.0281
MHNCI5192	-30.0331	-51.2300	MCN879	-25.8389	-52.0281
MHNCI5193	-30.0331	-51.2300	MCN880	-25.8389	-52.0281
MHNCI5195	-30.0811	-51.0233	MCN1052	-25.8389	-52.0281
MHNCI519	-30.0811	-51.0233	MCN1053	-25.8389	-52.0281
MHNCI5197	-30.0811	-51.0233	MCN1054	-25.8389	-52.0281
MHNCI5198	-30.0811	-51.0233	MCN1055	-25.8389	-52.0281
MHNCI5199	-30.0811	-51.0233	MCN1056	-25.8389	-52.0281
MHNCI5200	-30.0811	-51.0233	MCN1058	-25.8389	-52.0281
MHNCI5359	-30.0811	-51.0233	MCN1059	-25.8389	-52.0281
MHNCI6630	-30.0811	-51.0233	MCN1061	-26.2381	-51.0783
MHNCI6933	-30.0811	-51.0233	MCN1155	-24.5200	-48.1081
MHNCI6983	-30.0811	-51.0233	MCN1163	-26.3044	-48.8456
MHNCI6984	-30.0811	-51.0233	MCN1164	-26.2300	-51.0864
MHNCI7073	-30.0811	-51.0233	MCN1165	-26.7673	-48.6770
MHNCI7119	-30.0811	-51.0233	MCN1166	-25.4278	-49.2731
MHNCI7227	-30.0811	-51.0233	MCN1168	-25.4278	-49.2731
MHNCI7442	-30.0811	-51.0233	MCN1392	-25.4278	-49.2731
MHNCI7513	-30.0811	-51.0233	MCN1393	-22.9194	-42.8186
MHNCI7699	-30.0331	-51.2300	MCN1442	-26.1169	-48.6161
MHNCI8086	-30.0331	-51.2300	MCN1550	-24.8931	-52.2028
MHNCI8159	-30.0811	-51.0233	MCN1600	-25.6956	-51.6597
MHNCI8994	-30.0331	-51.2300	MCN1784	-25.4278	-49.2731
MHNCI9026	-30.0331	-51.2300	MCN1864	-25.4417	-49.0633
MHNCI9164	-30.0331	-51.2300	MCN1944	-25.4278	-49.2731
MHNCI9397	-30.0331	-51.2300	MCN1956	-26.3364	-49.9064
MHNCI9398	-30.0331	-51.2300	MCN1957	-26.3364	-49.9064
MHNCI9641	-30.0331	-51.2300	MCN1958	-25.4278	-49.2731
MHNCI9662	-30.0331	-51.2300	MCN1960	-25.7263	-48.9479
MHNCI9667	-30.0331	-51.2300	MCN1961	-25.8175	-48.5428
MHNCI9668	-30.0331	-51.2300	MCN1962	-25.8175	-48.5428
MHNCI9742	-30.0331	-51.2300	MCN1966	-25.8389	-52.0281
MHNCI9744	-30.0331	-51.2300	MCN1967	-25.8389	-52.0281
MHNCI9746	-30.0331	-51.2300	MCN1968	-25.9411	-52.1756
MHNCI10067	-30.0331	-51.2300	MCN2080	-26.2300	-51.0864
MHNCI10091	-30.0331	-51.2300	MCN2415	-26.2769	-52.7839
MHNCI10107	-30.0331	-51.2300	MCN2428	-26.3958	-52.4708
MHNCI10123	-30.0331	-51.2300	MCN2429	-26.3958	-52.4708
MHNCI10267	-30.0331	-51.2300	MCN2430	-25.5931	-49.4103
MHNCI10456	-30.0331	-51.2300	MCN2612	-25.9281	-49.1989
MHNCI10532	-30.0331	-51.2300	MCN2634	-25.8175	-48.5428
MHNCI10608	-30.0331	-51.2300	MCN2694	-28.5978	-49.4244
MHNCI10667	-30.0331	-51.2300	MCN2725	-25.5200	-48.5092

MHNCI10712	-29.9511	-51.0939	MCN2896	-26.9194	-49.0661
MHNCI10757	-29.9511	-51.0939	MCN2897	-25.6417	-52.1028
MHNCI10997	-29.9511	-51.0939	MCN2902	-27.4942	-48.6556
MHNCI11224	-29.9511	-51.0939	MCN2903	-26.1169	-48.6161
MHNCI11400	-29.9511	-51.0939	MCN2904	-23.6203	-45.4131
MHNCI11663	-29.9511	-51.0939	MCN2906	-25.4278	-49.2731
MHNCI11922	-29.9444	-50.9919	MCN2907	-26.1614	-51.5525
MHNCI12042	-30.0331	-51.2300	MCN2932	-25.7263	-48.9479
MHNCI12068	-30.0331	-51.2300	MCN2933	-26.0267	-48.8550
MHNCI12290	-29.9444	-50.9919	MCN3004	-30.0331	-51.2300
MHNCI12291	-30.0331	-51.2300	MCN3125	-30.0331	-51.2300
MHNCI12392	-30.0331	-51.2300	MCN3127	-25.4452	-51.9360
MHNCI12460	-30.0331	-51.2300	MCN3238	-25.4452	-51.9360
MHNCI12461	-30.0331	-51.2300	MCN3556	-25.4452	-51.9360
MHNCI12462	-29.9178	-51.1836	MCN3702	-25.4452	-51.9360
MHNCI12602	-30.0331	-51.2300	MCN3800	-25.4452	-51.9360
MHNCI12603	-29.9444	-50.9919	MCN4071	-25.4452	-51.9360
MHNCI12604	-28.0233	-48.6133	MCN4098	-25.4452	-51.9360
MHNCI13779	-30.0331	-51.2300	MCN6067	-28.5978	-49.4244
MHNCI13815	-28.5978	-49.4244	MCN6638	-26.3044	-48.8456
MHNCI13917	-28.5978	-49.4244	MCN6640	-26.3044	-48.8456
MHNCI15836	-30.0331	-51.2300	MCN8029	-25.5200	-48.5092
MuRAU004	-30.0331	-51.2300	MCN8122	-27.6342	-52.2739
MUZAR106	-29.6750	-50.2072	MCN8646	-28.1702	-52.4711
MUZAR22	-30.0331	-51.2300	MCN9094	-28.1702	-52.4711
MUZAR52	-30.0331	-51.2300	MCN9529	-28.1702	-52.4711
MUZAR53	-30.0331	-51.2300	MCN12802	-28.1702	-52.4711
MUZAR54	-27.8750	-51.1722	MCN15565	-28.1702	-52.4711
MUZAR55	-26.7597	-52.1911	MCN15566	-28.1702	-52.4711
MUZAR58	-26.7597	-52.1911	MCN15567	-28.1702	-52.4711
MUZAR62	-26.7597	-52.1911	MCN15568	-28.1702	-52.4711
MUZAR63	-26.7597	-52.1911	MCN15569	-28.1702	-52.4711
MUZAR64	-27.8750	-51.1722	MCN15570	-28.1702	-52.4711
MUZAR67	-26.7597	-52.1911	MCN15572	-28.1702	-52.4711
MUZAR71	-26.7597	-52.1911	MCN15574	-28.1702	-52.4711
MUZAR83	-27.8750	-51.1722	MCN15614	-28.1702	-52.4711
MUZAR86	-27.6892	-51.1300	MCN15615	-28.1702	-52.4711
MUZAR88	-27.6892	-51.1300	MCN15623	-28.1702	-52.4711
MUZAR90	-27.8750	-51.1722	MCN15801	-28.1702	-52.4711
MUZAR96	-27.4017	-51.2250	MCN16336	-28.1702	-52.4711
MUZAR106	-27.6342	-52.2739	MuZARSN	-28.1702	-52.4711

S2 Appendix. Environmental variables used for species distribution modeling for *O. fragilis* in south of Neotropical region.

Variables	**Dataset name**	**Spatial resolution**	**Year**	**Source**
Land cover	GlobCover Land; Cover version v2.3	300 meters	2009	ESA GlobCover Project
Altitude	Alt = altitude	30 arc-second	2005	WorldClim global climatic layers
Bioclimatic	Bio1 = annual mean temperature	30 arc-second	2005	WorldClim global

variables	Bio2 = mean diurnal range Bio3 = isothermality Bio4 = temperature sazonality Bio10 = mean temperature of warmest quarter Bio12 = annual precipitation Bio13 = precipitation of wettest month Bio14 = precipitation of driest month Bio15 = precipitation seasonality Bio17 = precipitation of driest quarter Bio18 = precipitation of warmest quarter Bio19 = precipitation of coldest quarter	climatic layers

CONCLUSÃO GERAL

O presente trabalho contribuiu para o entendimento dos fatores envolvidos na variação morfológica de *O. fragilis*, buscando uma abordagem integrada, baseada nos conceitos da ecomorfologia, analisando tanto as variáveis abióticas quanto bióticas às quais os organismos encontram-se submetidos. Os resultados obtidos permitem concluir que *O. fragilis* apresenta padrões morfológicos determinados pelo ambiente. As formações campestres, de substrato mais maleável e volume de presas menor, levaram à seleção de organismos menores e mais robustos. Já as formações florestais, de substrato mais denso e maior volume de presas, originou organismos maiores, mais gráceis e alongados.

Nossas hipóteses de que as diferenças de habitat resultariam em padrões morfológicos distintos para a espécie foram corroboradas. As características de habitat que influenciam a distribuição e a variação morfológica nesta espécie são relacionadas à precipitação, temperatura e cobertura do solo, que definem o tipo de recurso alimentar e de substrato disponíveis para os organismos. Nossas conclusões apresentam profundas implicações para a conservação dessa espécie, já que as mudanças globais irão causar modificações significativas em seu habitat, alterando as principais variáveis que influenciam a disponibilidade dos recursos dos quais dependem e também sua atividade metabólica. Contudo, estudos mais aprofundados ainda se fazem necessários, no sentido de elucidar se os padrões verificados são adaptações ou simplesmente resultado da plasticidade fenotípica da espécie.

Como perspectivas de continuidade, pretendemos realizar estudos relacionados a adequabilidade de habitat. Pretendemos investigar se crescer em um ambiente que fornece condições mais adequadas de temperatura, precipitação e recursos alimentares resulta na seleção de indivíduos mais simétricos e também se essa adequabilidade ambiental está de alguma forma influenciando a biologia reprodutiva destes organismos.