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Predator morphology affects prey consumption: evidence from an anuran population in subtropical wetlands

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Morphology and diet are key factors in the ecology of organisms, determining aspects of the natural history and evolution of the species. In this work, we evaluated the diet-morphology relationship in an anuran population, measuring the influence of morphological traits on the variation in the diet of individuals of *Leptodactylus luctator*. For this purpose, we collected individuals from a natural grassland habitat in southern Brazil. We analysed the stomach content of individuals and classified the consumed food items up to the classification level of order. We also measured four morphological traits per individual of *L. luctator*: distance between eyes, relative limb length, relative mouth width (gape) and snout-vent length. We applied Linear Mixed Effect Models to evaluate the relationship of anuran morphological traits, number of prey taxa and volume of consumed prey. We tested the hypothesis that the configuration of predator morphological traits determines variations in prey consumption patterns. Our results indicate that the body size of *L. luctator* was not directly related to the diet composition but the individuals' gape is directly and positively related to the number of consumed taxa. This suggests that gape limitation could be a limiting factor in prey selection. The capacity to consume a wide variety of prey taxa could be an advantage in unpredictable environments, especially those with great daily thermal amplitudes such as the subtropical Brazilian grasslands.

Keywords: Leptodactylus luctator, diet, amphibian, ecomorphology, functional ecology,

INTRODUCTION

Amphibians are important predators of small organisms, which represent a considerable portion of the biomass present in ecosystems (Wells, 2007; Rowland et al., 2016). The diet of most amphibian species consists almost exclusively of arthropods, however, although several species have specialised feeding habits, anurans are known for having generalist foraging habits, preying on a wide variety of invertebrate and vertebrate orders (Duellman, 2005; Moser et al., 2019; Oliveira et al., 2022). Among the aspects of the natural history of amphibians, diet is recognised as one of the most important, reflecting their evolutionary history (Duellman & Trueb, 1994; Da Rosa et al., 2002).

Most studies on anuran diet are based on the quantification and description of food items and their relative importance for the species' trophic ecology (Moser et al., 2017; Farina et al., 2018; Moser et al., 2019). However, current ecological studies reinforce the importance of using approaches that integrate the species' ecological-evolutionary aspects (e.g. Queiroz et al., 2015; Leite-Filho et al., 2017; Marques et al., 2019; Dalmolin et al., 2019), which include the relationship

within functional traits (such as morphological traits) and ecological variables. Using this approach, the processes that determine the ecological-evolutionary aspects of species become clearer (Marques & Nomura, 2015; Tonkin et al., 2016), and this includes their feeding behaviour (Tozetti & Martins, 2019). Thus, diet stands out as an important factor associated with the ecological and morphological traits of each taxon (Sih & Christensen, 2001).

Foraging strategy is considered a determining factor of the diet in anurans (Toft, 1981; Santos et al., 2004; Piatti & Souza, 2011). Among species that feed on invertebrates, those that are active foragers tend to consume smaller prey that have social habits and slow movements (such as ants and termites) (Toft, 1981). On the other hand, species that have a sit-and-wait type of foraging behaviour generally consume larger and solitary prey such as beetles, orthopterans, and spiders (Strüssmann et al., 1984; Magnusson et al., 1985; Pough & Taigen, 1990). Diet variation is also driven by prey availability (Michelin et al., 2020; Moroti et al., 2021), in particular in generalist species which tend to eat the most abundant prey in their habitat (Maneyro et al., 2004; López et al., 2009; Rebouças & Solé, 2015).   However, a substantial

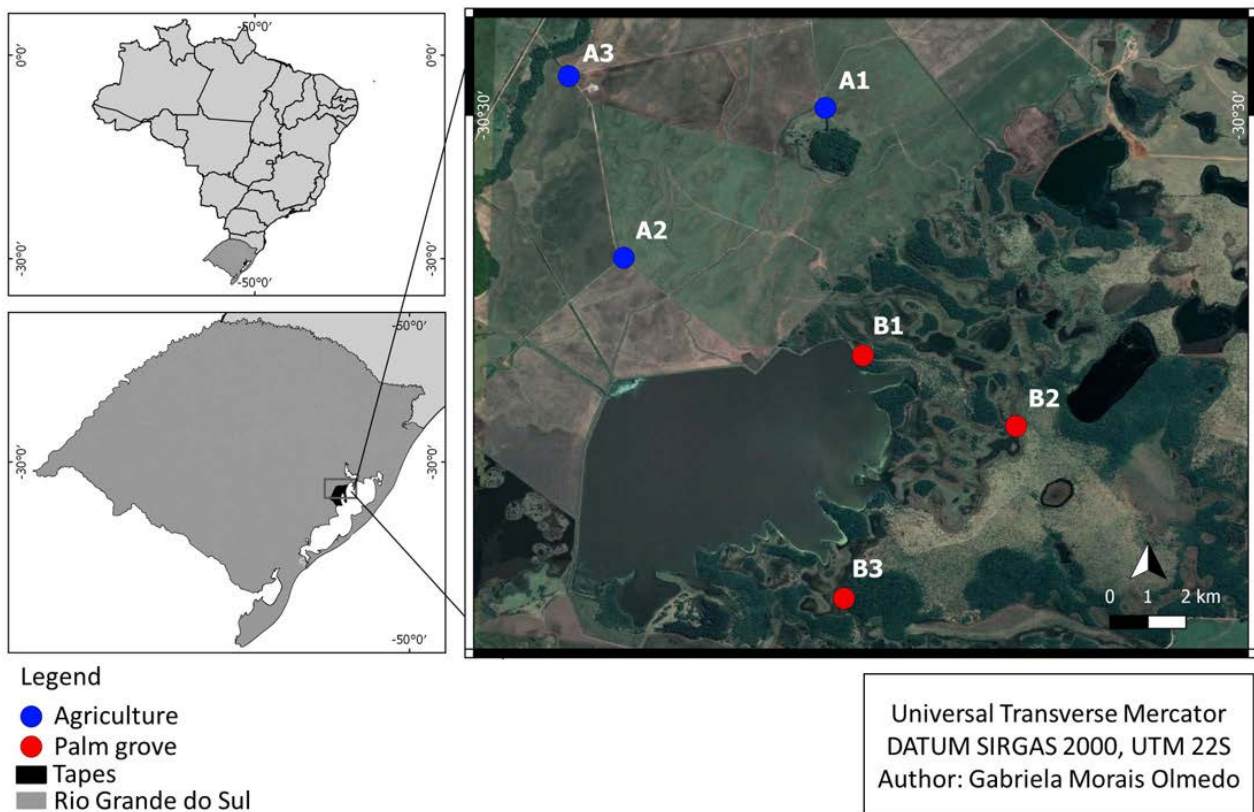*Correspondence: Camila Moser (camila-moser@hotmail.com)*

Figure 1. Study area in the municipality of Tapes, Rio Grande do Sul, Brazil. Sampled areas are represented by blue (agriculture matrix) and red (natural palm grove matrix) circles.

part of the variation in diet can emerge in response to inter/intra species functional divergence (Simon & Toft, 1991; Piatti & Souza, 2011). In these cases, the behavioural aspects would be important, but also those characteristics related to the species' physiology and morphology.

In anurans, the association between morphology and diet may become more obvious when individuals of the same species are compared. The morphology of the skull structures, for example, has a great influence on the consumed prey types and have great inter and intra species variation (Emerson & Bramble, 1993; Duellman & Trueb, 1994; Metzger & Herrel, 2005; Cvijanović et al., 2014). Gape size for example, affect the patterns of consumed prey or prey size (Emerson, 1985; Menzies & Parker, 2018). An obvious assumption is that predator body size defines their ability to subdue prey and creates a limit to the maximum size of potential prey. Consequently, the relationship between predator and prey sizes affects the species' trophic niche, as well as on the patterns of divergence in the diet between individuals with different body sizes (Strüssmann et al., 1984; Shine, 1991; Forsman & Lindell, 1993; Araújo et al., 2007). Intrapopulational variation in prey preferences can work as a mechanism to avoid competition, which favours the co-occurrence of close related individuals (Guimarães et al., 2011; Piatti & Souza, 2011). Recently, individual specialisation has gathered attention from ecologists due their contribution to the understanding of trophic specialisations (Bolnick et al., 2003; Xia et al., 2020).

Based on previous studies, many aspects related to the diet of predators (e.g. species composition and biomass) are affected by their morphological traits (such as body size and maximum gape; Araújo et al., 2007; Solé et al., 2017; Tozetti & Martins, 2019). In this work, we evaluated the relationship between the descriptors of feeding behaviour (richness and volume of consumed prey) and the morphological traits of *Leptodactylus luctator* in southern Brazil. Specifically, we tested the hypothesis that a predator's morphological traits (snout-vent length, relative limb length, distance between eyes, and gape) determine the richness and volume of prey consumption. We predicted that the richness and volume of consumed prey have a positive relationship with morphological traits, especially with snout-vent length and gape. As reported by other species, anurans eat the whole prey, the mouth gape being a limiting factor to their ability to ingest (Vitt et al., 2000; Tozetti & Martins, 2019).

MATERIALS & METHODS

Study area
We conducted the study in natural grassland habitats located in the municipality of Tapes, State of Rio Grande do Sul, Brazil (51° 22' 36.8'' S; 30° 25' 58.3'' W; Fig. 1), at 10 m above sea level. The study site covers an area of 1,294.5 ha and includes well-preserved areas of the Pampa Biome (in particular, sandbank formations; Becker et al., 2007). The area stands out for having one of the last

Figure 2. Habitat types present in the study area - **A.** natural palm-grove grasslands, and **B.** agriculture grasslands with irrigated rice and soybean cultivation.
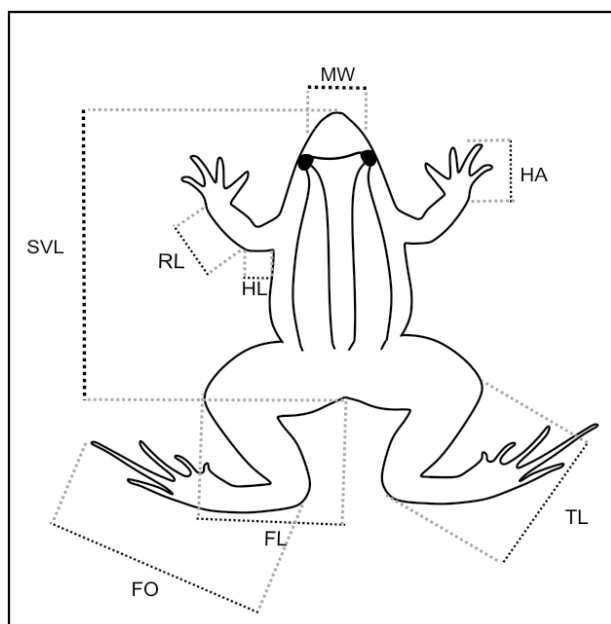
Table 1. Morphological traits measured in adults of *Leptodactylus luctator*

Morphological Trait	Levels	Ecological relevance
Distance between eyes	mm	These traits are associated with the number of individuals and richness of consumed prey orders
Snout-vent length	mm	
Mouth width	Distance between mouth ends (mm)	
Relative limb length	(femur length + tibia length + foot length) / (arm length + forearm length + hand length) - mm	Limb length is associated with the capacity of individuals to search and explore different microhabitats

Figure 3. Morphological metrics evaluated in adults of *Leptodactylus luctator*: SVL = snout-vent length; TMP = third metacarpal and phalanx length; RL = radius length; HL = humerus length; FMP = fourth metatarsal and phalanx length; TL = tibia length; FL = femur length; MW = mouth width.

remnant palm grove habitats formed by *Butia odorata* (Barb. Rodr.) Noblick in Brazil. There is an estimated number of 70,000 individuals of *B. odorata* forming a single continuous palm grove spreading over an area of 750 ha (Fig. 2A). The average annual temperature and rainfall in the study region are 18 °C and 1,200 mm, respectively (Maluf, 2000). The area adjacent to the palm groove is used for agricultural activities and is subject to the conventional planting systems. This area has a size of about 800 ha where irrigated rice and soybean are cultivated.

Data collection

We adopted the nomenclature presented by Magalhães et al. (2020) in which the studied frog population, formerly considered as *L. latrans*, was updated to *L. luctator.* We performed the sampling of individuals of *L. luctator* from September to December 2018. For this purpose, we used visual search (Crump & Scott Jr, 1994) in breeding sites between 20:00 h and 02:00 h. We sampled each area monthly for three consecutive days (N = 12 days). The search was performed by four researchers for one hour in as many breeding sites as possible. Thus, our total sampling effort was 288 search hours. To avoid any effects of ontogeny in our analysis, we restricted collection to adult individuals. The search was conducted in six breeding sites distributed throughout the study area that included a great variety of habitats. Considering this, we selected three breeding sites in natural, preserved grasslands (in the palm groove area) and three breeding sites in grasslands adjacent to agricultural areas (irrigated rice and soybean cultivation; Fig. 2). The choice of the sampled areas occurred so that we could assess the influence of different environmental conditions on the species' diet.

The captured specimens (N = 47), were placed in plastic bags and kept in refrigeration equipment to decrease digestive activity until euthanasia (Moser et al., 2017). The time between capture and euthanasia was less than 2 hours. The collections were carried out under the authorisation of the Federal Agency (SISBIO - authorisation number 66513). Subsequently, individuals were euthanised with xylocaine, fixed with 10% formaldehyde, and preserved in 70% ethanol. In the laboratory, we removed the gastrointestinal contents of each individual, which were also kept in 70% ethanol. We performed the screening of the samples using a stereomicroscope with a magnification range of 10x to 45x. We identified the consumed prey items up to the level of order based on regional literature (Ribeiro-Costa & Rocha, 2002). We then macerated and spread each individual's stomach contents in a Petri dish. Graph paper

Table 2. Results of LMM models showing the relationship between descriptors of feeding behaviour and morphological traits of *Leptodactylus luctator*. DF (degrees of freedom); AICc (Akaike's Information Criterion); R^2m (fixed effects); R^2C (fixed + random effects).

| Descriptors	Morphological traits	DF	*F*	*p*	AICc	R^2m	R^2C
Consumed prey diversity	Distance between eyes	47	0.99	0.32			
	Mouth width	47	4.02	0.04			
	Relative limb length	47	0.04	0.83	16.18	0.12	0.12
	Body size (snout-vent length)	47	0.83	0.37			
Total volume	Distance between eyes	47	0.04	0.85			
	Mouth width	47	1.50	0.23			
	Relative limb length	47	0.01	0.98	659.25	0.18	0.18
	Body size (snout-vent length)	47	8.32	< 0.001			
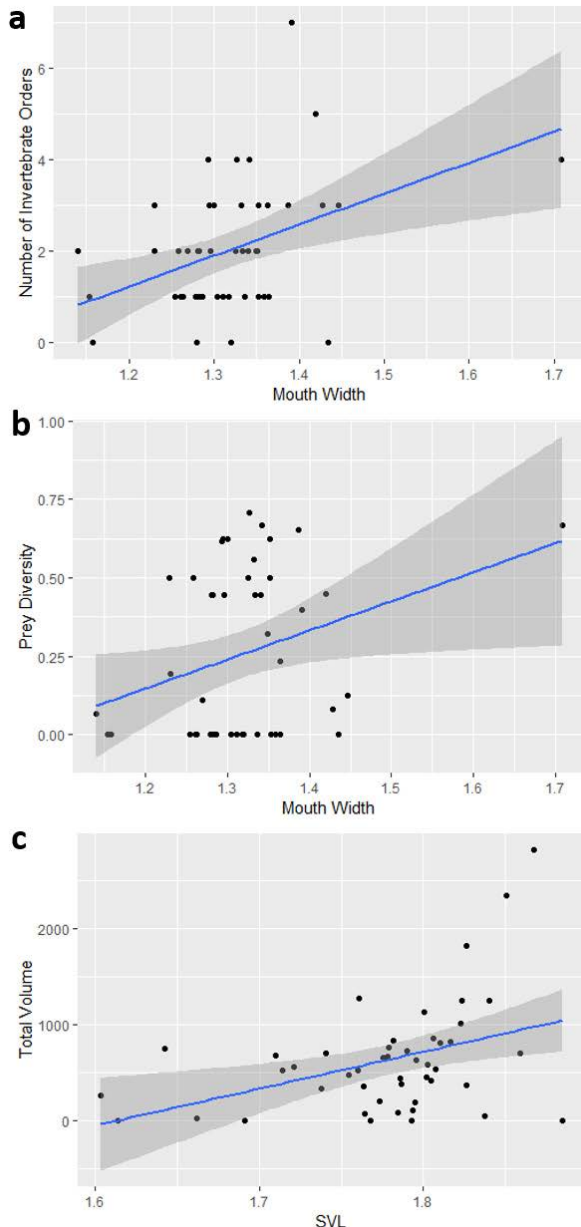
Figure 4. Diet-morphology relationships in *Leptodactylus luctator*. **A.** Relationship between the number of consumed invertebrate orders and gape; **B.** Relationship between the consumed prey diversity and mouth width; **C.** Relationship between total volume of consumed prey and snout-vent length.

(1 mm x 1 mm) was placed under the plate and used to measure the volume (V) and the number of identifiable orders found when categorising the prey (see Moser et al., 2020 for additional details). Prey items were then pressed with a pistil until the entire macerated layer was homogeneous and uniform with a height of 1 mm (Fig. 3). The individuals of *L. luctator* were deposited in the scientific collection of the Laboratório de Ecologia de Vertebrados Terrestres of the Universidade do Vale do Rio dos Sinos. The voucher numbers are available in the supplementary material.

Trait measurement
We evaluated four morphological traits of each individual: distance between eyes, relative limb length, relative mouth width (gape), snout-vent length and anatomical components as RL (radius length), HL (humerus length), FMP (fourth metatarsal and phalanx length), TL (tibia length) and FL (femur length; Fig. 3). We chose these traits based on literature (Marquéz-García et al., 2009) as well on perceived importance for determining the diet composition in several anuran species, including *L. luctator*. The morphological traits were characterised according to the metrics presented in Fig. 3 and Table 1 and based on Marquéz-García et al. (2009).

Statistical analysis
We tested the possible existence of relationships between descriptors of feeding behaviour (consumed prey diversity, total volume and number of consumed invertebrate orders) and morphological traits (distance between eyes, relative limb length, relative mouth width [gape] and snout-vent length) by using Linear Mixed Models (LMM). We used the Rao's quadratic entropy (Q) to assess the diversity of consumed prey. The Rao's quadratic entropy is a measure of diversity which is based on the proportion of the abundance of species present in a sample; in statistical terms, Rao quadratic entropy is equivalent to the Gini-Simpson index, and the dissimilarity range from 0 to 1 (Rao, 1982).

We generated individual models for each descriptor of feeding behaviour. Collection date and habitat were used as random effects. We log-transformed the values of morphological traits before the analysis, and also tested the collinearity between them by using Variance Inflation Factor analysis (VIF; Lin et al., 2011). Results

did not indicate a significant correlation between any of the evaluated traits. We used the Quasi-Poisson as link function to model the distribution of the total volume and number of consumed invertebrate orders in relation to the functional traits, in order to avoid or decrease the chances of the overdispersion in our data (Davison & Snell, 1991). For the diversity of consumed prey, we used the gaussian link function, which is specific for data which range from 0 to 1. We tested the significance of each diet-morphology relationship by ANOVA. We then ran these analyses with the packages "MuMin" and "vegan" within R software.

RESULTS

The LMM analysis revealed that the distribution of data related to the total volume of prey consumed was overdispersed (overdispersion > 1). It means that the amount of data that did not adjust to the distribution of the predictor variables (i.e. traits) was preponderant (i.e. excessive amount of residues). On the other hand, data distribution in the model with the number of consumed order showed a relatively low overdispersion (overdispersion = 0.83). In this way, we limited the following analyses to the models in which the number of both prey orders and diversity was considered.

We found a significant and positive relation between gape and the number of consumed prey order and prey diversity (Table 2; Fig. 4a and 4b). Also, the fixed effects (morphological traits) accounted for the total explained variation in both models.

DISCUSSION

Our results showed evidence that variations in some morphological traits are accompanied by differences in the dietary composition of individuals of *L. luctator*. The morphological traits affected each of the evaluated components (prey composition) differently. We found that: (i) body size (snout-vent length) was not directly related to the diet composition and (ii) the larger an individual's gape, the more diverse its dietary composition will be (larger number of prey taxa in the gut). These results are relevant because they highlight a little-explored dimension regarding an anuran diet: intraspecific dietary variation.

In general, species of Leoptodactylidae are considered generalist predators since they consume a great variety of food items (Protázio et al., 2015). This is a common characterisation for many species whose diet is known (Rodrigues et al., 2004; Pazinato et al., 2011; Sugai et al., 2012; Dias et al., 2018). However, we draw attention to the fact that variation in foraging, even subtle ones, can be found when examining the diet at the individual level. In the last decades, the number of studies with focus on anuran diet has been increasing (Piatti & Souza, 2011). More than a description of food items, the idea of testing intrapopulation variation in diet, as well as the relationship between frog size and diet, was well explored by previous studies (Araújo et al., 2007; Borges

et al., 2019). On the other hand, our study presents a new approach by adding morphology as a possible driver for dietary differences among individuals. We observed, for example, that body size (snout-vent length) is one of the traits related to dietary variation in *L. luctator*. This relationship is somewhat intuitive since larger animals would theoretically have the greater prey-storage capacity in their digestive tracts (Tozetti & Martins, 2019).

The stomach size of individuals generally increases with body size, so that larger individuals tend to hold a larger volume of prey (Sugai et al., 2012). This hypothesis is reinforced by studies in Uruguayan populations of *L. luctator* (Maneyro et al., 2004), which reported a positive correlation between the body size and the size of consumed prey. In our study, data from prey volume did not fit in our models. In a similar study, Solé et al. (2009) evaluated the diet of the same species in north-eastern Brazil and found no significant correlation between the size of individuals and the volume of consumed prey. These contradictions reinforce the need for more detailed studies between morphological parameters related to pray/predator relationship.

Our data allow us to infer that the dietary patterns of *L. luctator* are determined by gape. While the latter affects the ability to subdue prey, gape acts as a limiting factor in prey selection (Araújo et al., 2007; França et al., 2004; Maneyro et al., 2004). Limits in the gape can restrict the size and, consequently, the variety of prey that can be ingested (Huckembeck et al., 2018). Still, the trend is that the relationship between mouth width and the diversity of consumed prey is linear and positive since animals with a larger mouth opening can consume a wide range of prey categories, which would contain prey items of all sizes (De Carvalho Batista et al., 2011; Sales et al., 2011). These hypotheses are reinforced by the fact that our data indicate gape as the main predictor of prey diversity. The fact that we did not find a relationship between limb length and diet suggests that only specific morphological traits related to foraging affect feeding behavior (Bonte et al., 2012). Relative limb length does not seem to have a major contribution to foraging in anurans (Jeltsch et al., 2013; Bredeweg et al., 2019), although this trait is a conditional factor for access to habitats.

The relationship between a predator's body size and the amount of prey it eats is an ecological consequence of feeding ecology (MacArthur & Pianka, 1966; Charnov, 1976; Duelmann & Trueb, 1994). The possibility of ingesting a larger volume of prey can be an important attribute in unpredictable environments and environments subjected to anthropic modification, especially those with great daily thermal amplitudes (e.g. agricultural areas; Lopez et al., 2015). In this type of environment, sudden temperature drops can decrease the activity of invertebrates, reducing prey availability for anurans (Gibbs & Stanton, 2001; Lopez et al., 2009; Battles et al., 2013). In this case, larger individuals would have accumulated reserves in their stomachs from nights of successful foraging.

Our data reinforce the need to consider aspects of the functional diversity of anurans — especially those

related to their morphology — in future studies that are interested in the diet and trophic ecology of this group. Given the fact that anurans have high degrees of phylogenetic conservation in several traits (including morphological and behavioural traits; Campos et al., 2019), we suggest that these patterns of trait-diet relationship can be extended to other species of the clade Leptodactylidae.

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