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Feeding ecology of *Erythrolamprus jaegeri jaegeri* (Günter, 1858) and *Erythrolamprus poecilogyrus sublineatus* (Cope, 1860) in the coastal zone of Subtropical Brazil (Serpentes, Dipsadidae)

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ABSTRACT

The snakes *Erythrolamprus jaegeri jaegeri* and *Erythrolamprus poecilogyrus sublineatus* are sympatric and syntopic in the coastal region of southern Brazil. Herein, we analyzed the diet composition to evaluate the niche breadth and the prey selection by both species. We examined 192 specimens, and analysis of stomach contents revealed that both species predominantly consume anurans. However, the diet of *E. j. jaegeri* consists mainly of fish and amphibians, whereas that of *E. p. sublineatus* is broader, including fish, amphibians, reptiles and mammals. The Standardized Levins Index presented lower values for *E. j. jaegeri* (BA = 0.17) than for *E. p. sublineatus* (BA = 0.61), evidencing specialist and generalist strategies for each species, respectively. Regarding prey selection, *E. p. sublineatus* presented a larger snout-vent length, head, mouth and lower jaw than *E. j. jaegeri* and fed on larger prey. In addition, positive correlations between the size and weight of predators and prey were confirmed in both species. The results show the development of different mechanisms for co-occurrence of the two species, such as prey selection by size, such that the size of the predator is related to the size of their prey, or by developing different strategies to decrease niche overlap between species.

Key words: diet, ophidians, prey, size, niche.

INTRODUCTION

The ecological niche, defined as the set of physical and environmental variables in multi-dimensional space (Hutchinson 1957), encompasses three dimensions: spatial niche, feeding niche and temporal niche (Pianka 1982). The feeding niche is one of the most important dimensions among snakes and may influence biological and ecological features such as use of habitat, predatory behavior and period of activity (Toft 1985).

By the snakes eating vertebrate and invertebrate animals, we can call them carnivorous anyway (Mushinsky 1987, Greene 1997). This diversity is possible due to the development of morphological and biochemical mechanisms that facilitate snakes' detection of prey (Pough et al. 2008). Researchers have identified the following among the evolutionary events that influenced the foraging success of snakes: cranial and muscular adaptations that allow the ingestion of prey wider than the predator itself (Pough et al. 2008, Greene 1997); the development of different mechanisms for prey detection (chemoreception, accurate

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vision, heat orientation) and subjugation (strike, constriction, poisoning) (Greene 1997, Burghardt and Krause 1999, Pough et al. 2008, De Fraga et al. 2013); and occupation of different habitats (Quintela and Loebmann 2009, De Fraga et al. 2013).

Erythrolamprus jaegeri jaegeri (Günter, 1858) and *Erythrolamprus poecilogyrus sublineatus* (Cope, 1860) are semi-aquatic dipsadid snakes, sympatric in southernmost Brazil (Quintela et al. 2006, Quintela and Loebmann 2009, Santos et al. 2012). *Erythrolamprus j. jaegeri* can reach 550 mm in total length (Giraudo 2001) and is distributed in southeastern and southern Brazil and Uruguay (Dixon 1989). Over its southern distribution, it has been found mainly associated with wet habitats (Carreira et al. 2005, Quintela and Loebmann 2009), where underwater foraging and inactivity are documented (De Lema 2002). The adaptations for semiaquatic life observed in the species include the presence of a vestibule preventing the entry of water into the nasal cavity and the *fenestra narina* in dorsal position (Schmitt and Deiques 2009). *Erythrolamprus p. sublineatus* grows up to 700 mm in total length (Giraudo 2001) and is distributed throughout Argentina, Uruguay and the Rio Grande do Sul state of southernmost Brazil (Dixon and Markezick 1992), where it inhabits such varied habitats as grasslands, wetlands forests and coastal dunes (Carreira et al. 2005, Winck et al. 2007, Quintela and Loebmann 2009).

Studies have demonstrated that the competition between congeneric species is intense due to the sharing of habitat and resources (Darwin 1872, Losos 1994, Steen et al. 2014). Thus, different strategies emerge from phylogenetically close species to decrease competition and favor co-occurrence in a specific habitat (Pianka 1973). As a result, the level of resources shared by sympatric species is quantified by the analysis of niche breadth and overlap (Hurlbert 1978).

Given the sympatric condition of *E. j. jaegeri* and *E. p. sublineatus* in southernmost coastal Brazil, we investigated the diet composition of both species aiming to answer two questions: (1) Does *E. p. sublineatus* feed on larger prey, seeing that larger predators forage larger prey (Shine 1991)? (2) Considering the high association of *E. j. jaegeri* with wet habitats (De Lema 2002, Quintela and Loebmann 2009), does this species feed on more prey of aquatic origin compared with *E. p. sublineatus*?

MATERIAL AND METHODS

STUDY AREA

This study was conducted in the municipalities of Rio Grande and São José do Norte (31°47’02” - 32°39’45” S; 52°03’50” - 52°41’50” W), Rio Grande do Sul (RS) coastal plain, southern Brazil. The climate in the region is classified as warm temperate and fully humid (Kottek et al. 2006), with an annual average of 18°C. The annual precipitation is 1162 mm, and droughts may occur during the spring (Maluf 2000).

The southern RS coastal plain is characterized by low altitudes (generally under 3 m above sea level) and the predominance of open physiognomies such as grasslands, savannic grasslands, sandy fields and dunes (Vieira 1984). Forest formations are restricted to *restinga* patches, generally associated with water courses (riparian forest) and elevated groundwater areas with sandy or muddy soil (sandy and peat forests, respectively) (Waechter 1985, Marchiori 2004). Major hydrographical elements include the Patos-Mirim lagoon complex, coastal lagoons, wetlands and coastal streams (Vieira 1984).

DATA SAMPLING

Specimens were collected in different habitats of the study area (e.g., wetlands, grasslands, *restinga* forests) and were euthanized promptly after capture. From these, we obtained the following biometric measurements using a flexible ruler to the nearest 1.0 mm and a digital caliper to the nearest 0.01 mm: snout-vent length (SVL), head length (HL), head width (HW), maximum head height (HH), mouth length (ML), mouth width (MW), mandible length (IML) and wet weight (W). Specimens examined in this study are deposited in the Herpetological Collection of the Universidade Federal do Rio Grande (CHFURG), Rio Grande, Brazil (Appendix).

The digestive tracts of the analyzed specimens were removed through incisures made from esophagus to cloaca. All of the digestive tract contents were extracted, and the fresh and partially digested items were selected. The total length (TL) and weight (W) of fresh items were measured. The digested items for which total length was possible to obtain also had their body mass estimated by comparison with biometric data from specimens stored in the herpetological and ichthyological collections of FURG. For this, three collection specimens with equal length were selected, and the mean of their body masses was used as an estimated value for the prey body mass. In the case of items at an advanced stage of digestion, well-preserved structures (e.g., femur) were used to estimate total length and body mass. For this, the means of total length and body mass of three collection specimens with equal dimensions of the selected structure were used as estimated values for the prey total length and body mass. The direction of ingestion (headfirst or tail-first) was recorded whenever possible. The food items were identified to the lowest possible taxonomic category. All items were conserved in 70% alcohol and stored in the Laboratory of Vertebrates, Biological Sciences Institute, Universidade Federal do Rio Grande (FURG), Rio Grande, Brazil. All procedures were carried out according to the international practices for animal use and approved by the internal committee of ethics for animal use of the Universidade Federal do Rio Grande, Brazil.

DATA ANALYSIS

Qualitative and quantitative methods were applied to our database as proposed by Hyslop (1980). The qualitative method consisted of the analysis of the frequency of occurrence (FO%) of each identified taxon, calculated by the rate of number of stomachs containing such taxon over the total number of analyzed stomachs.

The first quantitative method applied was the numeric abundance index (N%) of each identified taxon, obtained by calculating the rate of the absolute number of prey of such taxon over the sum of prey of all identified taxa. The following method consisted of determining the percentage weight (W%) of each identified taxon, given by the rate of the sum of the weights of prey of such taxon over the sum of the weight of prey of all identified taxa (Hynes 1950). The Index of Relative Importance (IRI) [Hacunda (1981), modified from Pinkas et al. (1971)] of each identified taxa was obtained by applying the following formula: IRI = FO%(N% + W%).

To verify the niche breadth of the two species, we applied the Levins index (Krebs 1999), given by BA = [(1/Σpi2)-1]/n-1, where BA is the standard, pi is the frequency of occurrence of the taxon i in the whole sample, and n is the number of all taxa identified in the whole sample. The obtained values can vary from zero to one, such that a value close to one implies a well-distributed diet (item of the distinct taxa consumed in equivalent proportions; generalist dietary pattern), whereas a value close to zero implies that items of few taxa were consumed in high proportion and items of most taxa where consumed in low proportion (specialist dietary pattern).

The existence of significant differences between *E. p. sublineatus* and *E. j. jaegeri* SVL means and the means of total length and weight of prey categories “fishes” and “amphibians” were examined with a Student t test. Similarly, we tested the difference between measurements of HL, HW, HH, ML, MW and IML between the species.

A linear regression method was used to verify the correlation between the log-transformed weights of prey and its respective predators. The level of correlation was measured using the Spearman Correlation Coefficient.

RESULTS

DIET COMPOSITION

A total of 74 specimens of *E. j. jaegeri* were analyzed, 20 of which showed stomach contents. The 28 prey items consisted of anuran amphibians (82.2%), fishes (10.7%) and isopods (7.1%). Anuran prey consisted of *Leptodactylus latrans* (35.7%), *Physalaemus gracilis* (28.6%) and *Pseudopaludicola falcipes* (3.6%) and fish prey of *Phallocerus caudimaculatus* (10.7%). Isopods could not be identified at the species level (Table I).

A total of 44 of the 118 analyzed *E. p. sublineatus* specimens had stomach contents. We found 111 prey items, which included anurans (54.1%), fishes (42.3%), reptiles (2.7%) and mammals (0.9%). Anuran items included *L. latrans* (26.1%), *Odontophrynus maisuma* (10.8%),

TABLE I
Food items and their respective abundance in the diets of *Erythrolamprus jaegeri jaegeri* and *Erythrolamprus poecilogyrus sublineatus*.

PREY TAXON	*Erythrolamprus jaegeri jaegeri*				*Erythrolamprus poecilogyrus sublineatus*			
	PREY N=28		STOMACH		PREY N=111		STOMACH	
	N	%	N	%	N	%	N	%
ARTROPODA								
Isopoda								
Unidentified	2	7.1	2	9.5				
FISHES								
Anablepidae								
Jenynsia multidentata					2	1.8	1	2.0
Characidae								
Unidentified					6	5.4	1	2.0
Poeciilidae								
Phallocerus caudimaculatus	3	10.7	1	4.8	39	35.1	1	2.0
AMPHIBIANS								
Bufonidae								
Rhinella gr. *granulosa*					6	5.4	6	12.1
Hylidae								
Hypsiboas pulchellus					2	1.8	2	4.1
Unidentified	1	3.6	1	4.8				
Leptodactylidae								
Leptodactylus gracilis					3	2.7	3	6.1
Leptodactylus latrans	10	35.7	6	28.6	29	26.1	17	34.7
Physalaemus gracilis	8	28.6	7	33.3	2	1.8	2	4.1
Pseudopaludicola falcipes	1	3.6	1	4.8				
Unidentified	2	7.1	2	9.5	2	1.8	2	4.1
Odontophrynidae								
Odontophrynus maisuma					12	10.8	7	14.3
Microhylidae								
Elachistocleis bicolor					2	1.8	2	4.1
Unidentified	1	3.6	1	4.8	2	1.8	2	4.1
REPTILES								
Gymnophtalmidae								
Cercosaura schreibersii					3	2.7	2	4.1
MAMMALS								
Unidentified					1	0.9	1	2.0

Rhinella gr. *granulosa* (5.4%), *P. gracilis* (1.8%), *Leptodactylus gracilis* (2.7%), *Elachistocleis bicolor* (1.8%) and *Hypsiboas pulchellus* (1.8%). Fish prey consisted of *P. caudimaculatus* (35.1%), specimens of Characidae that could not be identified at the species level (5.4%) and *Jenynsia multidentata* (1.8%). Reptile items consisted of the small lizard *Cercosaura schreibersii* (2.7%), and the hair of an unidentified small mammal was found in a single stomach (Table I).

The anurans *L. latrans* and *P. gracilis* were the items with the highest abundance, weight, frequency of occurrence and IRI in the *E. j. jaegeri* diet. All of the remaining prey taxa showed comparatively low values for all indexes (Table II).

The most abundant item in the contents of *E. p. sublineatus* stomachs was the poeciliid *P. caudimaculatus*, which presented low values of weight, frequency of occurrence and IRI. *Leptodactylus latrans* was the second-most abundant item and showed high values of weight, frequency of occurrence and IRI. The third most abundant taxon, *O. maisuma*, also presented high values for weight, frequency of occurrence and IRI (Table III).

TABLE II
Numeric abundance (N%), weight percentage (W%), frequency of occurrence (FO%) and Index of Relative Importance (IRI) of prey taxa recorded in digestive tract of *E. j. jaegeri* specimens. Items are listed by increasing order of abundance.

Prey	N%	W%	FO%	IRI (Pinkas)
Leptodactylus latrans	35.71	49	30	2549.86
Physalaemus gracilis	28.57	51	35	2775.06
Phallocerus caudimaculatus	10.71	0.001	5	53.58
Isopoda	7.143	0.0004	10	71.43
Leptodactylidae	7.14	0	10	71.43
Unidentified anurans	3.57	0	5	17.86
Hylidae	3.57	0	5	17.86
Pseudopaludicola falcipes	3.57	0.001	5	17.86

TABLE III
Numeric abundance (N%), weight percentage (W%), frequency of occurrence (FO%) and Index of Relative Importance (IRI) of prey taxa recorded in digestive tract of *E. p. sublineatus* specimens. Items are listed by increasing order of abundance.

Prey	N%	W(%)	FO%	IRI (Pinkas)
Phallocerus caudimaculatus	35.13	1.33	2.27	82.87
Leptodactylus latrans	26.13	56.67	38.64	3199.12
Odontophrynus maisuma	10.81	19.70	15.91	485.42
Characidae	5.40	0.11	2.27	12.55
Rhinella gr. *granulosa*	5.40	14.43	13.64	270.50
Cercosaura schreibersii	2.70	0.61	4.54	15.06
Leptodactylus gracilis	2.70	3.72	6.821	43.81
Unidentified anurans	1.80	0	4.54	8.19
Elachistocleis bicolor	1.80	1.06	4.54	13.00
Hypsiboas pulchellus	1.80	1.51	4.54	15.04
Jenynsia multidentata	1.80	0.20	2.27	4.55
Leptodactylidae	1.80	0	4.54	8.19
Physalaemus gracilis	1.80	0.65	4.54	11.15
Unidentified mammal	0.90	0	2.27	2.05

NICHE BREADTH AND PREY SELECTION

The niche breadth measured by the Levins index was 0.17 for *E. j. jaegeri* and 0.61 for *E. p. sublineatus*. The direction of ingestion was possible to verify in 20 prey (71. 4%) of *E. j. jaegeri*; 18 of them (90%) showed headfirst ingestion, and only two prey (10%) were ingested tail-first. Prey total length ranged from 4 to 14% of predators' SVL (Table IV).

We could determine the direction of ingestion in 34 prey (30.6%) of *E. p. sublineatus*; 29 of them (85.3%) were ingested headfirst and five tail-first. Prey length varied from 2 to 17% of predators' SVL (Table V).

TABLE IV

Snout-vent length (SVL) of *E. j. jaegeri* specimens, prey total length (TL), rate TL/SVL showed in increasing order and direction of prey ingestion (headfirst = HF; tail-first = TF).

Prey Taxon	SVL predator (mm)	TL prey (mm)	TL/SVL	Direction of prey ingestion
Isopoda	307	12.06	0.04	HF
Physalaemus gracilis	453	24.62	0.05	HF
Physalaemus gracilis	453	30.28	0.07	TF
Leptodactylus latrans	266	19.87	0.07	HF
Leptodactylus latrans	280	19.31	0.07	HF
Physalaemus gracilis	371	24.64	0.07	HF
Leptodactylus latrans	255	19.87	0.08	HF
Leptodactylus latrans	280	21.70	0.08	HF
Leptodactylus latrans	280	22.27	0.08	HF
Physalaemus gracilis	315	25.96	0.08	HF
Leptodactylus latrans	252	22.57	0.09	HF
Leptodactylus latrans	252	23.04	0.09	TF
Leptodactylidae	182	18.02	0.10	HF
Leptodactylus latrans	280	27.37	0.10	HF
Leptodactylus latrans	281	29.92	0.11	HF
Physalaemus gracilis	200	22.11	0.11	HF
Pseudopaludicola falcipes	127	15.35	0.12	HF
Physalaemus gracilis	274	32.09	0.12	HF
Leptodactylus latrans	170	21.70	0.13	HF
Physalaemus gracilis	196	28.40	0.14	HF

TABLE V

Snout-vent length (SVL) of *E. p. sublineatus* specimens, prey total length (TL), rate TL/SVL showed in increasing order and direction of prey ingestion (headfirst = HF; tail-first = TF).

Prey Taxon	SVL predator (mm)	TL prey (mm)	TL/SVL	Direction of prey ingestion
Leptodactylus latrans	446	10.88	0.02	HF
Leptodactylus latrans	446	11.13	0.02	HF
Leptodactylus latrans	446	11.75	0.03	HF
Leptodactylus latrans	446	15.45	0.03	HF
Elachistocleis bicolor	473	20.00	0.04	HF
Leptodactylus latrans	446	18.35	0.04	HF
Odontophrynus maisuma	503	19.87	0.04	HF
Odontophrynus maisuma	503	22.27	0.04	TF
Leptodactylus gracilis	354	18.88	0.05	TF
Leptodactylus latrans	440	22.65	0.05	HF
Odontophrynus maisuma	397	19.58	0.05	HF

TABLE V (continuation)

Prey Taxon	SVL predator (mm)	TL prey (mm)	TL/SVL	Direction of prey ingestion
Leptodactylus latrans	436	24.08	0.06	HF
Leptodactylus latrans	313	23.34	0.07	HF
Rhinella gr. *granulosa*	307	22.12	0.07	HF
Rhinella gr. *granulosa*	528	39.58	0.07	HF
Rhinella gr. *granulosa*	547	38.48	0.07	TF
Rhinella gr. *granulosa*	602	44.24	0.07	HF
Leptodactylus latrans	297	24.65	0.08	HF
Leptodactylus gracilis	454	37.45	0.08	HF
Rhinella gr. *granulosa*	539	43.83	0.08	HF
Physalaemus gracilis	253	23.12	0.09	TF
Rhinella gr. *granulosa*	516	44.17	0.09	HF
Leptodactylus latrans	387	43.09	0.11	HF
Leptodactylus latrans	479	50.89	0.11	HF
Leptodactylus latrans	510	53.80	0.11	HF
Leptodactylus latrans	199	24.24	0.12	TF
Leptodactylus latrans	415	53.80	0.13	HF
Odontophrynus maisuma	192	24.08	0.13	HF
Leptodactylus latrans	302	41.41	0.14	HF
Leptodactylus latrans	508	68.66	0.14	HF
Odontophrynus maisuma	185	25.02	0.14	HF
Odontophrynus maisuma	305	41.79	0.14	HF
Odontophrynus maisuma	305	48.87	0.16	HF
Leptodactylus latrans	399	66.52	0.17	HF

No significant difference was found between the mean weight of *E. j. jaegeri* and *E. p. sublineatus* (p=0.l4), and the SVL means between the two species differed significantly (p=0.03). *Erythrolamprus j. jaegeri* SVL ranged from 127 to 453 mm, and *E. p. sublineatus* presented SVL ranging from 153 to 534 mm. Graphic bar representations for weight and SVL of both species are shown in Figures 1a and 1b, respectively.

Significant differences were found between the mean weight (p=0.002) and total length (p=0.05) of prey of the two snakes species, with higher values observed in *E. p. sublineatus* prey. Graphic bar representations for mean weight and total length of prey of both snake species are shown in Figures 1c and 1d, respectively.

The regression analysis indicated a moderate positive linear correlation between the weights of *E. j. jaegeri* specimens and their respective prey (Pearson Coefficient r= 0.5048) (Figure 2a). A moderate positive linear correlation was also observed between the SVL of *E. j. jaegeri* specimens and the total length of their respective prey (r= 0.5463) (Figure 2c).

A positive moderate linear correlation (r=0.6050; p<0.000) was observed between the weights of *E. p. sublineatus* specimens and their respective prey (Figure 2b). A weak positive linear correlation (r=0.2658; p=0.008) was detected between the SVL of *E. p. sublineatus* specimens and the total length of their respective prey (Figure 2d).

All graphic bars of the averages generated for measures of head (HL, HW, HH, ML, MW and IML) indicated a significant difference between species. For all variables, the highest values obtained corresponded to *E. p. sublineatus* (Figure 3).

DISCUSSION

DIET COMPOSITION

Although the diets of both *Erythrolamprus* species have demonstrated predominantly anurophagous

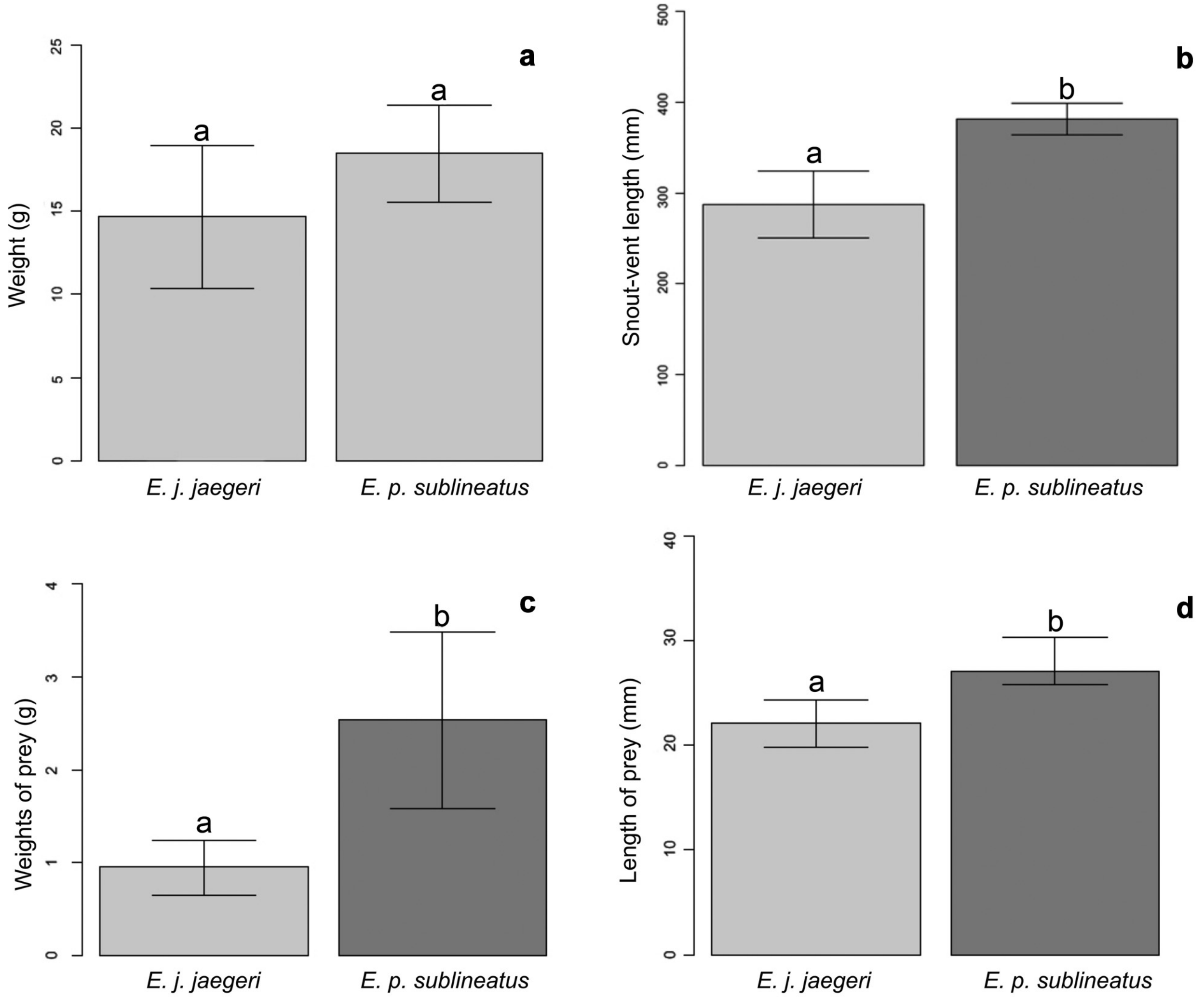

Figure 1 - Means ± standard deviation of weight (in grams) (**a**) and snout-vent length (SVL) (in millimeters) (**b**) of *Erythrolamprus jaegeri jaegeri* and *Erythrolamprus poecilogyrus sublineatus* in the present study; means ± standard deviation of weights (in grams) and total length (in millimeters) of prey found in digestive tracts of the snakes are presented in the figures **c** and **d**, respectively.

habits, agreeing with previous published data (De Lema 2002, Sawaya et al. 2008, Prieto et al. 2012), some divergent features may be considered. *Erythrolamprus j. jaegeri* presented a less diverse diet when compared with *E. p. sublineatus*, preying only on amphibians and fishes. Furthermore, it is probable that the isopods observed in the *E. j. jaegeri* diet may represent secondary items in light of the fact that, of the only two occurrences, one was associated with *Leptodactylus latrans*, a known isopod predator (Maneyro et al. 2004, Pazinato et al. 2011). *Erythrolamprus p. sublineatus*, in contrast, showed a more diversified diet, preying on almost all groups of vertebrates: fishes, amphibians, reptiles and mammals. Regarding the diet composition, we verified a higher abundance of aquatic origin items, contradicting our initial hypothesis of higher intake of terrestrial prey by this species when compared to *E. j. jaegeri*. However, even though the fish *P. caudimaculatus* represented the most abundant item, the intake of fish was absolutely casual (present in a single stomach) and resulted in low

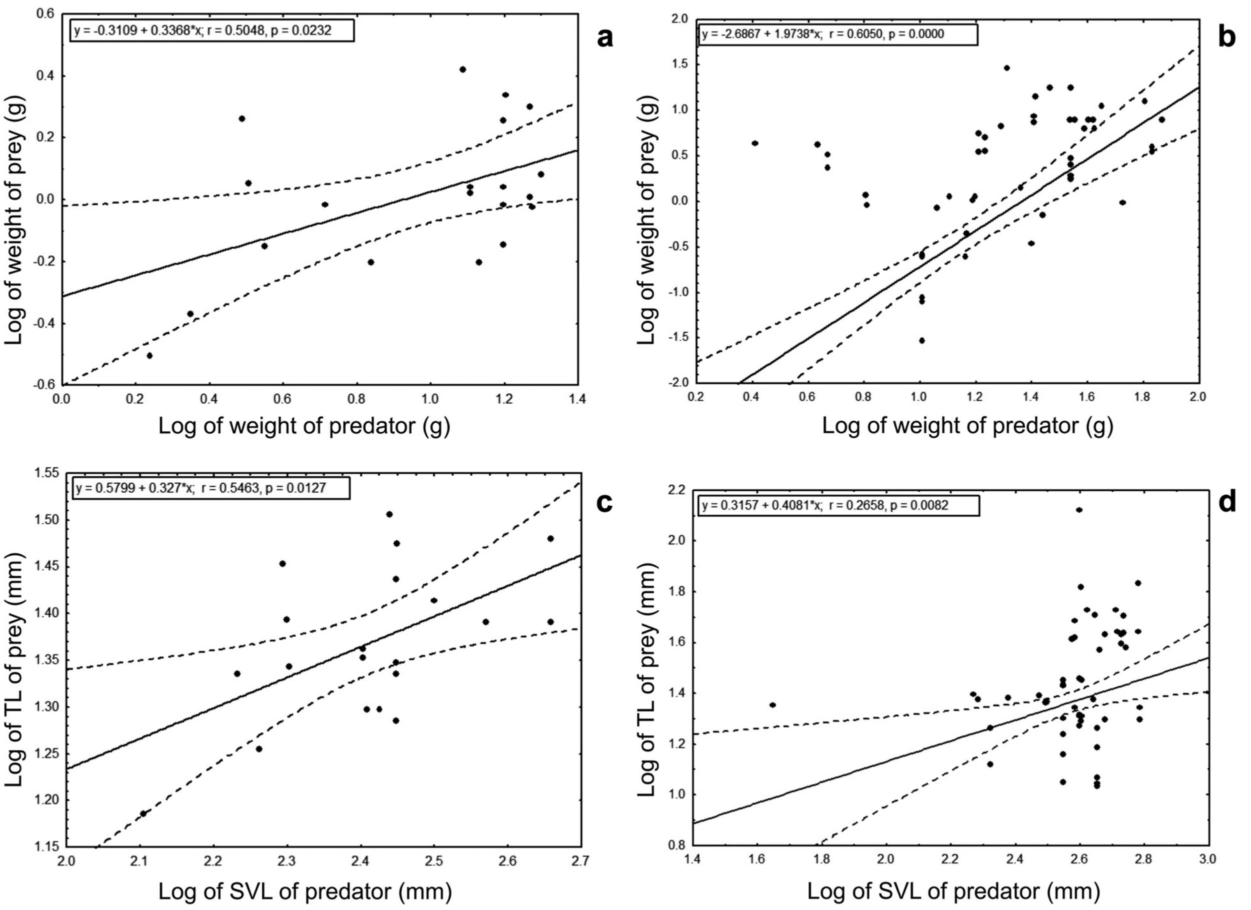

Figure 2 - Linear regression of prey weight as a function of predator weight for *Erythrolamprus jaegeri jaegeri* (**a**) and *Erythrolamprus poecilogyrus sublineatus* (**b**); linear regression of prey total length (TL) as function of predator snout-vent length (SVL) for *Erythrolamprus jaegeri jaegeri* (**c**) and *Erythrolamprus poecilogyrus sublineatus* (**d**).

values of IRI when compared with the amphibian contribution to the *E. p. sublineatus* diet. The same was verified for *E. j. jaegeri*.

The effectiveness of *E. j. jaegeri*'s fish predation was already documented (Santos et al. 2010), and, according to De Lema (2002), *E. p. sublineatus* preys on the fishes of the genera *Phallocerus* and *Jenynsia*, which was verified in the present study. However, the event here recorded may indicate an opportunist action, wherein the predator may have taken advantage of the high prey abundance while foraging. It should also be noted that the effort expended in aquatic foraging is greater when compared with terrestrial foraging due to the higher density and viscosity of the aquatic environment (Ricklefs 2003). Thus, it is fundamental that the energy obtained from food exceeds the energy expenditure of foraging (Gerking 1994, Ricklefs 2003). In this case, the unfavorably small size of the consumed fishes was compensated for by the intake of a high number of individuals (Table I), providing a satisfactory energy gain. It is also possible that the consumed fish were under easy-capture conditions, such as water bodies in drought, which enhanced their vulnerability to predation.

The prey with the highest importance, occurrence and contribution to weight in the *E. p. sublineatus* diet was *Leptodactylus latrans*, a large-sized frog species (Achaval and Olmos 2007) commonly found in grasslands, riparian forests, wetlands and even in urbanized environments (Maneyro and Carreira 2012). This anuran was also

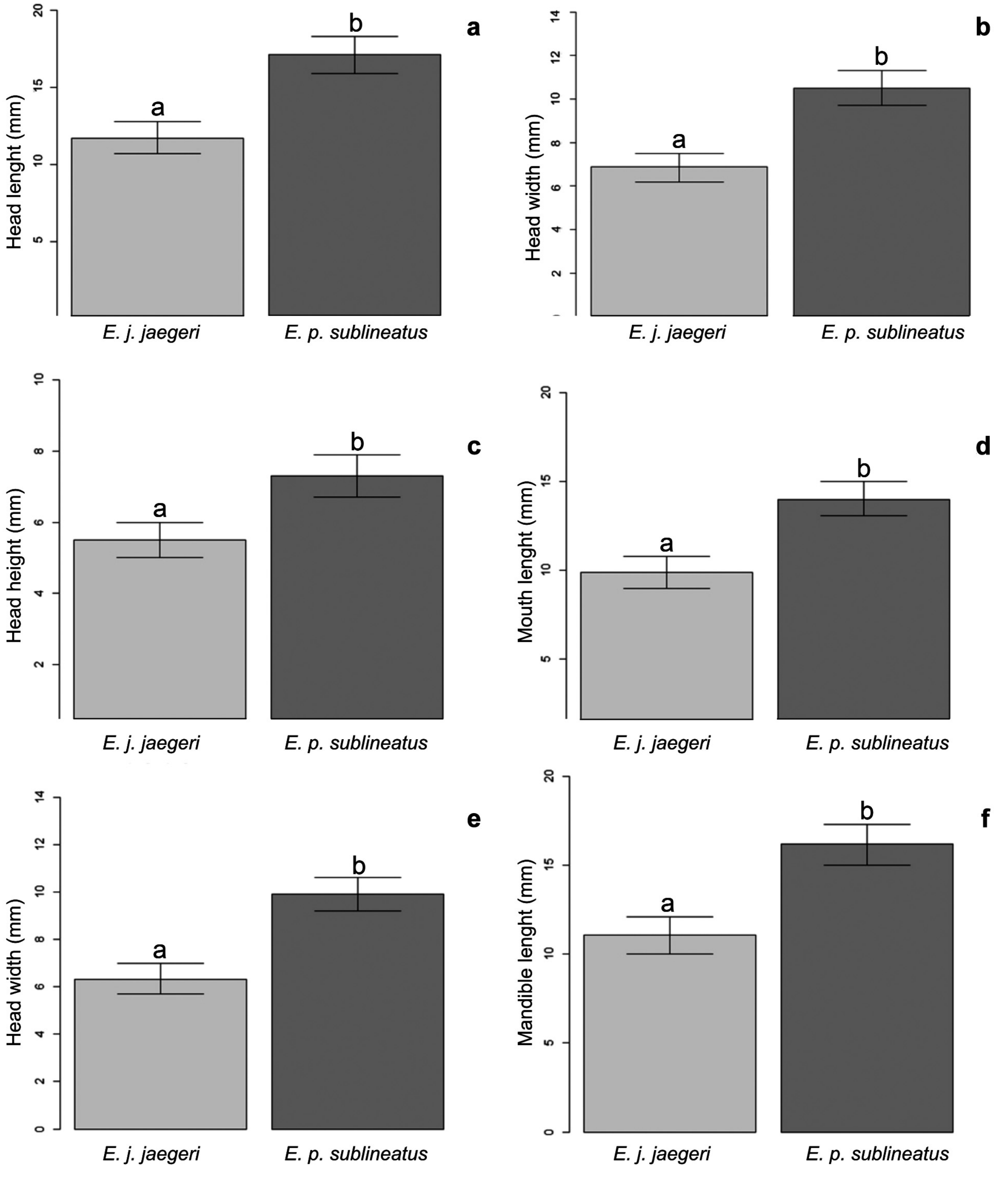

Figure 3 - Means ± standard deviation of head length (**a**), head width (**b**); head height (**c**), mouth length (**d**), mouth width (**e**), and mandible length (**f**) of *Erythrolamprus jaegeri jaegeri* and *Erythrolamprus poecilogyrus sublineatus* in the present study.

the second-most important and frequent item in the *E. j. jaegeri* diet. The dominance of this item in the *E. p. sublineatus* diet and its relevancy to the *E. j. jaegeri* diet could be related to the fact that foraging of large prey is advantageous, providing higher energy gain (Krebs and Davies 1996). The other fact that may have contributed to *L. latrans*' representativeness in the diet of both snake species could simply be its high abundance in the study area. Another relevant prey item in the *E. p. sublineatus* diet was *Odontophrynus maisuma*, a small sized but robust anuran with digging habits that occurs in terrestrial and periurban environments (Maneyro and Carreira 2012). The third-most important item in the *E. p. sublineatus* diet was medium-sized toads of the *Rhinella granulosa* group, which in the study area may correspond to *R. dorbigny* and/or *R. fernandezae.* Both species are robust toads that use from wet to severely dry environments (Narvaes and Rodrigues 2009). In sum, we can observe that the most relevant prey items for *E. p. sublineatus* showed robust size, indicating a strategy of foraging prey for potential energy gain (Pianka 1982).

The remaining amphibian species present in the *E. p. sublineatus* diet were, in order of importance, *Leptodactylus gracilis*, *Hypsiboas pulchellus*, *Elachistocleis bicolor* and *P. gracilis*, all of which showed IRI values lower than 15. Although they represent common species in the study area (Loebmann 2005), all of these anurans are characterized by small and slender bodies when compared with *L. latrans*, *O. maisuma* and *Rhinella* gr. *granulosa*, and their representation in the *E. p. sublineatus* diet may be related to the already discussed apparent preference for larger prey.

The item of highest importance, frequency of occurrence and weight in the *E. j. jaegeri* diet was the medium-sized anuran *P. gracilis*, an inhabitant of both natural and anthropic environments (Maneyro and Carreira 2012). Along with *L. latrans*, these two species confirmed the importance of leptodactylids in the diets of both studied snake species. The sharing of leptodactylids by the two *Erythrolamprus* species under verified syntopic conditions could be explained by the high abundance of the frog species in the studied area (Loebmann 2005). The interspecific competition here observed could be attenuated by the high availability of prey, resulting in resource partitioning (Toft 1985) or different feeding strategies adopted by the snakes (Mori and Vincent 2008).

The occurrence of an exclusively terrestrial item, the small lizard *Cercosaura schreibersii*, was recorded only in the *E. p. sublineatus* diet. *Cercosaura schreibersii* is an abundant lizard in grasslands and dunes of the study area (Quintela and Loebmann 2009), has cryptozoic habits (Deiques et al. 2007, Quintela and Loebmann 2009) and has been already found in the *E. poecilogyrus* diet in Uruguay (Carreira-Vidal 2002) and northeastern Argentina (Prieto et al. 2012). The reptiles here recorded, despite their abundance (Quintela and Loebmann 2009), represented sporadic predation events, and do not seem to consist of a usual *E. p. sublineatus* prey item.

The hairs of an unidentified small mammal were found in a single stomach. At least 15 species of small mammals, including sigmodontinae and caviid rodents and didelphid marsupials, occur in the study area (Bonvicino et al. 2008, Quintela et al. 2012, 2013, Sponchiado et al. 2012), and the rat species of genus *Oligoryzomys* seem to be the most common (Quintela et al. 2012, 2013, Sponchiado et al. 2012). The single record of small mammal predation indicates that this may represent an uncommon *E. p. sublineatus* prey item. Records of mammalian items in the *E. p. sublineatus* diet are restricted to one case in Uruguay (Carrera-Vidal 2002). Snakes that commonly feed on mammals present solenoglyphous dentition or kill by constriction and generally immobilize or kill the prey before intake (De Fraga et al. 2013).

Our data on the composition of the *E. p. sublineatus* diet corroborate the data obtained by Carrera-Vidal (2002) in Uruguay, where anurans (genera *Hypsiboas*, *Physalaemus* and *Rhinella*) appeared as the most-consumed item, followed by lizards (including *C. schreibersii*) and mammals in low proportions. The composition of the diet in our study area was also very similar to the *L. poecilogyrus* diet in the wetlands of northeastern Argentina (Prieto et al. 2012), where the same anuran families were recorded, with the exception of the lizard *C. schreibersii*. *Erythrolamprus p. poecilogyrus*, in contrast, presented a strictly anurophagous diet in southeastern Brazil (Pinto and Fernandes 2004), composed of bufonids and hylids. Microhylids were also recorded in the diet of *E. p. schotti* (Cacciali and Motte 2010). Fishes, absent in our samples, have already been recorded in the *E. poecilogyrus* diet (Skuk 1985, Palmuti et al. 2009).

Regarding *E. j. jaegeri*, only anurans and fishes were found by J.G. da Frota (unpublished data) in the stomach contents of specimens along the whole distribution of the subspecies, indicating that these may represent the most utilized resources. Insects were sporadically recorded (Michaud and Dixon 1989, Achaval and Olmos 2007) and may represent occasional prey.

NICHE BREADTH AND PREY SELECTION

The Levins index indicated distinct feeding strategies between the two *Erythrolamprus* species. Although the value of 0.61 obtained for *E. p. sublineatus* does not correspond to a completely generalist diet (indicated by values very close to 1), this contrasts with the value of 0.17 obtained for *E. j. jaegeri*, indicative of a high level of feeding specialization. The prey availability is a factor that contributes to the differences in diet compositions of the congeneric species (Teixeira and Fonseca 2003). However, considering that the analyzed species under sympatric conditions have access to the same resources, it is possible that the capability to exploit a greater diversity of habitats and niches by *E. p. sublineatus* is the main factor determining such a discrepancy. The broader feeding niche of *E. p. sublineatus* in relation to *E. j. jaegeri*, was therefore verified.

The direction of prey ingestion was verified as anteroposterior in most cases. This was expected; anteroposterior ingestion reduces the risk of injuries caused by prey limbs and resistance to ingestion, reducing the time and energy spent during this process (Greene 1976, De Fraga et al. 2013).

Data on the rate of prey TL over predator SVL indicated that *E. p. sublineatus* feed on larger prey when compared with *E. j. jaegeri*. Such results provide support for the experimental hypothesis that *E. p. sublineatus*, due to its larger size, feeds on larger prey. A possible explanation could be that the optimal prey size for maximum energy gain in this subspecies could be larger, considering its larger size (Pitcher and Hart 1982). It is also possible that *E. j. jaegeri*, due to its smaller size, encounters difficulties in the capture and subjugation of larger prey (Shine 1991), limiting its foraging to smaller prey. It is noteworthy that the larger *E. j. jaegeri* prey recorded in our study, a 32 mm *P. gracilis*, corresponded to less than half the length of the larger *E. p. sublineatus* prey, a 68 mm *L. latrans*.

The regression analysis indicated a moderate positive correlation between the weights of both snakes and their prey and between *E. j. jaegeri* SVL and length of respective prey. Positive correlation between weights of predator and prey is well documented in snakes (Mushinsky 1987, Shine 1991, Bryant et al. 2012). Juveniles generally ingest smaller prey to avoid the risks of injuries and even death caused by a poor assessment of prey (Garland and Arnold 1983, Sazima and Martins 1990, Nogueira et al. 2013). Throughout development, individuals increase their capacity to ingest larger prey, as well as the range of the consumed items (Arnold 1993). The higher coefficient of correlation generated for *E. p. sublineatus* in relation to *E. j. jaegeri* in weight analysis could also have been influenced by the higher number of prey found in the first subspecies (111 compared with 28 in *E. j. jaegeri*), inducing a better fit of the model. However, the low coefficient observed between the length of *E. p. sublineatus* and its prey may have been generated by the high variability found in prey size, resulting in outliers.

The differentiated head morphology between the subspecies was statically significant. *Erythrolamprus p. sublineatus* has a larger head, considering the length and the height dimensions (Figure 3). Larger preys were also observed for this subspecies, and this may be related to the larger head structures. It is known that gape is a limiting factor for prey selection (Greene 1997, Arnold 1993). Thus, larger head, mouth and mandible dimensions, as verified for *E. p. sublineatus*, could favor the intake of larger items (Shine 1991, Arnold 1993, Webb and Shine 1993). Similarly, the shorter head structures of *E. j. jaegeri* may limit its foraging to smaller prey (Webb and Shine 1993). The overlap of prey species that differ only in size, such as *L. latrans*, could likely be explained by the differences in head, mouth and mandible structure sizes between *E. p. sublineatus* and *E. j. jaegeri*. Considering the condition of sympatry, high abundance and partial dietary superimposition of the subspecies herein studied, it is probable that the asymmetric competition could be attenuating the resource partitioning, allowing co-occurrence. This type of competition acts by the utilization of different strategies, microhabitats or any other mechanism that reduces the level of competition between the involved taxa (Ricklefs 2011).

In the present study, we verified a divergence in the niche breadth between the two analyzed subspecies. The specialist *E. j. jaegeri* occupies a narrow niche, and the generalist *E. p. sublineatus* exhibits exclusive habits and forages on larger prey, which attenuates the competition between these congeneric sympatric forms.

RESUMO

As serpentes *Erythrolamprus jaegeri jaegeri* e *Erythrolamprus poecilogyrus sublineatus* são simpátricas e sintópicas na região costeira do extremo sul do Brasil. Aqui analisamos a composição da dieta para avaliar a amplitude de nicho e a seleção de presas por ambas as espécies. Foram examinados 192 espécimes, e a análise dos conteúdos estomacais revelou que ambas as espécies predominantemente consomem anuros. No entanto, a dieta de *E. j. jaegeri* consiste principalmente de peixes e anfíbios, enquanto a de *E. p. sublineatus* é mais ampla, incluindo peixes, anfíbios, répteis e mamíferos. O Índice Padronizado Levins apresentou valores mais baixos para *E. j. jaegeri* (BA = 0,17) do que para para *E. p. sublineatus* (BA = 0,61), evidenciando estratégias especialistas e generalistas para cada espécie, respectivamente. Em relação à seleção das presas, *E. p. sublineatus* apresentou maior comprimento rostro-cloacal e maior cabeça, boca e mandíbula do que *E. j. jaegeri* e se alimenta de presas maiores. Além disso, foram confirmadas correlações positivas entre tamanho e peso de predadores e presas, em ambas as espécies. Os resultados mostram o desenvolvimento de diferentes mecanismos para a coocorrência das duas espécies, tais como seleção de presa por tamanho, de tal modo que o tamanho do predador esteja relacionado ao tamanho de sua presa; ou pelo desenvolvimento de estratégias diferentes para diminuir a sobreposição de nichos entre as espécies.

Palavras-chave: dieta, ofídios, presas, tamanho, nicho.

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APPENDIX

Material examined from the herpetological collection of Universidade Federal do Rio Grande (FURG).

Erythrolamprus jaegeri jaegeri. Rio Grande do Sul: ESEC TAIM - CHFURG 1077; CHFURG1190; CHFURG1736; CHFURG1737. Rio Grande – CHFURG1023; CHFURG1027; CHFURG1028; CHFURG1030; CHFURG1031; CHFURG1034; CHFURG1077; CHFURG1082; CHFURG1083; CHFURG1084; CHFURG1085; CHFURG1086; CHFURG1089; CHFURG1090; CHFURG1254; CHFURG1258; CHFURG1261; CHFURG1262; CHFURG1575; CHFURG1576; CHFURG1577; CHFURG1578; CHFURG1579; CHFURG1580; CHFURG1581; CHFURG1582; CHFURG1583; CHFURG1584; CHFURG1585; CHFURG1586;

CHFURG1587; CHFURG1588; CHFURG1589; CHFURG1590; CHFURG1591; CHFURG1599; CHFURG1601; CHFURG1602; CHFURG1654; CHFURG1656; CHFURG1663; CHFURG1664; CHFURG1691; CHFURG1720; CHFURG1727; CHFURG1778; CHFURG1781; CHFURG1785; CHFURG1790; CHFURG1791; CHFURG1792; CHFURG1793; CHFURG1794; CHFURG1799; CHFURG1803; CHFURG1805; CHFURG1806; CHFURG1807; CHFURG1808; CHFURG1809; CHFURG1813; CHFURG1814; CHFURG1817; CHFURG1824; CHFURG1828; CHFURG1934; CHFURG1935; CHFURG1936; CHFURG1939; CHFURG1940.

Erythrolamprus poecilogyrus sublineatus. Rio Grande do Sul: ESEC TAIM – CHFURG1037; CHFURG1074; CHFURG1250; CHFURG1268; CHFURG1269; CHFURG1270; CHFURG1442; CHFURG1443; CHFURG1444; CHFURG1445; CHFURG1464; CHFURG1463; CHFURG2311. Rio Grande - CHFURG768; CHFURG773; CHFURG791; CHFURG792; CHFURG810; CHFURG812; CHFURG830; CHFURG831; CHFURG844; CHFURG845; CHFURG 846; CHFURG853; CHFURG854; CHFURG859; CHFURG863; CHFURG865; CHFURG880; CHFURG887; CHFURG889; CHFURG897; CHFURG905; CHFURG913; CHFURG915; CHFURG919; CHFURG920; CHFURG924; CHFURG959; CHFURG960; CHFURG1025; CHFURG1032; CHFURG1033; CHFURG1256; CHFURG1257; CHFURG1259; CHFURG1260; CHFURG1263; CHFURG1264; CHFURG1268; CHFURG1269; CHFURG1270; CHFURG 1365; CHFURG1548; CHFURG1608; CHFURG1646; CHFURG1631; CHFURG1636; CHFURG1297; CHFURG1298; CHFURG1300; CHFURG1301; CHFURG1302; CHFURG1303; CHFURG1304; CHFURG1305; CHFURG1306; CHFURG1407; CHFURG1408; CHFURG1410; CHFURG1663; CHFURG1665; CHFURG1666; CHFURG1667; CHFURG1668; CHFURG1669; CHFURG1670; CHFURG1671; CHFURG1672; CHFURG1673; CHFURG1674; CHFURG1675; CHFURG1685; CHFURG1686; CHFURG1687; CHFURG1688; CHFURG1689; CHFURG1690; CHFURG1692; CHFURG1693; CHFURG1698; CHFURG1703; CHFURG1725; CHFURG1726; CHFURG1728; CHFURG1729; CHFURG1735; CHFURG1736; CHFURG1777; CHFURG1779; CHFURG1780; CHFURG1782; CHFURG1783; CHFURG1784; CHFURG1786; CHFURG1787; CHFURG1788; CHFURG1789; CHFURG1791; CHFURG1792; CHFURG1794; CHFURG1802; CHFURG1815; CHFURG1816; CHFURG1932; CHFURG1933; São José do Norte - CHFURG1948.