



Natural history data of a common snake suggest inter-population variation and conservatism in life history traits: the case of *Erythrolamprus poecilogyrus*

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Documenting intraspecific variation is essential to understanding the ecology and evolution of natural populations. Here we provide information on sexual maturity, sexual size dimorphism, fecundity and diet of *Erythrolamprus poecilogyrus* from the region of the Aimorés Hydroelectric Power Plant, southeastern Brazil, based on specimens deposited in the Herpetological Collection of the Museu de Ciências Naturais da Pontifícia Universidade de Católica de Minas Gerais. We also compare our results with those from previously published studies. We measured snout-vent length and tail length, and counted ventral and sub-caudal scales of each specimen. We also recorded reproductive aspects and diet identified to the lowest possible taxonomic level. *Erythrolamprus poecilogyrus* differed in overall body and clutch size between geographic regions, following a pattern inverse to Bergmann's rule. In general, females attained larger body size than males, but do not have a higher number of vertebrae. We did not find intersexual differences in tail length, which may be related to a low degree of intersexual competition among males. Diet composition was very similar throughout the species' range, and characterises *E. poecilogyrus* as an anuran specialist. Females maintained their feeding activity while gravid, suggesting that *E. poecilogyrus* is an income breeder, which is an adaptive strategy when foraging success is predictable during reproductive periods.

Key words: diet, income breeding, *Liophis*, reproductive biology, Xenodontini

INTRODUCTION

The study of life history unites behaviour, ecology, population biology and evolution to yield in a broader understanding of the responses of organisms and populations to their environments (Ricklefs, 2000). With regard to snakes in the Neotropics, life-history studies focusing on a single species however often fail to mention aspects of intraspecific variation (e.g., Pinto & Fernandes, 2004; Scartozzoni et al., 2009; Maschio et al., 2010), and few studies explore broader patterns (geographic, taxonomic, and ecological) of the inter-population variation within life history aspects of snake species (Luiselli, 2006), such as those related to diet or reproductive biology (e.g. Luiselli, 2006; Pizzatto & Marques, 2006; Barros et al. 2012). As variability is widespread in nature (Darwin, 1859; Grant & Grant, 2002; Glaudas et al., 2008), documenting variation in life-history traits is essential to understand the ecology and evolution of natural populations (Glaudas et al., 2008). Thus, natural history data from different populations of snakes are essential. Moreover, since at least in part morphology predicts the ecology of an organism (Ricklefs

& Travis, 1980; Wainwright & Reilly, 1994; Foote, 1997), species of snakes that present a great morphological diversity and a wide geographic distribution could also be characterised by inter-population variation in ecological traits (e.g. Pizzatto & Marques, 2006; Santos et al. 2008).

The genus *Liophis* (*sensu* Dixon, 1980, Dipsadidae: Xenodontinae: Xenodontini) comprises more than 60 species ranging from Central to South America (Dixon, 1989; Zaher et al., 2009; Grazziotin et al., 2012; Uetz et al., 2012). Detailed interspecific relationships among *Liophis* species are still unresolved, and it has been suggested that the genus is polyphyletic (Vidal et al., 2000; Curcio et al., 2009; Zaher et al., 2009; Grazziotin et al., 2012). Zaher et al. (2009) and Grazziotin et al. (2012) synonymised *Liophis* along with *Umbrivaga* to *Erythrolamprus* and revalidated *Lygophis* previously included in the genus *Liophis*. Thus, *Erythrolamprus* currently comprises 50 species (Grazziotin et al., 2012), 35 of them occurring in Brazil (Bérnils & Costa, 2012), including the widely distributed *Erythrolamprus poecilogyrus* (Wied-Neuwied, 1825).

Erythrolamprus poecilogyrus occurs in South America from south-eastern Venezuela and eastern Guyana to the Argentinian Pampas and Chaco (Fernandes, 2006; Uetz et al., 2012). Dixon & Markezich (1992) split *E. poecilogyrus* into four subspecies due to its great variability in colour patterns, and in meristic and morphological traits throughout its distribution. The subspecies comprise *E. poecilogyrus poecilogyrus* (Wied-Newied, 1985), *E. p. caesius* (Cope, 1862), *E. p. schotti* (Schlegel, 1837) and *E. p. sublineatus* (Cope, 1860). Due to its wide geographic distribution and morphological diversity, *E. poecilogyrus* is a good candidate for studies exploring intraspecific variation in life history traits.

Information regarding the ecology of *E. poecilogyrus* can be found primarily in studies focusing on Neotropical snake assemblages (e.g., Sawaya et al., 2008; Palmuti et al., 2009). Studies providing detailed information on the reproductive and feeding biology of *E. poecilogyrus* are restricted to Pinto & Fernandes (2004) and Prieto et al. (2012). In general, *E. poecilogyrus* is active both during the day and night, is a terrestrial and oviparous species and feeds mainly on anurans (Pinto & Fernandes, 2004; Sawaya et al., 2008; Prieto et al., 2012), typical for Xenodontini species (Marques et al., 2001; Pizzatto et al., 2008). In the present study, we provide additional data on sexual maturity, sexual size dimorphism, fecundity and diet of a population belonging to the *E. p. poecilogyrus* subspecies from a single locality in Minas Gerais state, southeastern Brazil. Because reproductive

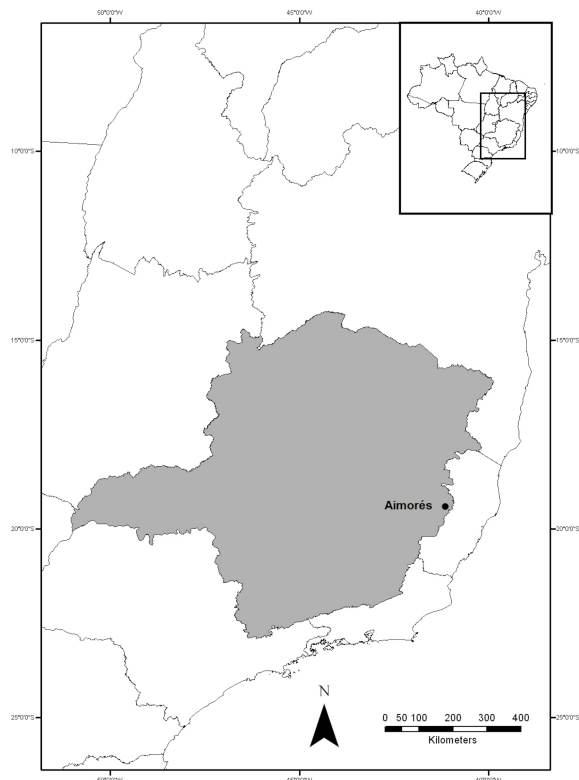


Fig. 1. Map showing the location of the Aimorés Hydroelectric Power Plant (UHE Aimorés) region, Minas Gerais state, southeastern Brazil, where the specimens of *Erythrolamprus poecilogyrus* were collected.

Table 1. Diet composition of *Erythrolamprus poecilogyrus* from Aimorés Hydroelectric Power Plant (UHE Aimorés) region, Minas Gerais state, Brazil. MCNR corresponds to the catalogue collection number of each specimen. F=female, M=male, A=adult, J=juvenile, H=hatchling, S=stomach, G=gut.

MCNR	Sex/maturity	Prey
874	FJ	Two legs of Leptodactylidae (G)
967	MJ	An arm and leg of <i>Leptodactylus</i> sp. (S)
832	J	A leg of Bufonidae (G)
869	FJ	Two Hylidae legs (S)
841	H	A leg of Bufonidae (S)
812	FA	A leg of <i>Leptodactylus</i> sp. (G)
892	FJ	Lizard tail and remains of an Hylidae (G)
851	FA	<i>Rhinella</i> gr. <i>granulosa</i> (S)
875	FA	<i>Rhinella</i> gr. <i>granulosa</i> (S)
842	MA	A leg of <i>Rhinella</i> sp. (G)
820	MA	A leg of <i>Leptodactylus</i> sp. (G)
1398	MA	A Hylidae leg (S)
1399	MA	Two legs of Bufonidae (G)
1750	M	<i>Rhinella</i> gr. <i>granulosa</i> (S)
755	x	<i>Rhinella</i> gr. <i>granulosa</i> (S)
862	x	Two legs of <i>Leptodactylus</i> sp. (G)
1534	H	A Gekkonidae tail (S)
858	FA	<i>Rhinella</i> gr. <i>granulosa</i> (S)
815	FJ	A leg of Bufonidae (G)

and diet aspects are known to vary across sites in snakes (e.g., Gregory & Larsen, 1996; Holycross & Mackessy, 2002; Pizzatto & Marques, 2006; Orofino et al., 2010), we compare our results with those from Pinto & Fernandes (2004) and Prieto et al. (2012). Specifically, we want to explore if life history aspects in *E. poecilogyrus* differ in disparate geographic populations.

MATERIALS AND METHODS

We examined 74 specimens of *E. p. poecilogyrus* deposited in the Herpetological Collection of the Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCNR, PUC Minas, see Appendix). Specimens were collected from 1997 to 2004 in the Aimorés Hydroelectric Power Plant (Usina Hidrelétrica - UHE Aimorés) region (19° 29' 33.84" S, 41° 03' 59.26" W), in the municipalities of Aimorés, Itueta, and Resplendor, eastern Minas Gerais, Brazil (Fig. 1).

The study area is located in the Atlantic Forest domain on the Doce River. The climate is tropical with a mean annual high temperature of 31.2°C and a mean low of 19.4°C. The annual average rainfall is 1162.6 mm. The region is characterised by a rainy season (October to March) and a dry season (April to September, Prefeitura Municipal de Aimorés, 2012).

For each specimen, we recorded snout-vent length (SVL) and tail length (TL) using a flexible ruler to the nearest mm, and counted the number of ventral (Nv) and sub-caudal scales (Nsub), corresponding with the number of body and tail vertebrae in the majority of snakes (Lindell et al., 1993). We recorded the reproductive condition of males and females through a ventral incision. We considered males and females as reproductive when they presented highly convoluted deferent ducts and turgid testis (Shine, 1977a) and vitellogenic follicles (>8 mm in diameter) or eggs in the oviduct (Shine, 1977b), respectively. The smallest reproductive individuals

determined minimum size at maturity for each sex, and all individuals above this size were considered adults (e.g. Alencar et al., 2012). Specimens with a SVL below 300 mm and between 300 mm and the minimum size at maturity were considered as hatchlings and juveniles, respectively. We also recorded the number of vitellogenic follicles and/or eggs and recorded the presence of prey items in the stomach and/or gut. Prey items were identified to the lowest possible taxonomic level.

We used the Levene and Kolmogorov-Smirnov tests to evaluate the assumptions of homoscedasticity and normality, respectively. We used student *t* tests to analyse sexual size dimorphisms (SSD) for SVL and Nsub. We performed an Analysis of Covariance (ANCOVA) to evaluate intersexual differences in TL using tail length as the dependent variable, sex as factor and SVL as the covariate. We tested for intersexual differences in Nv through a Wilcoxon test and for the association between female SVL and clutch size using a Spearman rank correlation. We log-transformed SVL, Nsub and TL prior to analyses and performed all analyses with the software Statistica v. 10 (StatSoft, 2011) and the R environment (R Core Team, 2012). We performed the analyses of sexual differences in SVL and TL using only adult specimens, whereas for Nv and Nsub we also included juveniles.

RESULTS

We were able to determine sex and maturity of 65 out of 74 specimens. We recorded 16 adult females, 11 adult males, 18 juveniles (13 females, four males, and one of undetermined sex) and 20 hatchlings (SVL<300 mm). Snout-vent length of adult females and males ranged between 452 mm and 682 mm (550.4±74.31 mm) and 417 and 543 mm (478.54±38.54 mm), respectively. SVL of juvenile females and males ranged between 316 and 444 mm (377.90±146.44 mm, *n*=13) and 312 and 410 mm (446.82±102.45 mm, *n*=4), respectively. Hatchling

Table 2. Comparison of the main results found by the present study, Pinto & Fernandes (2004) and Prieto et al. (2012) on the natural history of *Erythrolamprus poecilogyrus*. *=Snout vent length+tail length, **=Total length, ns=non significant, xxx=broken tail.

	Adult range size (mm)		Sexual size dimorphism				Clutch		Diet	Stop feeding while gravid?
	Females	Males	SVL	Nv	TL	Nsub	Size	Correlation with female body size?		
Present study	452+111*– 682+154*	417+113* –543+xxx	females> males	ns	ns	ns	2–9	yes	Primarily anurans, mainly Bufonids	no
Pinto & Fernandes (2004)	604**– 1121**	447–864**	females> males*	-	-	-	6–15	no	Exclusively anurans, mainly Hylids and Bufonids	no
Prieto et al. (2012)	250–571	211–451	females> males	ns	females> males	ns	-	-	Primarily anurans, mainly Bufonids	no

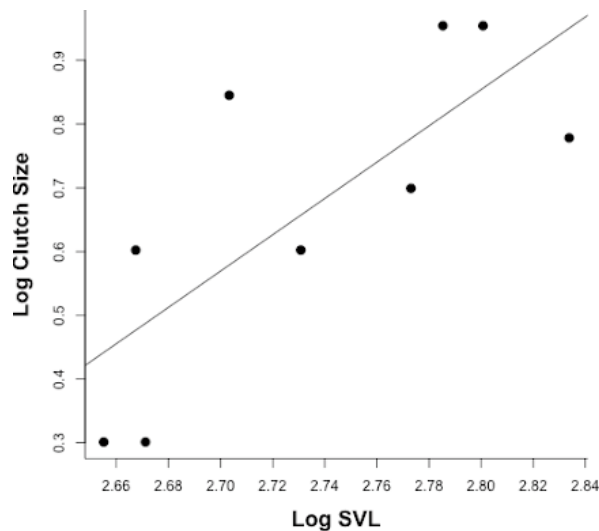


Fig. 2. Relationship between the number of vitellogenic follicles/eggs (clutch size) and body size (SVL, snout vent length) in females of *Erythrolamprus poecilogyrus*.

SVLs ranged between 150 and 283 mm (199.2 ± 42.41 mm, $n=20$). The number of ventral and subcaudal scales ranged from 161 to 172 (165 ± 62.26 , $n=23$) and 55 to 64 (60 ± 21.17 , $n=27$) respectively in females and from 158 to 168 (165.5 ± 54.69 , $n=16$) and 56 to 64 (60 ± 22.46 , $n=14$) respectively in males.

SVL of adult females was significantly larger than male SVL ($t_{24} = -2.95$, $p < 0.01$). Males and females showed no significant differences in Nv ($W=220$, $p=0.15$), tail length ($F_{1,22} = 1.31$, $p=0.26$; adults only), and Nsub ($t_{37} = -0.12$, $p=0.98$). Five females had vitellogenic follicles and six had eggs in the oviducts. Clutch size varied from two to nine vitellogenic follicles/eggs (5.1 ± 2.6) and was correlated to female SVL ($r=0.75$, $p < 0.05$, Fig. 2).

We found prey items in the stomach and gut of 19 (25.6%) individuals (four adult females, four adult males, eight juveniles/hatchlings and three individuals with undetermined sex/maturity). Prey consisted mainly of anurans, including lizards (Table 1). The family Bufonidae represents 55.5% of all anurans found, followed by Leptodactylidae (27.8%) and Hylidae (16.7%). Two females carrying eggs had each a specimen of *Rhinella gr. granulosa* (a bufonid) in their stomachs.

A comparison between our data and those from Pinto & Fernandes (2004) and Prieto et al. (2012) is shown in Table 2. The population from the UHE Aimorés region comprises smaller specimens than those analysed by Pinto & Fernandes (2004) but larger than those in Prieto et al. (2012). Females are larger than males in all the three studies and the female specimens analysed by Prieto et al. (2012) have longer tails than males. *Erythrolamprus poecilogyrus* from the UHE Aimorés region has a smaller clutch size than the specimens analysed by Pinto & Fernandes (2004). Female body size is related to clutch size in the present study, although Pinto & Fernandes (2004) failed to find this relationship. *Erythrolamprus poecilogyrus* is an anuran specialist feeder throughout, although Pinto & Fernandes (2004) found hylids and not bufonids being the primary diet. Gravid females were found with prey items in their stomach in all three studies.

DISCUSSION

Body size can vary greatly among snake populations (e.g., Ashton, 2001; Zuffi et al., 2009) and the inter-population differences described in this study could result from adaptation to local environmental conditions or phenotypic plasticity (King, 1989; Madsen & Shine, 1993; Luiselli, 2006). Differences in diet composition are frequently associated with body size variation in snakes, and a higher consumption of large prey or prey with high energy content may allow animals to attain larger body sizes (Forsman, 1991; King, 1993). However, diet composition in *E. poecilogyrus* was very similar among the three study sites considered. Body size variation in *E. poecilogyrus* followed a pattern inverse to Bergmann's rule (populations or species living in colder climates are generally larger than those living in warmer regions, Mayr, 1956), as previously suggested for squamate reptiles (Mousseau, 1997; Ashton, 2001; Zuffi et al., 2009). According to Mousseau (1997), this trend is related to the physiological time available for development, which is smaller in higher latitudes and cooler climates. However, Pinto & Fernandes (2004) and Prieto et al. (2012) classified adults as individuals with vitellogenic follicles above 3 mm in size, contrasting with the 8 mm considered in the present study. It is therefore likely that Pinto & Fernandes (2004) and Prieto et al. (2012) included specimens here considered as juveniles, decreasing mean body size of adults. In fact, although the population studied by Prieto et al. (2012) has the smallest body sizes, this seems not to be the case in Pinto & Fernandes (2004). The last authors studied the same subspecies as in the present study (*E. poecilogyrus poecilogyrus*) but considered specimens from different localities. Thus, inter-population variation for body size may exist at the subspecies level.

In all three studies, females of *E. poecilogyrus* attain larger body sizes than males. This is a common pattern found in snakes (Pizzatto & Marques, 2006; Maritz & Alexander, 2011; Alencar et al., 2012) usually attributed to fecundity selection (Cox et al., 2009). We found a positive association between female body size and the number of vitellogenic follicles/eggs, suggesting that larger females carry larger clutches. Interestingly, Pinto & Fernandes (2004) did not observe this trend when considering total length as a proxy of body size. Tail length is not the target of fecundity selection and thus could have biased their results.

The number of vertebrae can vary between the sexes in snakes (e.g., Lindell et al., 1993; Shine, 2000). Intraspecific variation in the number of ventral scales, representing the number of body vertebrae, have accordingly been demonstrated (e.g., Kelley et al., 1997; King, 1997; Aubret et al., 2004), and Lindell et al. (1993) suggested that it may be a result of intersexual differences in growth rates. However, neither Prieto et al. (2012) nor the present study found intersexual differences in the number of body vertebrae in *E. poecilogyrus*.

Sexual differences in relative tail length are common in snakes, with males usually having longer tails than females (King, 1989; Shine et al., 1999; Pinto et al., 2008;

Oliveira et al., 2011; Alencar et al., 2012). Males might benefit from longer tails because tails accommodate the hemipenes and associated muscles, or enhance the ability to actively remove other males during mating (see King, 1989 and Shine et al., 1999). This trend was not found in *E. poecilogyrus* from the UHE Aimorés region. If sexual competition among males is not intense, then the strength of selection for male mating ability may be reduced, resulting in the absence of sex divergence in tail length (see King, 1989). Surprisingly, Prieto et al. (2012) found that females have longer tails than males in *E. poecilogyrus* from northeastern Argentina, an atypical pattern among snakes.

The diet of *E. poecilogyrus* from the UHE Aimorés region is mainly composed of anurans, as previously documented for this species by Pinto & Fernandes (2004) and Prieto et al. (2012). However, juveniles and hatchlings of *E. poecilogyrus* also feed on lizards in the UHE Aimorés region and in northeastern Argentina (Prieto et al., 2012). A diet specialised on anurans may be a conserved feature of *E. poecilogyrus*, which appears to be largely the case for the whole tribe Xenodontini (Lopes, Alencar & Martins, unpublished data). Hylids and bufonids were the most frequent food items found by Pinto & Fernandes (2004) for *E. poecilogyrus* but bufonids were by far the most commonly consumed prey in the UHE Aimorés region and northeastern Argentina (Prieto et al., 2012). The discrepancies could reflect local differences in prey availability (e.g., Glaudas et al., 2008; Santos et al., 2008). Despite their high toxicity, frogs of the genus *Rhinella* were consumed by all populations of *E. poecilogyrus*, as is the case for Xenodontini species (e.g., Bernarde et al., 2000; Winkler et al., 2011) as well as other *Erythrolamprus* species (e.g., Michaud & Dixon, 1989; Albarelli & Santos-Costa, 2010).

Females of *E. poecilogyrus* maintain their feeding activity while gravid and thus may be defined as an income breeder, which fuel reproductive expenditure through active food intake during the reproductive period, whereas capital breeders would rely upon energy gathered previously (Bonnet et al., 1998; Langford et al., 2011). This dichotomy could be related to the environmental variability, and income breeding is likely adaptive in systems where foraging success is predictable during reproductive periods (Winne et al., 2006; Dyke et al., 2012). Additionally, ambush predators are usually characterised as capital breeders whereas active foragers, such as *E. poecilogyrus* (M. Martins, personal communication), are income breeders (Bonnet et al., 1998). This is probably related to the fact that the necessity to acquire energy prior to reproduction elevates metabolic costs of transport and increases exposure to predators (Shine, 1980; Dyke et al., 2012). Although capital breeding seems to be more common in ectotherms in general (Bonnet et al., 1998), some snakes have previously been classified as income breeders (e.g., Winne et al., 2006; Langford et al., 2011).

ACKNOWLEDGEMENTS

We thank T. Santos for the help during laboratory work, M. P. Gaiarsa for the map preparation and for reading the manuscript, C.A.B. Galdino for lizard identification, R.R. Carvalho Jr. for the information about the specimens and D. Fernandes for reading the manuscript and providing taxonomic and systematic information concerning the tribe Xenodontini. We also thank M. Zuffi for critically reading the manuscript and for the valuable suggestions. L.B.N. thanks Conselho Nacional de Desenvolvimento e Pesquisa (CNPq, Process 479457/2012-03), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, Process APQ-00683-12), and Fundo de Incentivo à Pesquisa of PUC Minas (FIP/PUC Minas) for financial support.

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Accepted: 1 November 2013

APPENDIX

Specimens examined: MCNR 749, MCNR 750, MCNR 751, MCNR 752, MCNR 753, MCNR 754, MCNR 755, MCNR 756, MCNR 812, MCNR 813, MCNR 814, MCNR 815, MCNR 816, MCNR 817, MCNR 818, MCNR 819, MCNR 820, MCNR 821, MCNR 822, MCNR 825, MCNR 826, MCNR 827, MCNR 828, MCNR 829, MCNR 830, MCNR 831, MCNR 832, MCNR 841, MCNR 842, MCNR 843, MCNR 844, MCNR 845, MCNR 846, MCNR 849, MCNR 851, MCNR 852, MCNR 853, MCNR 855, MCNR 856, MCNR 858, MCNR 860, MCNR 861, MCNR 862, MCNR 863, MCNR 864, MCNR 865, MCNR 866, MCNR 867, MCNR 868, MCNR 869, MCNR 870, MCNR 871, MCNR 873, MCNR 874, MCNR 875, MCNR 890, MCNR 892, MCNR 901, MCNR 964, MCNR 965, MCNR 966, MCNR 967, MCNR 1393, MCNR 1395, MCNR 1397, MCNR 1398, MCNR 1399, MCNR 1527, MCNR 1530, MCNR 1533, MCNR 1534, MCNR 1750, MCNR 1753, MCNR 1800.