Penny and penny laid up will be many: Large Yellow anacondas do not disregard small prey

Article *in* Journal of Zoology · November 2016

DOI: 10.1111/jzo.12417

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Journal of Zoology. Print ISSN 0952-8369

Penny and penny laid up will be many: large Yellow anacondas do not disregard small prey

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Keywords
sexual size dimorphism; Boidae; intersexual niche divergence; ontogeny; predator-prey size ratio; intraspecific competition; prey size; diet variation.

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Editor: Mark-Oliver Rödel

Received 25 May 2016; revised 3 October 2016; accepted 7 October 2016

doi:10.1111/jzo.12417

Abstract

The study of diet may help to predict the consequences of ontogeny and sexual size dimorphism in resource use. Although diet changes are expected in dimorphic species, ontogeny can be a factor in determining the degree of diet variation within a species. We studied large sexually dimorphic predator, the Yellow anaconda *Eunectes notaeus*, to learn how influences of sex and size on diet might lead to intersexual niche divergence, therefore avoiding intraspecific competition. We tested the consequences of sexual size dimorphism via two foraging metrics: prey size and feeding frequency. To test the consequences of ontogeny on trophic niche metrics, we related changes in feeding frequency and maximum prey size to increase in anaconda body size. Finally, we tested whether diet composition changed between sexes to the point where it could lead to reduced competition. While females (the larger sex) did eat larger prey compared to males, this effect disappeared when we removed the effect of body size. Females ate more frequently than males, even with body size effect was removed. Predator-prey size ratios were positively affected by maximum prey size, and as expected from foraging theory, did not increase minimum prey size. Feeding frequency did not display any ontogenetic effects. While diet composition varied between sexes, overlap is high. This indicates that variations in resource use as a product of sex-based differences in size are negligible in Yellow anacondas. Although females feed more frequently, this may be an effect of the greater energetic costs of reproduction. Ontogeny has a positive effect on maximum prey size, though this is a general trend, and has already been demonstrated for several other species. Finally, understanding of sex-based changes in resource use will be improved if it can be determined whether such phenomena are consequences rather than causes for sexual size dimorphism.

Introduction

Niche is an multi-axis hypervolume and food has been considered one of its main components (Hutchinson, 1957). Foraging theory predicts that animals should act to maximize energetic gains from feeding, while maximizing both breeding opportunities and individual safety (Stephens, Brown & Ydenberg, 2007). One predication of foraging theory is that body size may determine prey size. If a species shows sexual size dimorphism (SSD), it is expected that this may affect feeding habits (Shine, 1989). The ways in which niche and sexual dimorphism affect one each other has been intriguing scientists for decades (Fisher, 1930), and foraging theory offers a pathway to understanding the processes at work on intersexual dietary divergence.

Two main hypotheses have been developed to explain sexual dimorphism. Under the *ecological divergence hypothesis* (Shine, 1989), morphology of males and females would diverge as a consequence of variation in resource utilization between sexes. The *sexual selection hypothesis* (Darwin, 1859), on the other hand, predicts that dimorphism is a result of sexual selection that favors large males or females. Knowledge on diet has the potential to clarify the contribution of each of these processes to the evolution of sexual dimorphism.

Dietary variation as a consequence of ontogeny has been observed in a wide range of vertebrates, particularly for species with wide size variation, such as sharks (Kim *et al.*, 2012) and snakes (Natusch & Lyons, 2012). Differently sized individuals of the same species vary in their morphology, physiology and life-history constraints. It is therefore plausible different-sized conspecifics might also differ in their dietary requirements or have different selection criteria when foraging. Certainly, larger individuals have higher energetic needs, and can generally access larger prey (Carbone & Gittleman, 2002).

Prey composition of many vertebrate species have been described, including carnivorous mammals (Cavalcanti & Gese, 2010), predatory reptiles (Bhupathy, Ramesh & Bahuguna, 2014) and birds of prey (Miranda, 2015). Although several trends stand out, theoretical analysis of dietary data are still uncommon. For snakes, experiments on ontogeny effects on diet (Jayne, Voris & Heang, 1988; Shine, 1991) have been complemented by observational approaches (Natusch & Lyons, 2012). Regarding giant snakes, field observations do not record their feeding on small prey as they grow larger, contrary to what was predicted from experimental approaches or from foraging theory (Arnold, 1993).

Snakes are suitable models for studying sex-related dietary divergence and the effects of ontogeny on diet because they: (1) show a wide range of sizes (Andrews, 1982); (2) are gape-limited, making predator size a precise predictor of prey maximum size (Arnold, 1993); (3) are trophic-independent at any age; (4) have some species that are highly sexually dimorphic (Rivas, 2015). One limitation in the use of snakes in research is their low detectability in nature. This problem can be circumvented by taking samples from snake trade (Natusch & Lyons, 2012).

We investigated sex-based diet variation and potential ontogenetic shifts in prey consumption using gut contents of a giant snake species, the Yellow anaconda, *Eunectes notaeus* Cope 1862 (Fig. 1), sustainably managed in Argentina. To better understand food habits divergence between sexes and ontogenetic shifts on prey size in this species, we tested the following predictions: I – female anacondas will eat larger prey than males; II – females will eat more frequently than males; III – prey use varies between sexes; IV – body size will have a positive effect on feeding frequency; V – individual body size is positively related with maximum prey size but will have no effect on its minimum size.

Materials and methods

Study area

We worked at La Estrella, a marsh formed around 1960, from natural silting of a portion of the Pilcomayo River, in Formosa province, northern Argentina. La Estrella was established in Chaco vegetation, with extensive occurrence of hardwood species (Brown *et al.*, 2010). The decomposition resistance of the dead trees has helped determine the current physiognomy of La Estrella, as they have been colonized by lianas and epiphytic vegetation, forming structures locally known as 'champas', where Yellow anacondas bask during the old periods that occur during winter months. In addition to champas, there are lagoons, dense monodominant formations of Cattail (*Typha* sp.), and extensive areas of Caranday palms *Copernicia alba*. La Estrella has an abundance fish fauna that attracts aquatic birds (Brown *et al.*, 2010). Birds, together with rodents that become trapped in champas by flooding, form main prey of Yellow anacondas (Waller, Micucci & Alvarenga, 2007). Other large vertebrates as caimans *Caiman* spp., turtles *Phrynops hilarii*, capybaras *Hydrochoerus hydrochaeris* and nutrias *Myocastor coypus* are locally uncommon (pers. obs.). The marsh floods annually between February and May, and dries-out between October and December. During 1961–1990, the average monthly highest temperature (33.4°C) was recorded in January, and the lowest (12.1°C) in July (NOAA 2015).

Figure 1 Yellow anaconda lying in water at La Estrella marsh, Formosa province, Argentina. Reproduced with permission. [Colour figure can be viewed at wileyonlinelibrary.com].

Study species

The Yellow anaconda is commonly found along the Paraguay River Basin (Henderson *et al.*, 1995). Individuals range in mass from 0.101 kg in newborns to 27.5 kg in large females. The species shows high levels of SSD, with mean mass of 3.72 versus 7.16 kg, and 174 versus 216 cm snout-vent length for adult males and females, respectively (Waller *et al.*, 2007).

Anacondas forage widely on a variety of fish, reptiles, birds and their eggs, and mammals, occasionally including carrion in their diet (Strüssmann, 1997; Waller, Buongermini & Micucci, 2001). Like other anaconda species, they are persecuted as predators of domestic animals (Miranda, Ribeiro & Strüssmann, 2016), for their fat – traditionally used by its purported medicinal properties (Alves *et al.*, 2006), and for their valuable skin (Micucci & Waller, 2007). They are sustainably managed only in Argentina, through an initiative known as *Programa Curiyú*. The Red List status of this species has yet to be evaluated by the IUCN (International Union for Conservation of Nature), but it is included on Appendix II of the Convention on International Trade of Endangered Species – CITES.

Management program

The Programa Curiyú works on the basis of surplus yield models in an adaptive management context, having no specific hunting quotas for a given year. The harvest is limited by the number of hunters, length of the hunting season and minimum skin length. For management plan details, see Waller *et al.* (2007).

During the hunting season (winter), biologists collect data on prey found in anaconda guts. Snakes are usually slaughtered and skinned close to the capture site, with the carcass being discarded. We offered a monetary reward for hunters to bring us live snakes for dissection, in addition to data collected in previous year by program biologists. We complied with the valid laws of Ministerio de la Producción y Ambiente de la Provincia de Formosa at the study time (permit number 11004048/2015). All the studied animals were part of the ongoing management plan and no individuals were killed specifically for this study.

Field and laboratory protocols

After slaughtering, we waited for the spasms to subside and then dissected the snake to access the gut contents. These were identified visually when slightly digested, for all prey species excluding rodents. Highly digested prey species were identified by comparing feathers and feet for birds and scales for reptiles with material deposited at the Vertebrate Zoological Collection of Mato Grosso's Federal University, Brazil. Highly digested rodents where identified using trichology techniques (de Miranda, Rodrigues & Paglia, 2014). Body masses for avian species and their eggs were obtained from Dunning (1993) and Giacomo, (2005), with exception of Southern Screamer *Chauna torquata* eggs, which were weighed in the field. Reptile and mammal masses where obtained from Strüssmann (1992), Bonvicino & Almeida (2000), Pardiñas & Teta (2005) and Weksler & Bonvicino (2005). We used mean mass for each species unless prey remains suggested that a specimen was a sub-adult, when estimates were made visually. For rodent prey sampled previously by the Programa Curiyú (for which there were no voucher), we used the mean body mass of the largest non-Caviomorph rodent in our study area *Holochilus chacarius*. We made this conservative decision – based on the null hypothesis that prey increase in size as anacondas grow larger – considering that rodents are the smallest prey killed by Yellow anacondas, and that 80% of the rodents consumed belong to this species (Waller *et al.*, 2007).

Statistical analyses

As multiple prey can be captured in successive short-spaced predation events, when multiple bird eggs or rodents were found, individual items were not considered independent replicates. This was done to avoid pseudoreplication. We only considered multiple items to be indicative of multiple predation events if they could not have been feasibly killed together (i.e. the egg of one bird species and an adult of another).

To test the effect of sex on prey size (prediction I), we performed an ANCOVA (as a case of generalized linear model, GLM), using sex as categories and body mass as a covariate. Prediction II, which implies that females have a higher feeding frequency, was tested with another ANCOVA (in this case a GLM with a binomial distribution), using body size as a covariate, which also allows testing the effect of body size on feeding frequency (prediction IV). An ANOSIM was used to test differential prey composition between sexes where Pianka's Niche overlap combined with a null model approach (Gotelli & Entsminger, 2006), was used to test whether different diet compositions would result in differential resource use (prediction III). A quantile regression was used to test prediction V, using two τ values: 0.75, to test if size had a positive effect on maximum prey size, and 0.25, to test if body size had an effect on minimum prey size. We choose this method after noticing that it is the adequate model when the independent variable only controls maximum values of the dependent variable (Gotelli & Ellison, 2005). Alpha levels where established at 0.05 and statistical analyses were ran in R software, using the packages *Vegan*, *EcoSimR* and *QuantReg* (Gotelli & Entsminger, 2006; Oksanen *et al.*, 2007; Koenker, 2013).

Results

Hunters brought us 95 anacondas – 59 females and 36 males from La Estrella during the hunting season of 2015. These ranged from 1.56 to 13.7 kg. Of these, 65 (68.43%) contained prey. The Programa Curiyú data base provided information on gut contents of another 112 anacondas – 96 females and 16 males – hunted between 2001 and 2010, with masses ranging from 1.7 to 23.2 kg. Descriptive data about Yellow anacondas and their prey is given in Table 1. Most common prey items were aquatic birds, followed by rodents, bird eggs and reptiles (Table 2; Fig. 2).

Mean mass of prey taken by male anacondas was 247 g ($n = 30$), while mean mass of prey taken by females was 585 g ($n = 142$), significantly larger than the males' mean prey mass (prediction I; ANOVA, $n = 172$, $P < 0.01$). However, when we take into consideration the effect of body size, the sex effect disappear (ANCOVA, $P = 0.939$ for sex and <0.01 for size; Fig. 3). Sex had a positive effect on feeding frequency, with 83.05% of the females having fed, compared with 44.44% of males (prediction II; ANCOVA, $P < 0.05$, $n = 95$). Size had no effect on feeding frequency of anacondas (prediction III; $P = 0.723$). Prey composition was different between sexes (ANOSIM; $P = 0.002$, $n = 220$), with Pianka's

Table 1 Descriptive data regarding Yellow anaconda and their prey mean mass, its minimum and maximum values and standard error in La Estrella, Formosa, Argentina

	Mean mass (g)	Min–Max (g)	SD(±)
Males	3544	1560–8000	1363
Females	7777	2280–23200	3948
Male's prey	247	29–1890	474
Female's prey	585	14–6000	855

Table 2 Prey composition of Yellow anacondas *Eunectes notaeus* from La Estrella marsh, northern Argentina

	Female %		Male %	
Species and body mass (g)	Frequency	Biomass	Frequency	Biomass
Birds				
Cormorant *Phalacrocorax brasilianus*, 1576 g	9.4	30.5	5.1	28.0
Rosy-billed pochard *Netta peposaca*, 1510 g	2.2	6.9	0.0	0.0
Muskovy duck *Cairina moschata*, 2450 g	1.1	5.6	0.0	0.0
Maguari stork *Ciconia maguari*, 4057 g	0.6	4.6	0.0	0.0
Purple gallinule *Porphyrio martinicus*, 656 g	2.2	3.0	0.0	0.0
Roseate spoonbill *Platalea ajaja*, 1490 g	0.6	1.7	0.0	0.0
Whistling duck *Dendrocygna bicolor*, 710 g	1.1	1.6	2.6	6.3
Anhinga *Anhinga anhinga*, 1235 g	0.6	1.4	0.0	0.0
Brazilian teal *Amazonetta brasiliensis*, 595 g	1.1	1.4	0.0	0.0
Limpkin *Aramus guarauna*, 1080 g	0.6	1.2	0.0	0.0
Great egret *Ardea alba*, 882.2 g	0.6	1.0	0.0	0.0
Whistling duck *D. autumnalis*, 778.3 g	0.6	0.9	0.0	0.0
Silver teal *Anas versicolor*, 617 g	0.6	0.7	0.0	0.0
Chachalaca *Ortalis canicollis*, 539 g	0.6	0.6	0.0	0.0
Southern screamer nestling *C. torquata*, 500 g	0.6	0.6	0.0	0.0
Cattle egret *Bubulcus ibis*, 364 g	0.6	0.4	0.0	0.0
Snail kite *Rostrhamus sociabilis*, 320 g	0.6	0.4	0.0	0.0
Monk parakeet *Myiopsitta monachus*, 120 g	1.1	0.3	7.7	3.2
Striated heron *Butorides striata*, 226 g	0.6	0.3	0.0	0.0
Jacana *Jacana jacana*, 100.9 g	1.1	0.2	0.0	0.0
Guira cuckoo *Guira guira*, 141 g	0.6	0.2	0.0	0.0
Spotted sandpiper *Actitis macularius*, 40.4 g	1.1	0.1	2.6	0.4
Shiny cowbird *Molothrus bonariensis*, 40 g	0.6	0.0	2.6	0.4
Brushrunner *Coryphistera alaudina*, 30 g	0.0	0.0	5.1	0.5
Giant wood rail *Aramides ypecaha*, 708.2 g	0.0	0.0	2.6	6.3
Southern screamer egg *C. torquata*, 164 g	20.2	4.3	2.6	1.5
Limpkin egg *Aramus guarauna*, 59.3 g	5.6	0.7	7.7	1.6
Mammals				
Capybara *Hydrochoerus hydrochaeris*, 6000 g	0.6	6.8	0.0	0.0
Marsh rat *Holochilus chacarius*, 92 g	22.8	4.3	25.6	8.2
Unidentified rodent, 92 g	12.8	2.4	30.8	9.8
Guinea pig *Cavia aperea*, 637 g	0.6	0.7	0.0	0.0
Vesper mouse *Calomys callosus*, 29.9 g	1.7	0.1	2.6	0.3
Fornes' rice mouse *Oligoryzomys fornesi*, 14 g	3.3	0.1	0.0	0.0
Reptiles				
False water-cobra *Hydrodynastes gigas*, 1890 g	3.3	12.9	5.1	33.6
Yellow anaconda *Eunectes notaeus*, 1500 g	0.6	1.7	0.0	0.0
Sample size	180		40	

For each prey species, frequency and biomass (calculated as contribution of each species to total biomass consumed) are shown by sex.

niche overlap is 0.68, higher than expected by chance (prediction IV; $P < 0.01$). Anaconda body size had a positive effect on maximum prey size (prediction V; quantile regression, $P > 0.001$, $n = 173$, $\tau = 0.75$), but no effect on minimum size ($P = 1.0$, $\tau = 0.25$) (Fig. 4). Thus, the best fitting equation was prey size = $-66.44 + 0.14 \times$ anaconda size, for $\tau = 0.75$.

Discussion

Here, we show that sex play a small role in diet divergence between sexes in anacondas. If intersexual niche divergence has a parallel function to reproductive success in evolution of large sized females, it may be small. As diet divergence as a product of SSD has been demonstrated for a range of taxa (Weise, Harvey & Costa, 2010; for mammals; Natusch & Lyons, 2012 for reptiles; Cook *et al.*, 2013 for birds), this may be a secondary consequence of increases in fitness generated by larger body size in males and/or females. Although female anacondas prey is both larger and different from that of males, they feed more frequently, which may be related to fat accumulation associated with the higher costs of reproduction (Lourdais, Lorioux & DeNardo, 2013). This notion is supported by the fact that, while diverging in composition, males and females diet overlaps extensively, excluding the possibility of SSD being a way to reduce competition. Ontogenetic changes in diet increase maximum size of prey that anacondas

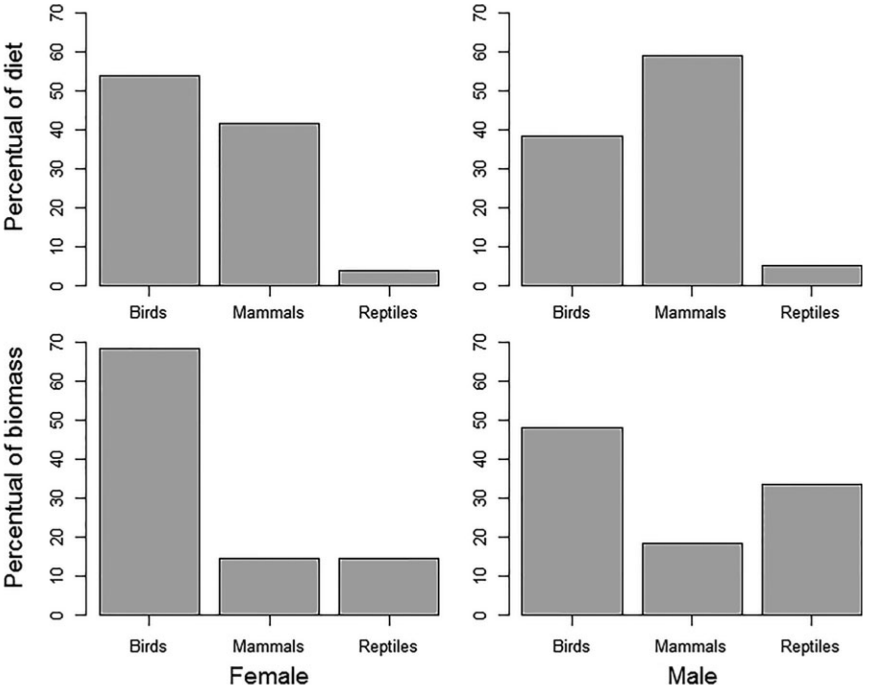

Figure 2 Prey composition of Yellow anacondas *Eunectes notaeus* from La Estrella marsh, northern Argentina. For each prey Class, bars represent frequency or biomass percentiles for each sex.

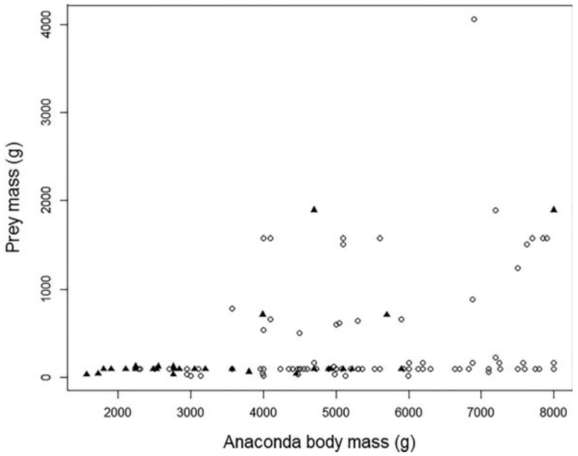

Figure 3 Effect of Yellow anaconda sex on prey body mass. Prey size is plotted against anaconda size; males (black triangles) do not eat smaller prey than females (open circles) ($P > 0.05$). Anaconda's size has been truncated by the largest male in order to afford a better view of data.

may catch, without affecting minimum prey size. This is predicted on both physiological and foraging theoretical grounds because energetic demands increase with size, despite greater efficiency in energy use by larger organisms (Makarieva, Gorshkov & Li, 2005; Stephens *et al.*, 2007).

The diet composition of Yellow anacondas from northern Argentina shows a high proportion of aquatic birds (Table 2). This is followed by small mammals and reptiles in frequency for females, while for males, small mammals are the most common prey. When we take biomass into consideration, the general trend of great avian importance is maintained for females, while for males, birds and reptiles become more important than mammals. The absence of amphibians is probably because La Estrella is mostly formed of open waters where amphibians are uncommon. Fish prey have been rarely recorded by us and other authors because the anacondas lacks the head morphology needed not reduce drag when striking at prey underwater (Vincent *et al.*, 2009). Therefore, predation on fish may be restricted to dry season, when they can be founded stranded or dying in shallow pools. Head morphology is considered a variable that can cause intersexual divergence on diet (Vincent, Herrel & Irschick, 2004). However, contrary to predictions of previous research (Vincent & Herrel, 2007), head size and shape does not show changes between sexes in Yellow anacondas (Waller *et al.*, 2007).

High predation of birds has been shown elsewhere for Yellow and Green anacondas (Strüssmann, 1997; Rivas, 2015). However, our records of rodents and other small prey were higher than recorded in other studies, which we believe may be due to the methodological constraint imposed by other studies use only of forced regurgitation to obtain stomach contents. This method may underestimate small-sized prey present in the snake's intestines because anacondas – like pythons – are large and muscular snakes and small prey may go unnoticed during

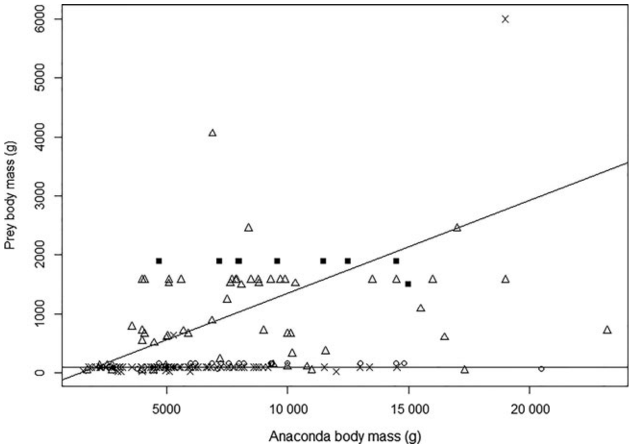

Figure 4 Yellow anaconda's size plotted against prey size, showing that anaconda feed on larger prey as they grow in size while continuing to eat small prey. Prey types: reptiles – closed squares; avian eggs – circles; birds – triangles; mammals – crosses. The quantile regression of prey size against predator size was significant for $\tau = 0.75$ (upper line, $P < 0.05$) but not for $\tau = 0.25$ (lower line, $P = 0.10$).

stomach palpation. If studying large snakes, we recommend using feces collection as a complement to forced regurgitation. Nevertheless, since large prey will make snakes produce more feces, some statistical correction would need to be undertaken (Ackerman, Lindzey & Hemker, 1984), otherwise strong pseudoreplication will occur (see Bhupathy *et al.*, 2014 for an example).

By finding 68% of anacondas fed we question a common notion that giant snakes feed infrequently, a premise for a number of research fields (Whelan & Schmidt, 2007; Andrew *et al.*, 2015). In other large species, as *Python reticulatus*, 37–45% individuals had prey in their guts (Shine, Harlow & Keogh, 1998). We stress that these are very high rates considering that animals were collected with methods allowed defecation and regurgitation before dissection. In the smaller sized scrub python *Morelia spilota*, 45% of the individuals had prey in their stomachs or intestines (Slip & Shine, 1988). Since digestion takes no more than 2 weeks for extremely large prey (Secor & Diamond, 1997a; Toledo, Abe & Andrade, 2003), we argue that giant snakes feed rather more frequently than is commonly supposed. In addition, research on the metabolic response to digestion shows a hypoalometric (Secor & Diamond, 1997b) or absent (Bedford & Christian, 2001) effect of large sized prey, strengthening this idea.

Another common assumption regarding giant snakes on which the data casts doubt is the widespread use of a sit-and-wait or ambush foraging strategy (Whelan & Schmidt, 2007; Secor, 2008), as this could not explain the high incidence of egg predation found in this study, suggesting that sit-and-wait strategy is just one part of a broader suit of foraging behaviors. It is possible that this is an idiosyncrasy caused by Yellow anacondas being an aquatic species. Locomotion costs are smaller in water, and this could permit individuals to forage more actively. However, a similar pattern of egg predation is found in the more terrestrial *Python molurus* in Everglades (Dove *et al.*, 2012), and in the terrestrial *Python natalensis* in South Africa (Alexander, 2012). Based on evidence regarding: (1) high feeding frequency; (2) presence of non-motile prey; and (3) presence of small-sized prey; we consider that the idea of the giant snake which sit-and wait to feed on enormous prey and later fast for months may have to be reassessed.

While sex has a strong effect on feeding frequency, its effect in prey size disappears when we make body size into account. Consequently, dietary divergence may result from SSD as well as from the ontogenetic relationship between body size and feeding frequency. Meanwhile, fitness-based differences between male and female body size are more parsimonious as an explanation for large body size in females (Shine, 1989). One could suggest that the strong differences in feeding frequency could be a misconception induced by our data on this being collected only during the winter months. But summer is the dry season in our study area; this is when anacondas reproduce (Waller *et al.*, 2007; Rivas, 2015), and individuals of neither sex feed often when reproductively active. Breeding season fasting has been shown to occur in several other snake taxa, including colubrids (Shine, 2003), pythonids (Madsen & Shine, 2000) and viperids (Madsen & Shine, 1993). Nevertheless, since La Estrella is a recently formed environment, we believe that data collection in seasons other than winter or in other study areas may reveal different diet composition.

Increases in maximum prey size along with increases in anaconda's body size while continuing to consume small prey reflect optimal choices under foraging theory. This theme has been the subject of a long discussion since some snakes are shown to consume small-sized prey in laboratory experiments (Shine, 1991). This, however, contrasted with field studies where relationship between snake size and prey size could be described as an 'ontogenetic shift', with an increase in the minimum prey size in larger snakes (Arnold, 1993). We believe that this is a misconception caused by: (1) increased performance of the digestive system in larger snakes (Secor & Diamond, 1997b); and (2) small sample sizes of truly large snakes (Shine *et al.*, 1998; Rivas, 2015). Both can act reducing detection of small prey, the first decreasing passing time and therefore reducing time to detection through dissection or regurgitation and the second reducing general detection probability for any prey species.

In anacondas, feeding data supports the predictions of the 'ontogenetic telescope' hypothesis, with size-based traits allowing larger animals to eat larger prey (Beerman *et al.*, 2015). Although it is difficult to accurately predict the evolutionary drivers for any morphological trait (Young & Brodie, 2004 and comments therein), our results are consistent with the hypothesis that SSD is an effect of increases in fitness resulting from larger body size in females (Rivas, 2015), while the moderate dietary divergence may be a side-effect of it. Fitness differences resulting from differential optimum size between males and females seem to be a sufficient proximal cause to explain SSD.

In summary, our study shows that there is little change in Yellow anacondas feeding habits resulting from SSD as size increases, while the ontogenetic relationship between body size and diet produces increases in maximum prey size. Our results indicate that the pattern of prey size shift by anacondas can therefore be considered general in indeterminate-growth species. Since these shifts might have evolved because of conserved physiological constraints related with increase in energetic demand by larger organisms, they may be worthy of consideration for research on foraging by indeterminate growth species. Further research on the effects of SSD on resource use will be relevant for development of our understanding of these changes as causes or consequences of differently sized males and females.

Acknowledgements

We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico for grants 130873/2014-4 (E. Miranda), PROPeq-UFMT 332/CAP/2013 (R. Ribeiro-Jr.), and 309541/2012–3 (C. Strüssmann), as well as for general financial support (Edital Universal, 456497/2014-5). We thank Fundação de Apoio à Pesquisa Científica e Tecnológica for financial support through Edital Universal 155536/2014, and for a grant to B. Camera. We are grateful for the financial support of PRONEM/FAPEMAT/CAPES through the Edital 008/2014, process number 23038.007261/2014-32, grant 3530/2014. The Office Vétérinaire Federal of Switzerland and Fundación Biodiversidad – Argentina provided since 2002 invaluable financial support for our fieldwork. We are grateful to Daigo Fujisono, Shinya Ono and Masahiro Yasuda, of JICA (Japan International Cooperation Agency) and JWRC (Japan Wildlife Research Center) for logistical support during field activities. Ministerio de la Producción y Ambiente de la Provincia de Formosa provided us the licenses for field activities. Adrian Barnett and Cristian Dambros improved the quality of an earlier manuscript by offering criticisms of the English and statistical analysis. We finally thank the hunters Francisco Victoriano Ruiz and Laudino Santillan, who offered us their skills which made this work possible.

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