Intraspecific variation in the diet of the Mexican garter snake *Thamnophis eques*

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Abstract

The Mexican Garter Snake (*Thamnophis eques)* is a terrestrial-aquatic generalist because it feeds on both aquatic and terrestrial prey. We describe size-related variation and slight sexual variation in the diet of *Thamnophis eques* through analysis of 262 samples of identifiable stomach contents in snakes from 23 locations on the Mexican Plateau. The Mexican Garter Snakes we studied ate prey items mostly fish, followed in lesser amounts, respectively, by leeches, earthworms, frogs, and tadpoles. Correspondence analysis suggested that the frequency of consumption of various

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prey items differed between the categories of age and sex of snakes, and the general pattern was a reduction of prey item diversity with size of snake. Snake length was correlated positively with mass of ingested prey. Large snakes consumed large prey and continued to consume smaller prey. In general, no differences were found between the prey taxa of male and female snakes, although males ate two times more tadpoles than females. Males and females did not differ in the mass of leeches, earthworms, fishes, frogs and tadpoles that they ate, and males and females that ate each prey taxon were similar in length. We discuss proximate and functional determinants of diet and suggest that the observed intraspecific variation in Mexican Garter Snakes could be explored by temporal variation in prey availability, proportions of snake size classes and possible sexual dimorphism in head traits and prey dimensions to assess the role of intersexual resource competition.

Key words: ontogenetic, size, sexual variation, *Thamnophis*.

Introduction

The Mexican Garter Snake (*Thamnophis eques*) is a medium-sized garter snake classified as a terrestrial-aquatic predator because it feeds on both aquatic and terrestrial prey; mostly frogs, tadpoles, and fish, supplemented by lizards and mice (Drummond & Macías Garcia, 1989; Manjarrez, 1998). Drummond & Macías Garcia (1989) found that *T. eques* at Tecocomulco, Hidalgo, is locally specialized in feeding on only two to three taxa. This snake forages in vegetative cover along the shore and an attack may include a sudden lunge across the surface toward prey (Drummond & Macías Garcia, 1989).

Thamnophis eques is widely distributed over the Mexican Plateau, however, despite the apparent widespread distribution, this species has a constricted distribution and low population densities (Rossman, Ford, & Seigel, 1996; Manjarrez, 1998). Its populations are severely fragmented and isolated due to its habitat requirements, loss of habitat, and disturbance of habitat

(Conant, 2003). Many populations of garter snakes show considerable intraspecific variation in ecology (Rossman, Ford, & Seigel, 1996), but data on diet are particularly scarce for Mexican populations of *T. eques*. Previous studies of Mexican populations revealed some differences in prey size between males and females, neonates and adults, and rainy and dry seasons (Sosa, 1982; Macías Garcia & Drummond, 1988; Drummond & Macías Garcia, 1989). At Lake Tecocomulco, Mexico, large snakes (> 44.0 cm SVL) fed mainly on aquatic vertebrates (fish, frogs, and salamander larvae), while small snakes (≤44.0 cm SVL) fed on aquatic invertebrates (earthworms and leeches). Seasonal variation in prey was associated with fluctuations in prey availability (Macías Garcia & Drummond, 1988). At Toluca, Mexico, *T. eques* were found to have eaten tadpole *Hyla* sp., earthworms, mice, and slugs (Manjarrez, 1998).

In this study, we provide the first broad description of the diet of the Mexican Garter Snake (*Thamnophis eques*) on the Mexican Plateau. We looked for variation in consumption of prey taxa and size-classes of snake. We analyzed sexual and size-related variation in diet using the data from three drainages. To permit more extensive and novel comparisons, we pooled our dietary records with those of Lozoya (1988) and Drummond & Macías Garcia (1989), (19% and 13%, respectively, of the total regurgitations examined in this study.

Sexual differences in snake diets are not well documented (Shine, 1993; Daltry, Wuster, & Thorpe, 1998) but females sometimes ingest larger prey than males (Seigel, 1996) and this difference is usually attributed to snakes' sexual dimorphism in body size when females are bigger that males. The maximum size of prey that can be ingested is constrained by a snake's gape (e.g. King, 2002), and in most species, larger snakes take larger prey and appear to drop small prey from their diet, although data from very young snakes is usually limited (review in Arnold, 1993). Garter snakes are sexually dimorphic in body size (Shine, 1993) and their diet can vary with age/size-classes (Mushinsky, 1987; Macías Garcia & Drummond, 1988). Female garter snakes are usually larger than males (Shine, 1994) but sexual differences in garter snake diets have not been well studied and may not exist (Seigel, 1996).

Thamnophis eques is sexually dimorphic with adult females being larger than males in snout-vent length (SVL) and head length (5.6% and 12%, respectively; Manjarrez & Macías García, 1993; Manjarrez, 1998; Manjarrez, Contreras-Garduño, & Janczur, 2014). Females reach sexual maturity at 39.5 cm SVL.

Materials & Methods

This study received the approval of the ethics committee of the Universidad Autónoma del Estado de México (Number 4047/2016SF). All subjects were treated humanely on the basis of guidelines outlined by the Society for the Study of Amphibians & Reptiles.

We collected snakes that we found under stones and other objects, and looked for basking snakes along streams, rivers, canals, ponds, and lakes. We measured each captured snake (SVL), and also recorded sex by visual inspection of the tail-base breadth (Conant & Collins, 1998). Then, we gently induced regurgitation of stomach contents by abdominal palpation (Carpenter, 1952). After processing, snakes were released promptly at their capture sites. We measured the wet mass of each prey item and then fixed them in 10% formalin and preserved them in 70% alcohol.

We sampled snake stomach contents at 23 sites on the Mexican Plateau (Lerma, Tula, and Nazas, drainages, Table S1) sporadically during the active reproductive season (February to November) over a period of 16 years on 1.5 ± 0.9 occasions each (mean ± SD; range: 1 – 5; Table S2). The sites in the Lerma and Tula drainages were sampled from 1980-1986 and 1991-1995. We obtained 194 regurgitations from 22 sites in Jalisco, Michoacán, México, Hidalgo, and Queretaro. The records obtained for these two drainages are partially reported by Lozoya (1988, 19% of the total regurgitations), a reference that is inaccessible to most readers.

In the Nazas drainage we obtained 68 regurgitations. The Nazas population inhabits an isolated 0.36 ha spring-fed cattle pond in the Chihuahuan Desert with a rainy season from June through October. The records were obtained during 27 2-4 day visits, bimonthly during April to November 1981, and monthly during February through December 1982, and February through November 1983. Drummond & Macías Garcia (1989) previously reported 13% of these records. Snakes were captured on the first two days of each visit and released on the second day to prevent repeat sampling during the same visit. We counted and classified prey items as fish, leeches, frogs, tadpoles, and earthworms.

Analysis

We classified snakes as newborns (< 20.5 cm SVL), juveniles (20.5–39.5 cm) or adults (> 39.5 cm), based on birth sizes and minimum sizes of gravid females (Manjarrez, 1998). Thirteen regurgitations (5.7% of total) included more than one prey species, and hence contributed more than one data point for some snakes. Percentages of regurgitations containing each prey taxon were normalized by arcsine transformation (Zar, 1984). We used MANCOVA (with snake length as a covariate) to explore variation in the mass of prey consumed by prey taxa and by the sex of each snake. We included complementary analyses of dietary variation in relation to snake size whenever these could contribute to understanding variation in diet. For analyses of prey mass we excluded taxa represented by fewer than five prey items. Prey mass and snake length were natural log transformed prior to calculating correlations. We report means ± 1.

The analysis of records from different locations and years can potentially reveal a pattern of geographical or temporal variation in the diet of *T. eques*, but in this study we focused on a description of the diet under ontogenetic and sexual criteria. Possible spatial or temporal variations of the diet will be discussed in a subsequent paper. To avoid making Type I or II errors when many X^2 tests are performed, we used a correspondence analysis to identify prey items consumed more frequently by the combination of two related categories of sex of snake (male-female) and three categories of snake size (newborns, juveniles, and adults). We also performed a cluster analysis to determine the categories of age and sex of snakes with similar consumption of prey. We used the Morisita index of similarity between frequencies of prey consumed, and the Ward's Method of amalgamation (Rencher, 2002).

Results

Prey items

We obtained identifiable stomach contents from 262 *T. eques*. Prey items were primarily fish (42.4%; *Girardinichthys multiradiatus*, *Carassius auratus*), followed by leeches (23.7%; *Erpobdella punctata* and *Mooreobdella* sp.), earthworms (10.6%; *Eisenia foetida* and *Eisenia* sp.), frogs (10.2%; *Rana berlandieri* and *Rana sp.*), and tadpoles (9.8%; *R. berlandieri, Rana sp*., and *Hyla* sp.). The remaining 3.6% were excluded from the analysis because they were recovered from only 6 stomachs (axolotls (*Ambystoma sp*.), a lizard, slug, and mouse within 1 stomach).

Correspondence analysis suggests that there are differences in the frequency of consumption of different prey between categories of age and sex of snakes ($X^2_{50} = 126.4$, P <0.001). Two of the dimensions of correspondence analysis provided 77.2% of the variation of the consumption frequencies in the two main categories (sex and size). Cluster analysis indicated three snake groups (Fig. 1) with similar consumption of prey: (1) adult females (consuming leeches, frogs and fishes; (2) juvenile males and females, and male adults (consuming earthworms, slugs, and tadpoles, and (3) newborn males and females (consuming earthworms and frogs while excluding fish and tadpoles). Juvenile females provided the largest contribution to the analysis ($X^2 = 34.9$). This grouping of snakes suggests a scheme of ontogenetic change in the taxon of prey, with lower relevance of the grouping by sex (Fig. 1)

Variation with snake length

Snakes of different sizes ate a changing diversity of prey types. The general pattern was a reduction of prey item with size of snake (Fig. 2). Snakes < 65 cm SVL ate all prey types of all sizes, including invertebrates (leeches and earthworms) and vertebrates (tadpoles, fish, and frogs). Vertebrate prey were taken by only the largest snakes (> 60 cm SVL). At 15 cm SVL, snakes eat leeches as one of two major prey items, but at 55 cm SVL consumption of leeches decreases drastically and disappears completely in larger snakes >65cm SVL (Fig. 2). The consumption of fish and tadpoles increases when snake body size increases. However, the longer snakes > 75 cm SVL consume only fish and tadpoles while excluding all other prey, possibly because longer snakes were a very small part of the entire sample (n = 7 stomach contents).

Snake length was correlated positively with mass of ingested prey (r = 0.42, $F_{1, 326}$ = 71.52, P < 0.001; Fig. 3). Large snakes consume large prey and continue to consume smaller prey. The same relationship was presented for leeches (r = 0.42, $F_{1,136}$ = 29.85, P < 0.00; Fig. 4A) and fish (r = 0.43, $F_{1,88}$ = 20.30, P < 0.001; Fig. 4C), but not correlated with earthworm (r = 0.14, $F_{1,32}$ = 18.32, P = 0.806) and tadpole mass (r = 0.2, $F_{1,25}$ = 2.36, P = 0.136).

Variation with snake sex

Mean body lengths of captured snakes did not differ between sexes (Student t_{243} = 0.44, P = 0.66), thus male and female snakes were similar in size.

No differences were found between the diets of male and female snakes. Pooling all sizes of snake, males (n = 124) and females (n = 121) ate similar proportions of the five main prey taxa (X^2 = 3.82, P = 0.43), both sexes eating mainly fishes, frogs, leeches, and earthworms, and in similar proportions. Males ate two times more tadpoles (0.13) than females (0.06).

Males and females did not differ in the mass of leeches, earthworms, fishes, frogs and tadpoles that they ate (MANCOVA $F_{1, 193}$ = 0.79, P = 0.37), and males and females that ate each prey taxon were similar in length ($F_{1, 235}$ = 0.91, P = 0.34).

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Discussion

In this study, we provide a broad description of the diet of the Mexican Garter snake *T. eques* on the Mexican Plateau. The results indicate 69% of total regurgitations contain two major prey: leeches and fish, while the other three main prey are ingested in similar percentages (earthworms, 10.6%; frogs, 10.2%; tadpoles, 9.8%). The diet of *T. eques* included amphibious prey (frogs), terrestrial prey (earthworms) and aquatic prey (leeches, fish and tadpoles), and occasionally other prey such as slugs, axolotls, lizards, and mice. The main prey include three vertebrates (65%) and two invertebrates (35%).

The studies that have analyzed the diet of *T. eques* in Mexico included four local descriptions and in each study *T. eques* is locally specialized in feeding on only 2-3 prey taxa (Table 1) (Drummond & Macías Garcia, 1989). This suggests a pattern of spatial variation in the diet of *T. eques*, presumably by the local availability of prey (Gregory & Nelson, 1991; Tuttle & Gregory, 2009).

The diet of *T. eques* can also present ontogenetic variations associated with individual size, changing from terrestrial to aquatic prey as snake size increases (Macías Garcia & Drummond, 1988; Drummond & Macías Garcia, 1989). Ontogenetic change by prey taxa in gartersnakes, could be attributed to proximate mechanisms such as morphological constraints that determine the size of ingested prey (Shine, 1991; Arnold, 1993), the availability of potential prey (Krebs, 2009), energy or nutritional needs (Britt, Hicks, & Bennett, 2006), habituation and learning (Halloy & Burghardt, 1990; Ford & Burghardt, 1993) or genetically programmed preferences (Arnold, 1977; Arnold, 1981; Britt, Hicks, & Bennett, 2006). In Tecocomulco, Hidalgo, the differential distribution of large and small snakes was interpreted as a possible cause of differences in diet of *T. eques* with differences in the pattern of foraging, so that the snake can be an effective predator in the air-water interface; preying on aquatic prey when they are particularly vulnerable and terrestrial prey being added to the diet only opportunistically (Drummond & Macías García, 1989).

In our study, the ontogenetic variation in diet of *T. eques* was also found in the relationship between snake size and prey mass. The ingested prey size gradually increases with snake size and large snakes continued eating small prey. This relationship could be interpreted as an ontogenetic telescope (Arnold, 1993), as previously reported for *T. eques* in a Zacatecas population with *Rana berlandieri* (Drummond & Macías García, 1989).

The ingestion of small prey by large snakes may also have a functional explanation in terms of reducing the costs of energy, foraging and predation (Shine, 1993; Rodriguez-Robles, 2002; Britt, Hicks, & Bennett, 2006), for example when snakes are in vulnerable state (small snakes) that limits their locomotor performance (Bonnet et al., 2000), and promotes anorexia (O´Donnell, Shine, & Mason, 2004; Britt, Hicks, & Bennett, 2006).

The absence of ontogenetic variation in the regurgitated samples of tadpoles and earthworms in *T. eques*, is common because in a previous study the annelids were ingested by *T. eques* regardless of snake body size (Macías Garcia & Drummond (1988). The proximate explanation for this phenomenon is the availability of these prey during the annual active period of the snake or by a stable ontogenetic preference for invertebrates (Ford & Burghardt, 1993). The proximate and functional diet determinants of intraspecific variation in Mexican garter snakes could be explored by local and temporal variation in prey availability and proportions of snake size classes collected.

The intersexual variation in food habits has been associated with sexual differences in body size (Shine et al., 1998). *Thamnophis eques* has been reported as sexually dimorphic in body size, with males smaller than females in SVL (Manjarrez, 1998); however in this study, the average size of male and female *T. eques* were similar and there were no sexual differences in diet, except that adult females ate more number of leeches, frogs and fish than other age-sex groups, as suggested by cluster analysis. This sexual difference in diet can probably be attributed to real diet preference by adult females because females and males that ate each of these three prey taxon were similar in length (leech: Student $t_{55} = 1.39$, $P = 0.17$; frog: $t_{23} = 1.07$, $P = 0.29$; fish: $t_{102} = 0.83$, $P = 0.41$). Generally, large samples revealed no differences between male and female snakes in variety of prey taxa, proportions of different prey taxa and taxon specific prey weight (Shine, 1993), and the males and females that ate each taxon were similar in size. Overall, male and female Mexican Garter Snakes differ little in size (Manjarrez, Contreras-Garduño, & Janczur, 2014), habitat use, seasonal foraging pattern (Drummond & Macías Garcia, 1989), and diet (Macías Garcia & Drummond, 1988). Males and females of this species do not appear to differ in microhabitat use (Venegas-Barrera, 2001) or, as was found in the present study, in the body size of prey and type of prey consumed. This may explain the lack of difference between sexes. Small differences in microhabitat and diet might be revealed by very large sample sizes. Prey size and energetic demands may determine developmental transitions to different prey sizes or taxa, whereas sex, in this snake lacking sexual size dimorphism, has little or no influence on diet. However, sexual dimorphism in head traits (i.e., teeth number) and ingested prey shape have rarely been explored and it will be necessary to measure head and prey dimensions for *T. eques* (i.e., head width and length) to assess the role of intersexual resource competition.

Conclusions

In this study, we provide the first broad broad description of the diet of the Mexican Garter snake on the Mexican Plateau. The two major prey were leeches and fish. The diet of *T. eques* included amphibious, terrestrial and aquatic prey with ontogenetic variations associated with individual size, changing from terrestrial to aquatic prey as snake size increases. The ontogenetic variation in diet of *T. eques* was also found in the relationship between snake size and prey mass. The average size of male and female *T. eques* were similar and there were no sexual differences in diet. The proximate and functional diet determinants of intraspecific variation in Mexican garter snakes could be explored by local and temporal variation in prey availability and proportions of snake size classes collected.

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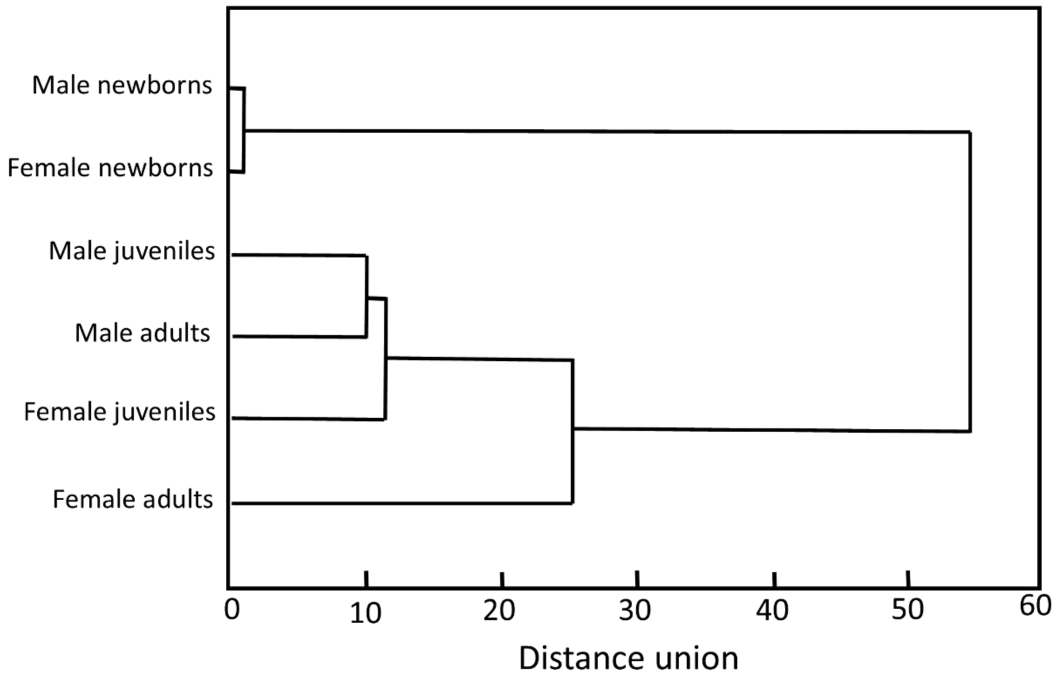
Table 1. Percentage of prey reported in the diet of *Thamnophis eques* in Mexico.

	Tecocomulco[1]	Cerrillo[2]	Toluca Valley[3]	Fresnillo[4]	Present study
	126 snakes	18 regurgitations	148 snakes	64 snakes	262 regurgitations
Invertebrate prey					
Earthworm	41	22	20.2	2.9	10.6
Leech	39	---	8.7	---	23.7
Other	1.0	5.5	---	---	0.4
Vertebrate prey					
Fish	11	---	29.0	---	42.4
Frog	5	28	10.1	69.0	10.2
Tadpole	1.5	33	22.2	23.4	9.8
Other	4.5	11.0	9.4	4.7	3.2

[1]Macías García & Drummond, 1988; [2]Manjarrez, 1998; [3]Manjarrez, Contreras-Garduño & Janczur; [4]Drummond & Macías García, 1989.



338 Fig. 1. Dendrogram for clustering the variables of age and sex of *T. eques* with similar consumption of prey using Ward's method of amalgamation.

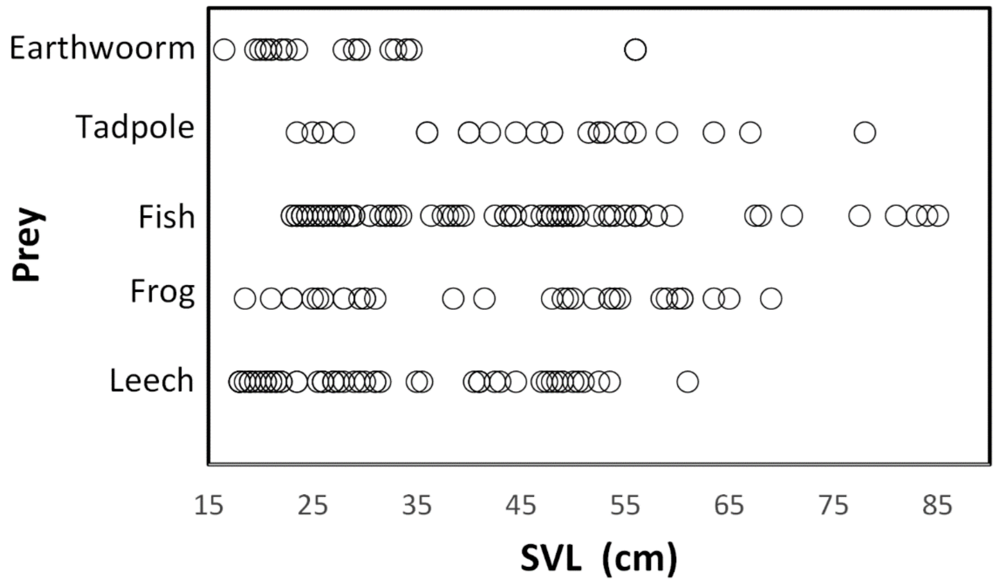
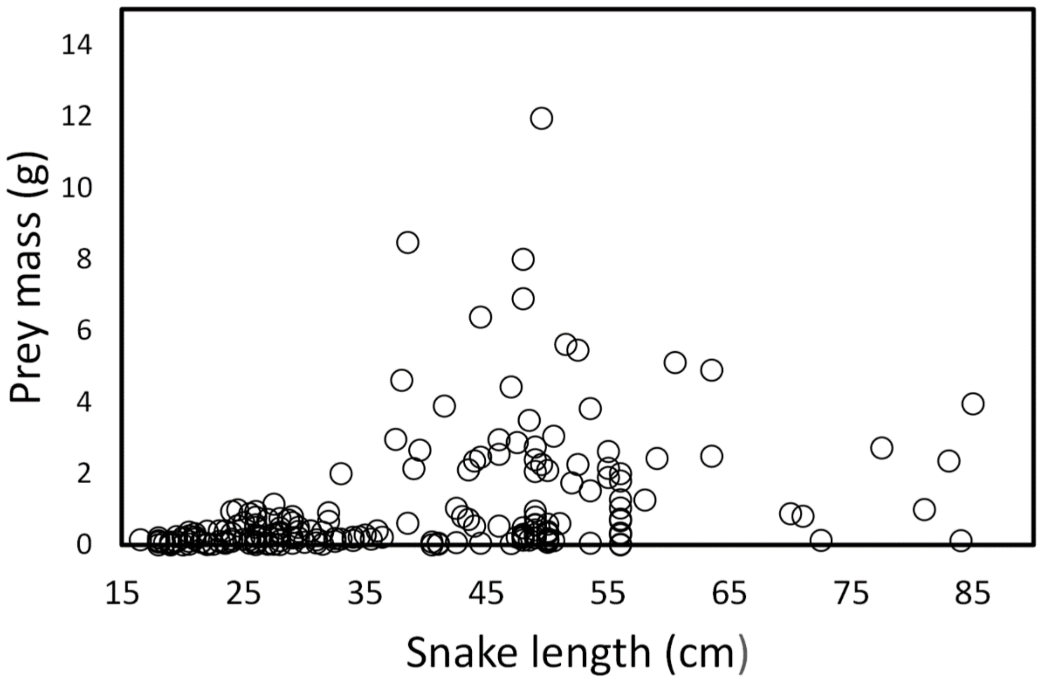


Fig. 2. Relationship between prey type and snake size (SVL, cm) of *T. eques* in México (n = 262). Each circle represents a single prey item.



344

345 Fig. 3. Prey mass as a function of snake length (SVL, cm) of (*T. eques*) in México. (N = 262).

346 Each dot represents an individual prey item.

347

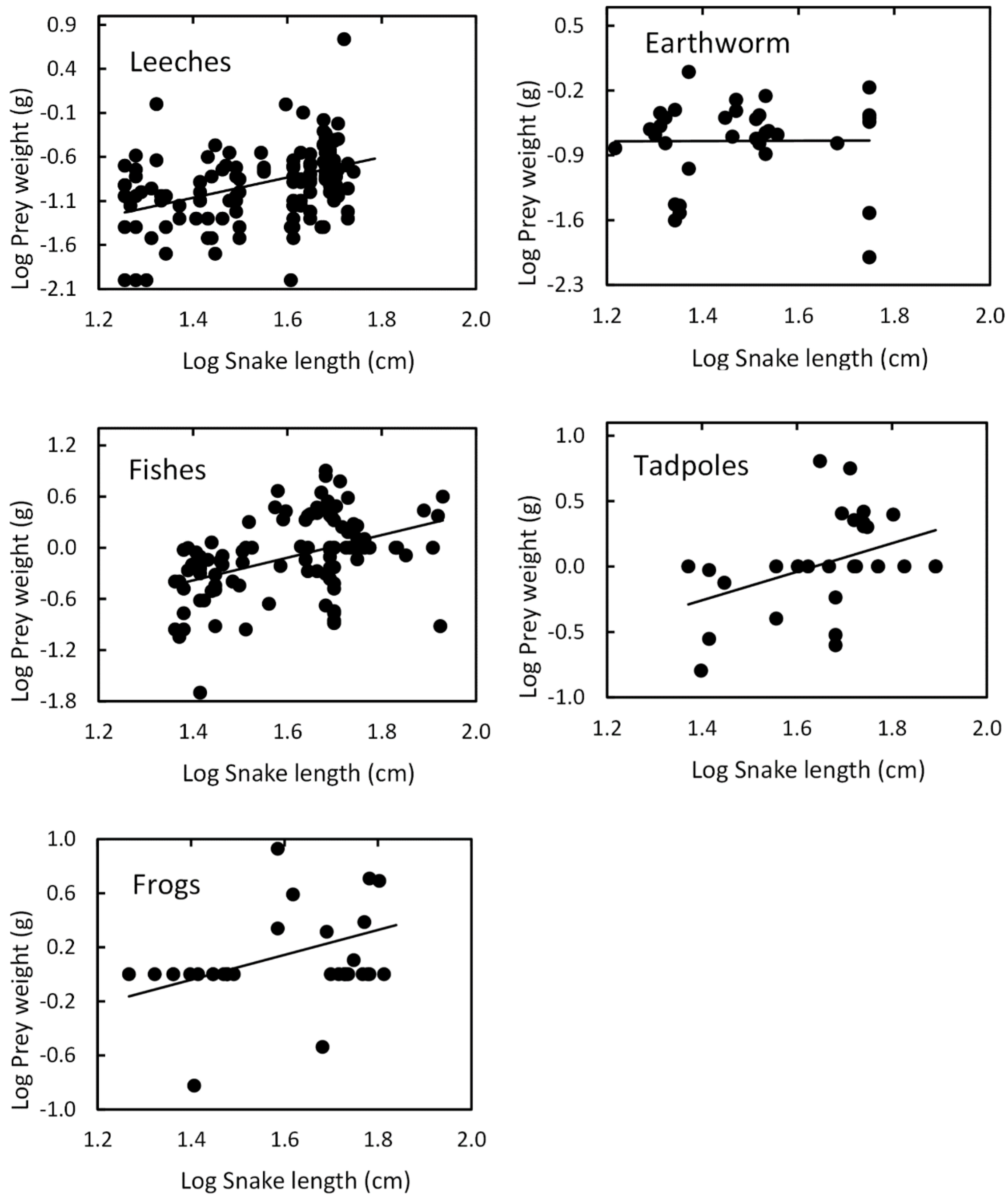


Fig. 4. Relation between prey mass and snake length of *T. eques*.