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

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The Mexican Garter Snake (*Thamnophis eques)* is a terrestrial-aquatic generalist that feeds on both aquatic and terrestrial prey. We describe size-related variation and sexual variation in the diet of *T. 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 consumed mostly fish, followed in lesser amounts by leeches, earthworms, frogs, and tadpoles. Correspondence analysis suggested that the frequency of consumption of various prey items differed between the categories of age but not between 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.

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Abstract

The Mexican Garter Snake (*Thamnophis eques)* is a terrestrial-aquatic generalist that feeds on both aquatic and terrestrial prey. We describe size-related variation and sexual variation in the diet of *T. 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 consumed mostly fish, followed in lesser amounts by leeches, earthworms, frogs, and tadpoles. Correspondence analysis suggested that the frequency of consumption of various prey items differed between the

24   categories of age but not between sex of snakes, and the general pattern was a reduction of prey

25   item diversity with size of snake. Snake length was correlated positively with mass of ingested

26   prey. Large snakes consumed large prey and continued to consume smaller prey. In general, no

27   differences were found between the prey taxa of male and female snakes, although males ate two

28   times more tadpoles than females. Males and females did not differ in the mass of leeches,

29   earthworms, fishes, frogs and tadpoles that they ate, and males and females that ate each prey

30   taxon were similar in length. We discuss proximate and functional determinants of diet and

31   suggest that the observed intraspecific variation in Mexican Garter Snakes could be explored by

32   temporal variation in prey availability, proportions of snake size classes and possible sexual

33   dimorphism in head traits and prey dimensions to assess the role of intersexual resource

34   competition.

35   **Introduction**

36   The Mexican Garter Snake (*T. eques*) is a medium-sized garter snake classified as a terrestrial-

37   aquatic predator because it feeds on both aquatic and terrestrial prey; mostly frogs, tadpoles, and

38   fish, supplemented by lizards and mice (Drummond & Macías Garcia, 1989; Manjarrez, 1998).

39   Drummond & Macías Garcia (1989) found that *T. eques* at Tecocomulco, Hidalgo, is locally

40   specialized in feeding on only two to three taxa. This snake forages in vegetative cover along the

41   shore and an attack may include a sudden lunge across the surface toward prey (Drummond &

42   Macías Garcia, 1989).

43   Although the Mexican Garter Snake is widely distributed over the Mexican Plateau, in

44   this area, the disturbance and loss of habitat have caused the isolation and fragmentation of their

45   populations (Conant, 2003; Manjarrez, Contreras-Garduño, & Janczur, 2014), with low

46   population densities and constricted distribution (Rossman, Ford, & Seigel, 1996; Manjarrez,

47   1998). A scenario that raises the possibility of intraespecific dietary differences by spatial

48   variation of the environment. In general, garter snakes show important ecological intraspecific

49   variation (Rossman, Ford, & Seigel, 1996), and reports on diet for *T. eques* in Mexico showed

50   sexual, ontogenetic (newborns- adults) and seasonal (rainy-dry) divergence in prey size (Macías

51   Garcia & Drummond, 1988; Drummond & Macías Garcia, 1989; Manjarrez, Contreras-Garduño,

52   & Janczur, 2014). For example, at Lake Tecocomulco, Mexico, small snakes fed mainly on

53   aquatic invertebrates (leeches and earthworms), while large snakes fed on aquatic vertebrates

54   (frogs, fish, and salamander larvae). Fluctuations in prey availability was associated with

55   seasonal variation in prey (Macías Garcia & Drummond, 1988). At Toluca, Mexico, Mexican

56   garter snake were detected to have eaten earthworms, tadpole, slugs and mice (Manjarrez, 1998;

57   Manjarrez, Contreras-Garduño, & Janczur, 2014).

58   In this study, we provide the first broad description of the diet of the Mexican Garter

59   Snake (*T. eques*) on the Mexican Plateau. We focused on a description of the diet under

60   ontogenetic and sexual criteria. We looked for variation in consumption of prey type, sex and

61   size-classes of snake from three different drainages. To permit more extensive and novel

62   comparisons, we pooled our dietary records with those of Lozoya (1988) and Drummond &

63   Macías Garcia (1989), as described in Materials and Methods.

64   Sexual differences in snake diets show that females sometimes ingest larger prey than

65   males (Shine, 1993; Seigel, 1996; Daltry, Wuster, & Thorpe, 1998) and this difference is usually

66   attributed to sexual dimorphism in body size when females are bigger that males. The maximum

67   size of prey that can be ingested is constrained by a snake's gape (e.g. King, 2002), and in most

68   species, larger snakes take larger prey and appear to drop small prey from their diet, although

69   data from very young snakes is usually limited (review in Arnold, 1993). Garter snakes are

70 sexually dimorphic in body size (Shine, 1993) and their diet can vary with age/size-classes

71 (Mushinsky, 1987; Macías Garcia & Drummond, 1988). Female garter snakes are usually larger

72 than males (Shine, 1994) but sexual differences in garter snake diets have not been well studied

73 and may not exist (Seigel, 1996).

74   *Thamnophis eques* is sexually dimorphic with adult females being larger than males in

75 snout-vent length (SVL) and head length (5.6% and 12%, respectively; Manjarrez & Macías

76 García, 1993; Manjarrez, 1998; Manjarrez, Contreras-Garduño, & Janczur, 2014). Females reach

77 sexual maturity at 39.5 cm SVL (Manjarrez, 1998).

78 **Materials & Methods**

79 This study received the approval of the ethics committee of the Universidad Autónoma del

80 Estado de México (Number 4047/2016SF). All subjects were treated humanely on the basis of

81 guidelines outlined by the American Society of Ichthyologists and Herpetologists (ASIH, 2004).

82   We collected snakes that we found under stones and other objects, and looked for basking

83 snakes along streams, rivers, canals, ponds, and lakes. We measured each captured snake (SVL

84 in cm), and also recorded sex in adults by visual inspection of the tail-base breadth or by

85 manually everting the hemipenis in small snakes (Conant & Collins, 1998). Although the snakes

86 were weighed, these data were not used in this study. Then, we gently induced regurgitation of

87 stomach contents by abdominal palpation (Carpenter, 1952). After processing, snakes were

88 released at their capture sites. We measured the wet mass of each prey item and then fixed them

89 in 10% formalin and preserved them in 70% alcohol.

90   We sampled snake stomach contents at 23 sites on the Mexican Plateau (Lerma, Tula, and

91 Nazas, drainages, Table S1) sporadically during the active reproductive season (February to

92 November) over a period of 16 years on 1.5 ± 0.9 occasions each (mean $\pm$ SD; range: $1 - 5$;

93   Table S2). The sites in the Lerma and Tula drainages were sampled from 1980-1986 and 1991-

94   1995. We obtained 194 regurgitations from 22 sites in Jalisco, Michoacán, México, Hidalgo, and

95   Queretaro. The records obtained for these two drainages are partially reported by Lozoya (1988,

96   19% of the total regurgitations), a reference inaccessible to most readers.

97   In the Nazas drainage we obtained 68 regurgitations. The Nazas population inhabits an

98   isolated 0.36 ha spring-fed cattle pond in the Chihuahuan Desert with a rainy season from June

99   through October. The records were obtained during 27 2-4 day visits, bimonthly during April to

100   November 1981, and monthly during February through December 1982, and February through

101   November 1983. Drummond & Macías Garcia (1989) previously reported 13% of these records.

102   Snakes were captured on the first two days of each visit and released on the second day to

103   prevent repeat sampling during the same visit. We counted and classified prey items as fish,

104   leeches, frogs, tadpoles, and earthworms.

105   **Analysis**

106   We classified snakes as newborns (< 20.5 cm SVL), juveniles (20.5–39.5 cm) or adults (> 39.5

107   cm; Manjarrez, 1998), based on birth sizes and minimum sizes of gravid females. Percentages of

108   regurgitations containing each prey taxon were normalized by arcsine transformation (Zar,

109   1984). We used MANCOVA (with snake length as a covariate) to explore variation in the mass

110   of prey consumed by prey taxa and by the sex of each snake. We included complementary

111   analyses of dietary variation in relation to snake size whenever these could contribute to

112   understanding variation in diet. For analyses of prey mass we excluded taxa represented by fewer

113   than five prey items. Prey mass and snake length were natural log transformed prior to

114   calculating correlations because of the lack of homoscedasticity and skewed distributions.

115   To avoid making Type I or II errors when many Chi square (X^2) tests are performed, we

116   used a Multiple Correspondence Analysis (MCA) to associate prey items consumed more

117   frequently (earthworm, tadpole, fish, frog and leech, considered as not continuous data) by the

118   combination of two categorical variables, the sex of snake (male-female) and snake size

119   (newborns, juveniles, and adults). The analysis is a modification of X^2 used to analyze

120   contingency tables and creates a Cartesian diagram based on the association between more than

121   three categorical variables (Legendre & Legendre, 2003). The diagram display simultaneously

122   the relative position (canonical position) of studied variables categories (Gotelli, 2001). The

123   nearest canonical positions of different variables represent a high association, while distant

124   categories show lower association. The degrees of freedom (*df*) and probability (*P*) for MCA

125   have no statistical relevance, because both were used only in two-way table, therefore, we do not

126   report these values. However, similar to X^2 test, the MCA estimate the differences between

127   observed and expected values, which allow estimate contribution of each variable to X^2 test

128   value. The analyses generates a coordinate system of reference that account variations of all

129   variables (dimensions), where we reported the first two dimensions, which represents the higher

130   variations. Finally, the center of graph (coordinate 0, 0) was the average of all variables,

131   therefore categories nearest to center of graph show a lower association to rest of categories.

132   Additionally, we performed a Cluster analysis to identify groups of categories of age and

133   sex of snakes with similar consumption of prey, we used the Morisita index of similarity between

134   frequencies of prey consumed, and the Ward's Method of amalgamation (Rencher, 2002).

135   Ward's Method attempts to minimize the Sum of Squares (SS) of any two hypothetical clusters

136   that can be formed at each step (Legendre & Legendre, 2003), and it is considered as very

137   efficient method, due reduce cluster long chains produced by other joining amalgamation

138   methods as nearest neighbor or UPGMA. The number of groups retained were determined by

139   graph of amalgamation schedule. The graph shows a line graph of the linkage distances at

140   successive clustering steps, the optimal cut-off to deciding how many clusters to retain is when

141   the linkage distance line forms a plateau. Multiple Correspondence and Cluster Analyses are

142   complementary, the MCA identify associations among categories of different categorical

143   variables, but cannot determine differences; while cluster create groups of different elements, but

144   we cannot know why they are different.

145   **Results**

146   **Prey items**

147   We obtained identifiable stomach contents from 262 (38%) of 690 *T. eques* collected. Thirteen

148   regurgitations (5.7% of total) included more than one prey species, and hence contributed more

149   than one data point for some snakes. In order of percentage of prey items identified we found

150   42.4% (n =111 regurgitations) consumed fish, 23.7% (n = 62) leeches, 10.6% (n = 28)

151   earthworms, 10.2% (n = 27) frogs, 9.8% (n = 25) tadpoles, and 2.3% (n = 6) axolotls

152   (*Ambystoma sp*.). Lizard, slug, and mouse were recovered from only 1 stomach each.

153   Our Multiple Correspondence Analysis (X^2 = 2,410.1) shows that prey type variable

154   contributes with 71.6% of X^2 test value (X^2 = 1,725.9), while snake size with 19.5% (X^2 = 468.6)

155   and sex with 8.9% (X^2 = 215.6). Canonical position of adult snakes was closer to tadpoles, frogs,

156   and axolots, therefore adults tend to feed more frequently these prey types than juveniles and

157   newborns snakes (Fig. 1). Juveniles consumed more likely earthworms, while newborns

158   principally leeches. Canonical position of male and female snakes showed a lower variation on

159   the prey type consumed (Fig. 1). Cluster analysis indicated that the three size classes differ in

160   prey type consumed (Fig. 2), where adult snakes were closer to juveniles, and both distant to

161 newborn. Prey types consumed by female and male snakes were similar, due linkage distance

162 nodes of males and females of the same size classes was lower than cutoff value. This grouping

163 of snakes suggests a scheme of ontogenetic change in the taxon of prey, with lower relevance of

164 the grouping by sex (Fig. 2).

165 **Variation with snake length**

166 Snakes of different sizes ate a changing diversity of prey types. The general pattern was a

167 reduction of number of prey item with size of snake (Fig. 3). Snakes < 65 cm SVL ate all prey

168 types of all sizes, including invertebrates (leeches and earthworms) and vertebrates (tadpoles,

169 fish, and frogs). Vertebrate prey were taken by only the largest snakes (> 60 cm SVL). At 15 cm

170 SVL, snakes eat leeches as one of two major prey items, but at 55 cm SVL consumption of

171 leeches decreases drastically and disappears completely in larger snakes > 65cm SVL (Fig. 3).

172 The consumption of fish and tadpoles increases when snake body size increases. However, the

173 longer snakes > 75 cm SVL consume only fish and tadpoles while excluding all other prey,

174 possibly because longer snakes were a very small part of the entire sample ($n = 7$ stomach

175 contents).

176 Snake length was correlated positively with mass of ingested prey ($r = 0.42$, $F_{1, 326} =$

177 71.52, $P < 0.001$; Fig. 4). Large snakes consume large prey and continue to consume smaller

178 prey. The same relationship was presented for leeches ($r = 0.42$, $F_{1,136} = 29.85$, $P < 0.00$; Fig. 5)

179 and fish ($r = 0.43$, $F_{1,88} = 20.30$, $P < 0.001$; Fig. 5), but not correlated with earthworm ($r = 0.14$,

180 $F_{1,32} = 18.32$, $P = 0.806$; Fig. 5) and tadpole mass ($r = 0.2$, $F_{1,25} = 2.36$, $P = 0.136$; Fig. 5).

181 **Variation with snake sex**

182   Mean body lengths of captured snakes did not differ between sexes of newborns (Student t_{20} =

183   0.08, $P = 0.94$), juveniles (Student $t_{94} = 0.95$, $P = 0.34$), or adults (Student $t_{131} = 0.13$, $P = 0.90$);

184   thus male and female snakes were similar in size.

185   No differences were found between the diets of male and female snakes. Pooling all sizes

186   of snake, males ($n = 124$) and females ($n = 121$) ate similar proportions of the five main prey

187   taxa ($X^2 = 3.82$, $P = 0.43$), both sexes eating mainly fishes, frogs, leeches, and earthworms, and

188   in similar proportions. Males ate two times more tadpoles (0.13) than females (0.06).

189   Males and females did not differ in the mass of leeches, earthworms, fishes, frogs and

190   tadpoles that they ate (MANCOVA $F_{1,\ 193} = 0.79$, $P = 0.37$), and males and females that ate each

191   prey taxon were similar in length ($F_{1,\ 235} = 0.91$, $P = 0.34$).

192   **Discussion**

193   In this study, we provide a broad description of the diet of the Mexican Garter snake *T. eques* on

194   the Mexican Plateau. The results indicate 69% of total regurgitations contain two major prey:

195   leeches and fish, while the other three main prey are ingested in similar percentages

196   (earthworms, 10.6%; frogs, 10.2%; tadpoles, 9.8%). The diet of *T. eques* included amphibious

197   prey (frogs), terrestrial prey (earthworms) and aquatic prey (leeches, fish and tadpoles), and

198   occasionally other prey such as axolotls, slugs, lizards, and mice. The main prey include three

199   vertebrates (65%) and two invertebrates (35%).

200   The studies that have analyzed the diet of *T. eques* in Mexico included four local

201   descriptions and in each study *T. eques* is locally specialized in feeding on only 2-3 prey taxa

202   (Table 1) (Drummond & Macías Garcia, 1989). This suggests a pattern of spatial variation in the

203   diet of *T. eques*, presumably by the local availability of prey, for example the temporal variation

204   of prey, which has not yet been explored for *T. eques* (Gregory & Nelson, 1991; Tuttle &

205   Gregory, 2009).

206   The diet of *T. eques* can also exhibit ontogenetic variations associated with individual

207   size, changing from terrestrial to aquatic prey as snake size increases (Macías Garcia &

208   Drummond, 1988; Drummond & Macías Garcia, 1989). Ontogenetic change by prey taxa in

209   gartersnakes, could be attributed to proximate mechanisms such as morphological constraints

210   that determine the size of ingested prey (Shine, 1991; Arnold, 1993), the availability of potential

211   prey (Krebs, 2009), energy or nutritional needs (Britt, Hicks, & Bennett, 2006), habituation and

212   learning (Halloy & Burghardt, 1990; Ford & Burghardt, 1993) or genetically programmed

213   preferences (Arnold, 1977; Arnold, 1981; Britt, Hicks, & Bennett, 2006). In Tecocomulco,

214   Hidalgo, the differential distribution of large and small snakes was interpreted as a possible

215   cause of differences in diet of *T. eques* with differences in the pattern of foraging, so that the

216   snake can be an effective predator in the air-water interface; preying on aquatic prey when they

217   are particularly vulnerable and terrestrial prey being added to the diet only opportunistically

218   (Drummond & Macías García, 1989).

219   In our study, the ontogenetic variation in diet of *T. eques* was also found in the

220   relationship between snake size and prey mass. The ingested prey size gradually increases with

221   snake size and large snakes continued eating small prey. This relationship could be interpreted as

222   an ontogenetic telescope (Arnold, 1993), as previously reported for *T. eques* in a Zacatecas

223   population with *Rana berlandieri* (Drummond & Macías García, 1989).

224   The absence of ontogenetic variation in the regurgitated samples of tadpoles and

225   earthworms in *T. eques*, is common because in a previous study the annelids were ingested by *T.*

226   *eques* regardless of snake body size (Macías Garcia & Drummond (1988). The proximate

227 explanation for this phenomenon is the high availability of these prey during the annual active

228 period of the snake or by a stable ontogenetic preference for invertebrates (Ford & Burghardt,

229 1993). The proximate and functional diet determinants of intraspecific variation in Mexican

230 garter snakes could be explored by local and temporal variation in prey availability and

231 proportions of snake size classes collected. Intraspecific differences in *Thamnophis* diet have

232 been described for different populations, seasons, years, size classes, and sexes (Rossman, Ford,

233 & Siegel, 1996). For example, in some species of *Thamnophis* have been described geographic

234 dietary differences (e.g., *T. elegans*, *T. radix*, and *T. sirtalis*; Kephart, 1982; Kephart & Arnold,

235 1982; Tuttle & Gregory, 2009) and explained by spatial variation in prey availability, whereas

236 proportions of stomachs containing particular taxa can vary temporally as prey populations

237 fluctuate (Kephart and Arnold, 1982; Seigel, 1996).

238   The intersexual variation in food habits has been associated with sexual differences in

239 body size (Shine et al., 1998). *Thamnophis eques* has been reported as sexually size dimorphic,

240 with males smaller than females in SVL (Manjarrez, 1998); however in this study, the average

241 size of male and female *T. eques* were similar and there were no sexual differences in diet,

242 except that males ate two times more tadpoles than females. This sexual difference in diet can

243 probably be attributed to real diet preference because females and males that ate each prey taxon

244 were similar in length. Generally, large samples revealed no differences between male and

245 female snakes in variety of prey taxa, proportions of different prey taxa and taxon specific prey

246 weight (Shine, 1993), and the males and females that ate each taxon were similar in size. Overall,

247 male and female Mexican Garter Snakes differ in size (Manjarrez, Contreras-Garduño, &

248 Janczur, 2014), microhabitat use (Venegas-Barrera, 2001), seasonal foraging pattern (Drummond

249 & Macías Garcia, 1989), and diet (Macías Garcia & Drummond, 1988; Manjarrez, Contreras-

250   Garduño, & Janczur, 2014). As was found, males and females of this species do not differ in the

251   body size of prey and type of prey consumed. The possible small differences in diet and

252   microhabitat can be expose by larger sample sizes. Prey size and energetic demands may

253   determine developmental transitions to different prey sizes or taxa, whereas sex, in this snake

254   lacking sexual size dimorphism, has little or no influence on diet. However, sexual dimorphism

255   in head dimensions, and eaten prey shape have seldom been searched and it will be essential to

256   measure prey and head traits for *T. eques* to evaluate the function of resource competition

257   between sexes.

258   **Conclusions**

259   In this study, we provide the first broad description of the diet of the Mexican Garter snake on

260   the Mexican Plateau. The two major prey were leeches and fish. The diet of *T. eques* included

261   amphibious, terrestrial and aquatic prey with ontogenetic variations associated with individual

262   size, changing from terrestrial to aquatic prey as snake size increases. The ontogenetic variation

263   in diet of *T. eques* was also found in the relationship between snake size and prey mass. The

264   average size of male and female *T. eques* were similar and there were no sexual differences in

265   diet. The proximate and functional diet determinants of intraspecific variation in Mexican garter

266   snakes could be explored by local and temporal variation in prey availability and proportions of

267   snake size classes collected.

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353   disponibilidad de alimento en la distribución y temperatura corporal de la culebra de agua

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356 **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 (*Eisenia foetida* and *Eisenia* sp.)
Leech	39	---	8.7	---	23.7 (*Erpobdella punctata* and *Mooreobdella* sp.)
Other	1.0	5.5	---	---	0.4
Vertebrate prey					
Fish	11	---	29.0	---	42.4 (*Girardinichthys multiradiatus, Carassius auratus*)
Frog	5	28	10.1	69.0	10.2 (*Rana berlandieri* and *Rana sp.*)
Tadpole	1.5	33	22.2	23.4	9.8 (*R. berlandieri, Rana sp*)
Other	4.5	11.0	9.4	4.7	3.2

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358 [1]Macías García & Drummond, 1988; [2]Manjarrez, 1998; [3]Manjarrez, Contreras-Garduño &

359 Janczur; [4]Drummond & Macías García, 1989.

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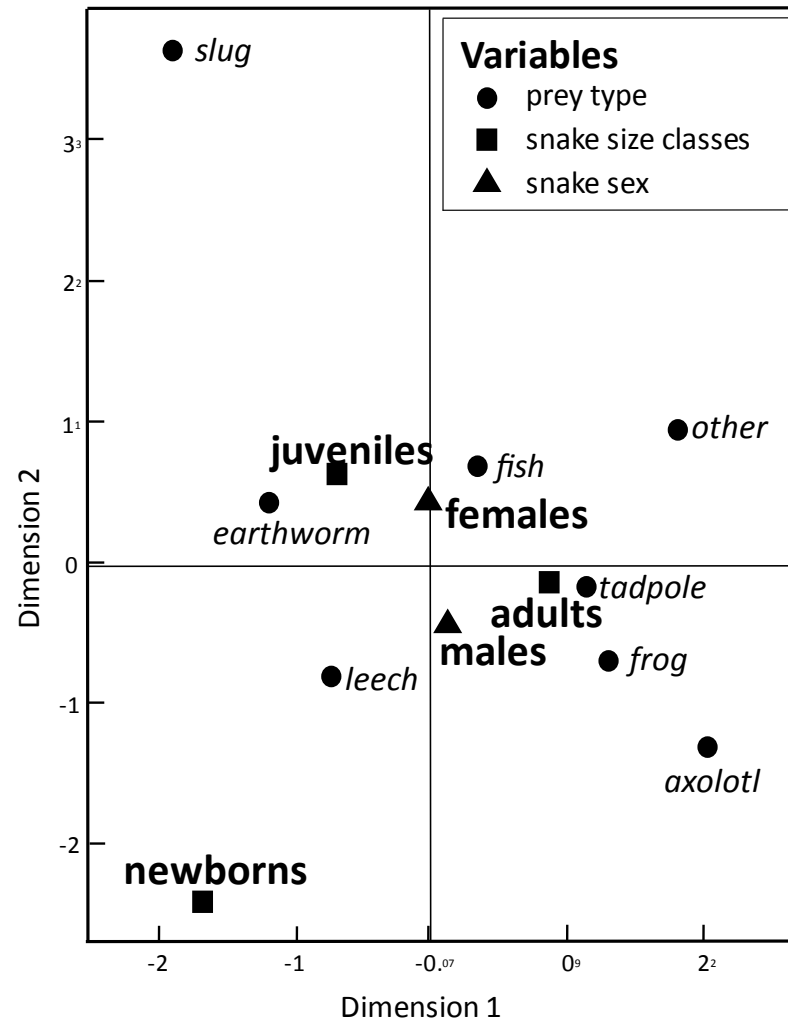
379   Fig. 1. Dimension variables obtained from a Multiple Correspondence Analysis to associate prey

380   items consumed by snake *T. eques* in the combination of snake sex (male-female) and snake size

381   classes (newborns, juveniles, and adults).

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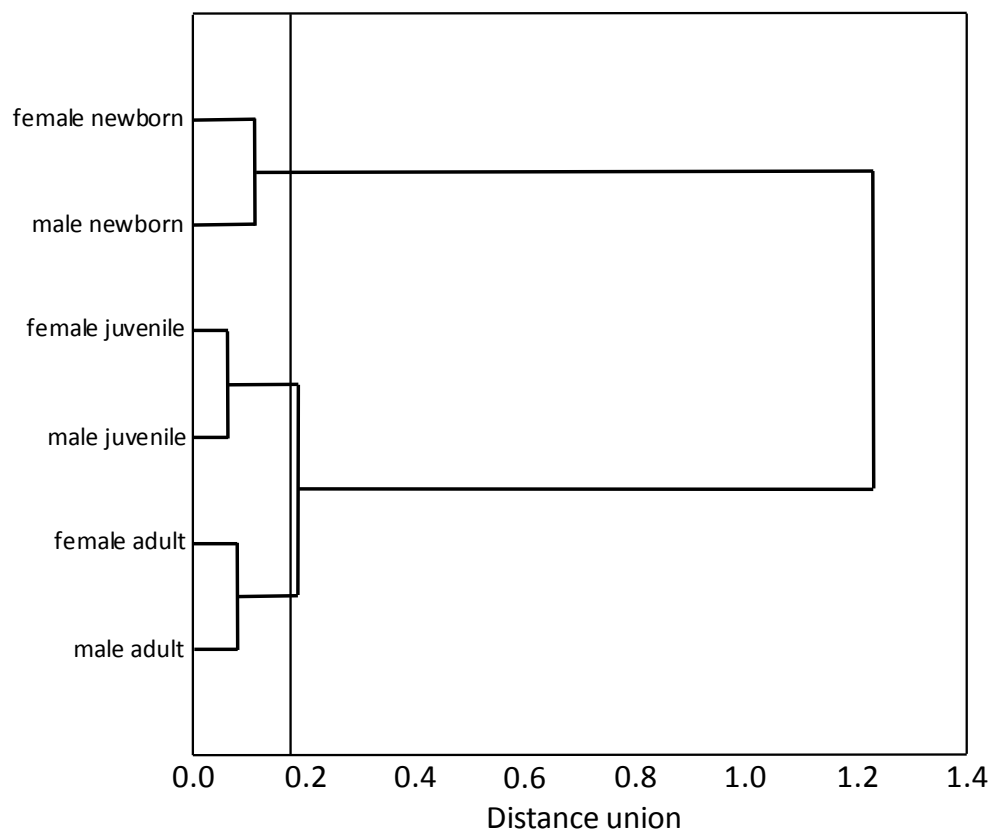
397   Fig. 2. Hierarchical tree produced agglomeration of size classes (newborns, juveniles and adults)

398   and sex (female and male) of *T. eques* snakes in function of prey type consumed. The

399   amalgamation schedule (Ward's Method) defined in 0.8 the cutoff value for the tree diagram.

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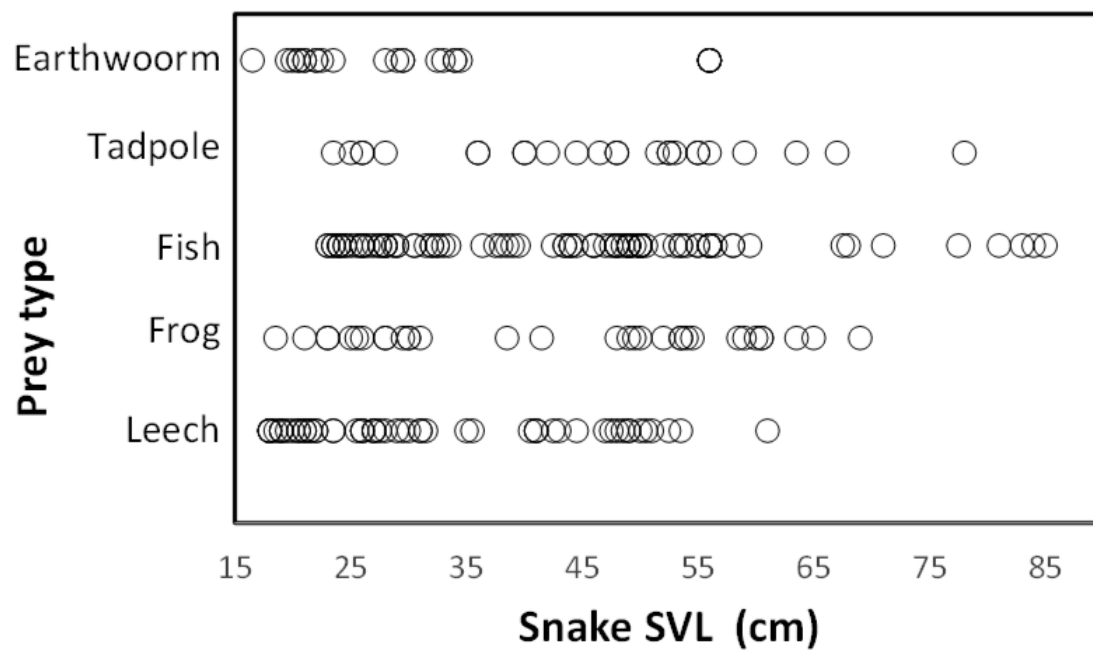
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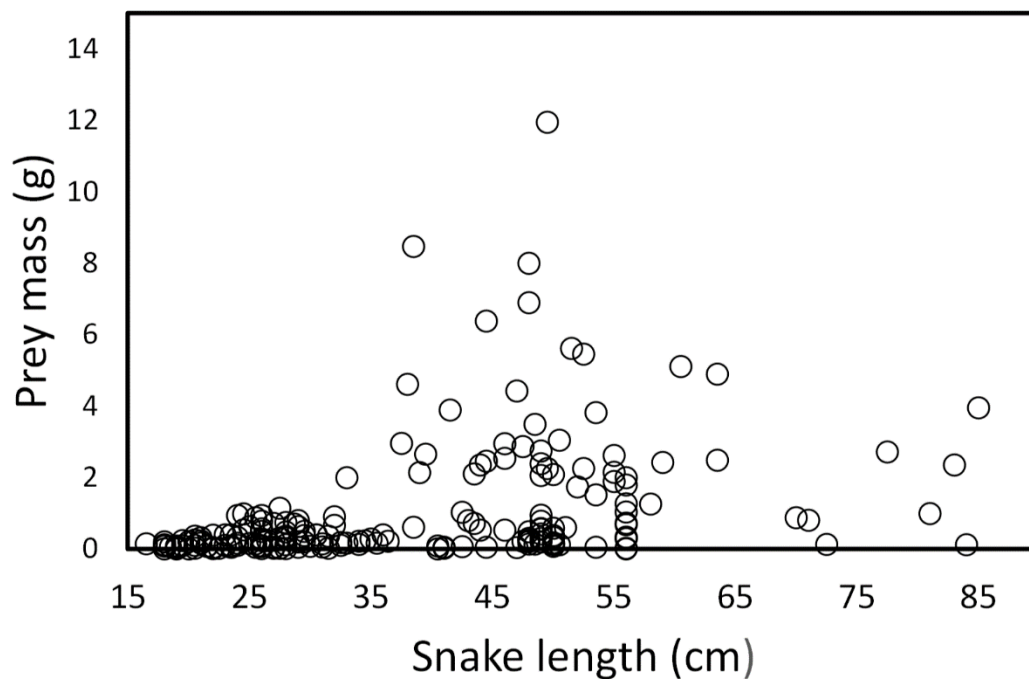
403   Fig. 3. Relationship between prey type and snake size (SVL, cm) of *T. eques* in México. Each

404   circle represents an individual snake with a type of prey item (262 regurgitations).

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406   Fig. 4. Prey mass as a function of snake length (SVL, cm) of (*T. eques*) in México. ($r = 0.42$, F

407    $_{1, 326} = 71.52$, $P < 0.001$). Each dot represents an individual prey item. The many circles on the

408   zero line of prey mass are because the low weights of leeches and earthworms.

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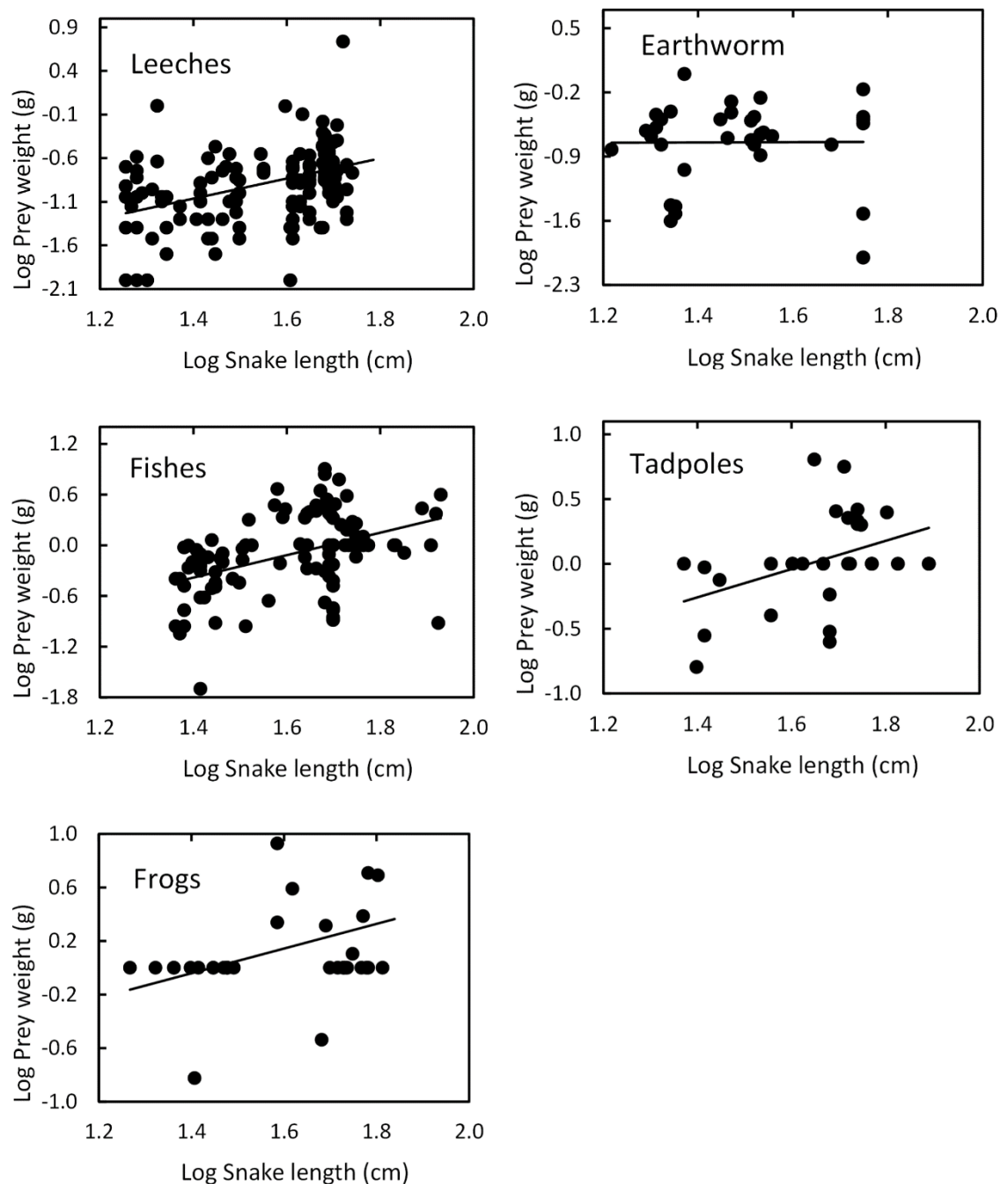
Fig. 5. Relation between prey mass and snake length of *T. eques*. Leeches ($r = 0.42$, $P < 0.00$),

fish ($r = 0.43$, $P < 0.001$), earthworm ($r = 0.14$, $P = 0.806$), tadpole ($r = 0.2$, $P = 0.136$), frogs (r

$= 0.597$, P < 0.001).