

Feeding ecology of two populations of *Sceloporus minor* (Squamata: Phrynosomatidae) inhabiting contrasting environments in central Mexico

AARON GARCÍA-ROSALES¹, RACIEL CRUZ-ELIZALDE¹,
AURELIO RAMÍREZ-BAUTISTA¹ & VICENTE MATA-SILVA²

¹Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Km 4.5 carretera Pachuca-Tulancingo, 42184, Mineral de La Reforma, Hidalgo, México

²Department of Biological Sciences, The University of Texas at El Paso, El Paso, Texas, USA
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Corresponding author: AURELIO RAMÍREZ-BAUTISTA, e-mail: ramibautistaa@gmail.com

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Abstract. Food resources have a significant effect on many characteristics of living organisms, such as growth, reproduction, and tissue repair, among others. These resources, however, can vary among localities and seasons of the year. In this study, we examined the feeding ecology of the lizard *Sceloporus minor* from two localities (La Manzana and El Enzuelado, Hidalgo) with contrasting environments in central Mexico. The analysis of the stomach contents revealed an omnivorous diet, composed by 14 prey categories. Comparing the two study sites, lizards from La Manzana consumed 13 prey categories, and lizards from El Enzuelado consumed 11 categories of prey. In both localities, adult coleopterans, hymenopterans, orthopterans, and plant matter showed the highest values of food importance. By sex, males and females from La Manzana consumed 11 prey categories each, whereas in El Enzuelado males consumed eight prey categories and females consumed 10 prey categories. By season, lizards consumed a higher number of prey categories in the dry season than in the wet season for both La Manzana and El Enzuelado. Niche breadth values were low by population, sex, and season; however, the overlapping values were high. The volume of stomach contents was not correlated with male and female SVL in either population. However, the volume of stomach content in females varied significantly through the three stages of the reproductive cycle, vitellogenesis, embryonic development, and post-reproductive period. Results showed that the diet of both populations of *S. minor* is omnivore, consuming mainly insects and plant material. Low diet amplitude and a high overlap between populations, sexes, and seasons of the year, indicated that these populations have a high preference for specific prey items. This study expands the knowledge of the feeding ecology of this species and, consequently, of their populations. Additionally, it provides specific information regarding the effect of food on female reproductive traits throughout the year.

Key words. Food resources, lizards, niche breadth, omnivorous diet, diet overlap, populations.

Introduction

Different populations of single species can display variation in their ecological, morphological, and behavioral attributes (MICHAUD & ECHTERNACHT 1995, HERNÁNDEZ-SALINAS et al. 2014). Variation of these characteristics are due to specific environmental conditions of the habitats where those populations are found, such as different intervals of temperature, humidity, or variation of the latter during the periods of drought and rain (HORVÁTHOVÁ et al. 2013, DU et al. 2014). Likewise, this variation can be due also to ecological factors, such as microhabitat availability, feeding habits, predation intensity, and population density (DUNHAM 1982, BENABIB 1994).

Food resources are an indispensable component for the maintenance and development of life history traits, such as growth rate, survival, reproduction, and tissue repair in lizard species (VITT & CALDWELL 2009); therefore, quality and quantity of food consumed by lizards will have an influence on these characteristics (SIMON 1975, BALLINGER & CONGDON 1980). The food spectrum used by lizards is determined by different factors, such as quality and quantity of the food in the environment and foraging mode (MC LAUGHLIN 1989, PERRY 2007). Historically, two foraging modes have been suggested, “active foraging,” where lizards actively search for their food (MILES et al. 2007, PERRY 2007), and “sit and wait” foraging, displayed when individuals perch on a site and subdue and eat any

prey that passes nearby (SCHOENER 1971, HUEY & PIANKA 1981, MCLAUGHLIN 1989, MILES et al. 2007). These foraging modes are generally maintained among species of the families Iguanidae, Phrynosomatidae, Agamidae, and Teiidae (MILES et al. 2007). Some species within these families, however, show another strategy of foraging, and are regarded as sit and wait or active foragers (COOPER & WHITING 2000, REILLY et al. 2007). In this sense, in general, foraging mode, including prey preference in diverse lizard groups is influenced by phylogeny rather than environmental and ecological factors (VITT & PIANKA 2005, MILES et al. 2007).

In addition to foraging mode, prey diversity of lizards is determined by the availability of food resources in the environment. Prey availability is determined by seasonal environmental conditions, such as precipitation and intra- and interspecific competition (HUEY & PIANKA 1981, NGO et al. 2015). Therefore, diet is an aspect that can vary both within and among populations in lizard species (REILLY et al. 2007, HAWLENA & PÉREZ-MELLADO 2009, WASIOLKA et al. 2009). For example, variation has been reported in diet composition of lizard populations of islands and mainland environments (DUTRA et al. 2011, HERNÁNDEZ-SALINAS et al. 2016), and among populations inhabiting different mainland environments (PARKER & PIANKA 1975, NGO et al. 2015). Therefore, diet among populations of a single species is determined by the type, size, and abundance of prey (VITT & COLLI 1994, HERREL et al. 2001). On the other hand, within a population, the diet of individuals can be limited by morphological and/or physiological factors. For example, morphological structures, such as SVL, head size, and structure of the jaw, limit the quantity and size of the prey that an individual is able to eat (ALDAPE-LÓPEZ et al. 2009). The amount of food consumed by gravid females is lower than that consumed by non-gravid females. In the former, the size of the body cavity (abdomen) is an important restriction to continue feeding as they carry the embryos (MÉNDEZ-DE LA CRUZ et al. 1992). Additionally, prey intake of gravid female lizards is limited physiologically because of a lack of appetite resulting from high progesterone production (CREWS & GARRICK 1980).

PYKE et al. (1977) demonstrated that the diet of an organism is optimal when it maximizes the energetic gains from the consumption of prey available in the environment; thus, lizards will choose prey types with greater energetic value (BARBAULT & MAURY 1981). Seasonal environmental conditions, such as precipitation and temperature, regulate prey diversity and abundance (BALLINGER 1977, BALLINGER & BALLINGER 1979), causing lizard diets to vary according to seasonal prey availability in the environment (DURTSCHKE 1995).

The genus *Sceloporus* (Phrynosomatidae) is currently represented by around 106 species (UETZ et al. 2018), which show a high variation in feeding behaviors (PERRY 2007), but most species have been classified as “sit and wait” foragers (COOPER 1995, REILLY et al. 2007). Based on their diet, the majority of species are regarded as carnivores (GADSDEN-ESPARZA & PALACIOS-ORONA 1995, LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010), with a few

species reported as being omnivorous (SMITH & MILSTEAD 1971, BALLINGER 1981, MÉNDEZ-DE LA CRUZ et al. 1992).

Sceloporus minor (COPE, 1885) is a Mexican endemic lizard restricted to the central and northern regions of the country (WIENS et al. 1999). Previous studies on populations of *S. minor* have shown differences in synchrony of reproductive cycles between sexes and among populations (RAMÍREZ-BAUTISTA et al. 2008, 2014), colour pattern (STEPHENSON & RAMÍREZ-BAUTISTA 2012, GARCÍA-ROSALES et al. 2017), and morphology (STEPHENSON 2010, RAMÍREZ-BAUTISTA et al. 2008, 2014, GARCÍA-ROSALES et al. 2017). Despite this information, currently there is no information regarding use of food resources between sexes and/or among populations of the species. Consequently, this study provides novel information on annual and seasonal diet composition among and within populations of *S. minor*, which is essential to understanding the ecology of this species.

Our main goal was to analyze the diet composition of two populations of *S. minor* from central Mexico that inhabit differing environments. Specifically, our aims were (i) to analyze the diets of each sex, between seasons (dry and wet), and populations (La Manzana and El Enzuelado), (ii) to determine the dietary niche breadth and overlap between sexes, populations, and seasons, (iii) to analyze the relationship between SVL and mandibular dimensions with stomach volume and prey size, respectively, and (iv) to evaluate the volume of stomach contents of females during pre-reproductive, reproductive, and post-reproductive period. We hypothesized that, outside of the already known variation in reproductive and morphological characteristics among populations, as a result of environmental conditions (RAMÍREZ-BAUTISTA et al. 2008, 2014, GARCÍA-ROSALES et al. 2017), we would also expect to find dietary variation between sexes, populations, and seasons.

Material and methods

Study area

This study was carried out with individuals of two populations located in differing environments, separated by a straight line distance of 65 km. The two localities are La Manzana (20°52'N, 99°13'W) and El Enzuelado (20°35'N, 98°37'W), and belong to the municipalities of Zimapan and San Agustín Metzquitlán, respectively, in the state of Hidalgo, Mexico. La Manzana is located at an elevation of 2,500 m, with vegetation composed of pine-oak forest (RZEDOWSKI 1978, STEPHENSON 2010), a mean annual temperature of 14°C, and precipitation of 565 mm. El Enzuelado is located at an elevation of 1,955 m, with vegetation represented by xerophilous scrub (RZEDOWSKI 1978), a mean annual temperature of 17.5°C, and precipitation of 496 mm (PAVÓN & MEZA-SÁNCHEZ 2009). In both localities, the dry season extends from October to May, whereas the wet season is from June to September (PAVÓN & MEZA-SÁNCHEZ 2009).

Data collection

The analyzed specimens are housed at the Collection of Amphibians and Reptiles of the Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo (Appendix 1), which were previously used in reproduction studies (see RAMÍREZ-BAUTISTA et al. 2014). These organisms were collected monthly from April 2008 to March 2009 in both localities. Lizards were humanely euthanized with a dose of anesthesia, later fixed with 10% formalin and then preserved in 70% ethanol (see RAMÍREZ-BAUTISTA et al. 2014). For all individuals, we recorded measurements of morphological characteristics such as snout–vent length (SVL: measured to the nearest ± 0.01 mm), jaw length (JL: ± 0.01 mm), and jaw width (JW: ± 0.01 mm) using a digital caliper; also, we recorded body mass of specimens using a Pesola spring scale (0.01 g).

Laboratory work and data analysis

The stomachs of the analyzed organisms were removed and weighed using an analytical balance (precision 0.0001 g). The stomach contents were removed and placed in Petri dishes where their dimensions of length, width, and height were recorded using a digital caliper (LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010). Each prey volume (mm^3) was obtained using the formula for the volume of an ellipsoid (DURÉ et al. 2009): $V = 4/3\pi (\text{length}/2) (\text{width}/2)^2$. Different types of prey were identified at the taxonomic ordinal level (TRIPLEHORN & JOHNSON 2005). Holometabolous insects (with complete metamorphosis) were classified into larval and adult stages, and each was considered as independent categories (ALDAPE-LÓPEZ et al. 2009, GADSDEN et al. 2011). Plant material also was considered a diet category in the diet analysis (FERIA-ORTIZ et al. 2001).

We calculated the Importance Value (ViI; ACOSTA 1982) of each prey item consumed by males and females from both populations utilizing the formula: $ViI = P_i + A_i + C_i$; where ViI = importance value of the taxon i , $P_i = P_i/\sum P_i$ (P_i = total weight of the taxon i ; $\sum P_i$ = total weight of all taxa), $A_i = A_i/\sum A_i$ (A_i = number of prey that belong to taxon i ; $\sum A_i$ = total number of prey), $C_i = C_i/\sum C_i$ (C_i = number of stomachs that contained taxon i ; $\sum C_i$ = total number of stomachs); ViI was calculated by population, sex, and season (dry and wet).

We calculated niche breadth using the LEVIN's standardized niche index (HURLBERT 1978), with the formula $B_i = ((1/\sum p_i^2) - 1)/(N - 1)$, where: p_i is the proportion (number of individuals) each prey category with respect to the total number of preys found in each group (sex or population), and N is the number of prey category in the diet of individuals. Diet overlap was assessed using PIANKA's O_{jk} index (PIANKA 1973), with the formula $O_{jk} = \sum_{i=1}^N P_{ij} P_{ik} / \sqrt{\sum_{i=1}^N P_{ij}^2 \sum_{i=1}^N P_{ik}^2}$, where P_{ij} and P_{ik} are the proportions of the i resource used by group (sex or population) j and k , respectively. Both

breadth and overlap were calculated between sexes and seasons, dry (October–May) and wet (June–September) for each population and between populations. Both indices were performed by using the Ecological Methodology software, version 6.1.1 (KREBS 1999).

We used a MANOVA test to assess differences in volume of stomach contents and prey abundance (number of prey items in the stomach) consumed between sexes and seasons (dry and wet) within and between populations. For this analysis, the response variables (volume and prey abundance) were orthogonalized with the formula $Z = (\bar{x} - \mu)/\sigma$, thus standardizing the data. Additionally, we used a Factorial ANOVA test to estimate differences of stomach content volume of females from each population by considering three stages of the reproductive cycle, vitellogenesis (July–November), embryonic development (November–April), and post-reproductive period (April–June) for both populations (RAMÍREZ-BAUTISTA et al. 2014). Finally, we evaluated with Pearson correlations the relationships between SVL of the lizards with the volume of stomach contents (the total volume considering all preys in the stomach) and number of total prey, as well as JL and JW with complete prey body volume (total body volume of the prey was included only when these were found complete), all the variables used in the Factorial ANOVA and in the correlation were transformed to \log_{10} to meet the assumptions of normality (ZAR 1999).

Results

Diet composition by species, populations and sexes

A total of 145 lizards was analyzed, 71 from La Manzana (39 females and 32 males) and 74 from El Enzuelado (37 females and 37 males). One specimen from El Enzuelado had an empty stomach, and, therefore, it was not considered in the analysis. From the 144 specimens with stomach contents, we identified a total of 1,463 prey items belonging to 14 different prey categories (Table 1). Of the total prey number recorded, 929 were consumed by lizards from La Manzana and 534 from El Enzuelado. Based on prey weight, it was revealed that the diet of the lizards from both populations is composed mainly of insects (84.4%), followed by plant material (17.0%), arachnids (0.06%), and gastropods (0.002%; Table 1).

The data on diet of lizards from La Manzana showed 13 prey categories (Table 1), represented by insect groups (84.61%), arachnids, and plant material (7.69%, each; Tables 1, 2). The categories of Hymenoptera, adult Coleoptera (A), plant material, and Hemiptera showed the highest values of food importance (ViI), as well as the greater number of consumed prey in the population (Table 1), and throughout the entire sampling period (Fig. 1a). When analyzing the diet by sex, we found that both sexes used 11 prey categories, but differed with respect to consumed prey type (Table 2). In both sexes, the consumed diet categories of Hymenoptera, Coleoptera and plant material showed the highest values of ViI, which were 1.368, 0.768,

Table 1. Dietary composition of *Sceloporus minor* from La Manzana and El Enzuelado. N = number of items, %N = percentage of N, F = frequency of occurrence, %F =percentage of F, W = weight (g) of prey category, %W = percentage of W, and ViI = value of feeding importance. A = adult, L = larvae.

| Prey categories | La Manzana | | | | | | | El Enzuelado | | | | | | |
|-----------------|------------|--------|-----|--------|-------|--------|-------|--------------|--------|-----|--------|--------|--------|-------|
| | N | %N | F | %F | W | %W | ViI | N | %N | F | %F | W | %W | ViI |
| Araneae | 2 | 0.215 | 2 | 1.015 | 0.008 | 0.092 | 0.013 | 6 | 1.124 | 6 | 2.927 | 0.115 | 0.695 | 0.047 |
| Coleoptera (A) | 172 | 18.515 | 50 | 25.381 | 2.198 | 27.092 | 0.710 | 219 | 41.011 | 58 | 28.293 | 5.972 | 36.111 | 1.054 |
| Coleoptera (L) | 2 | 0.215 | 1 | 0.508 | 0.037 | 0.459 | 0.012 | 2 | 0.375 | 2 | 0.976 | 0.313 | 1.890 | 0.032 |
| Dermaptera | 1 | 0.108 | 1 | 0.508 | 0.003 | 0.035 | 0.006 | 1 | 0.187 | 1 | 0.488 | 0.003 | 0.021 | 0.007 |
| Diptera | 2 | 0.215 | 1 | 0.508 | 0.001 | 0.006 | 0.007 | | | | | | | |
| Hemiptera | 25 | 2.691 | 17 | 8.629 | 0.367 | 4.518 | 0.158 | 31 | 5.805 | 18 | 8.780 | 0.409 | 2.476 | 0.171 |
| Homoptera | 8 | 0.861 | 4 | 2.030 | 0.005 | 0.063 | 0.030 | 1 | 0.187 | 1 | 0.488 | 0.000 | 0.002 | 0.007 |
| Hymenoptera | 657 | 70.721 | 69 | 35.025 | 3.814 | 47.019 | 1.528 | 171 | 32.022 | 35 | 17.073 | 1.069 | 6.462 | 0.556 |
| Lepidoptera (A) | 4 | 0.431 | 6 | 3.046 | 0.232 | 2.864 | 0.063 | | | | | | | |
| Lepidoptera (L) | 11 | 1.184 | 1 | 0.508 | 0.037 | 0.459 | 0.022 | 3 | 0.562 | 3 | 1.463 | 0.147 | 0.891 | 0.029 |
| Orthoptera | 5 | 0.538 | 5 | 2.538 | 0.121 | 1.487 | 0.046 | 71 | 13.296 | 52 | 25.366 | 6.268 | 37.905 | 0.766 |
| Phasmida | 1 | 0.108 | 1 | 0.508 | 0.105 | 1.294 | 0.019 | | | | | | | |
| Gasteropoda | | | | | | | | 1 | 0.187 | 1 | 0.488 | 0.003 | 0.021 | 0.007 |
| Plant Material | 39 | 4.198 | 39 | 19.797 | 1.185 | 14.613 | 0.386 | 28 | 5.243 | 28 | 13.659 | 2.237 | 13.527 | 0.324 |
| Totals | 929 | 100 | 197 | 100 | 8.112 | 100 | | 534 | 100 | 205 | 100 | 16.537 | 100 | |

Table 2. Dietary composition of *Sceloporus minor* from La Manzana and El Enzuelado by sex (male and female). N = number of items, F = frequency of occurrence, W = weight (g) of prey category, and ViI = value of feeding importance. A = adult, L = larvae.

| Prey Categories | La Manzana | | | | | | | | El Enzuelado | | | | | | | |
|-----------------|------------|----|--------|-------|--------|-----|--------|-------|--------------|-----|--------|-------|--------|-----|--------|-------|
| | Male | | | | Female | | | | Male | | | | Female | | | |
| | N | F | W | ViI | N | F | W | ViI | N | F | W | ViI | N | F | W | ViI |
| Araneae | | | | | 2 | 2 | 0.008 | 0.024 | 3 | 3 | 0.059 | 0.048 | 3 | 3 | 0.056 | 0.048 |
| Coleoptera (A) | 66 | 23 | 1.561 | 0.768 | 106 | 27 | 0.637 | 0.616 | 101 | 26 | 3.449 | 1.046 | 118 | 32 | 2.522 | 1.082 |
| Coleoptera (L) | 6 | 2 | 0.138 | 0.068 | 2 | 1 | 0.037 | 0.023 | 1 | 1 | <0.001 | 0.014 | 1 | 1 | 0.312 | 0.061 |
| Dermaptera | 1 | 1 | 0.003 | 0.014 | | | | | | | | | 1 | 1 | 0.026 | 0.017 |
| Diptera | 1 | 1 | <0.001 | 0.014 | 1 | 1 | <0.001 | 0.011 | | | | | | | | |
| Hemiptera | 13 | 7 | 0.304 | 0.177 | 12 | 10 | 0.062 | 0.131 | 21 | 14 | 0.316 | 0.258 | 10 | 4 | 0.093 | 0.086 |
| Homoptera | 7 | 3 | 0.005 | 0.053 | 1 | 1 | <0.001 | 0.011 | | | | | 1 | 1 | <0.001 | 0.013 |
| Hymenoptera | 235 | 31 | 1.725 | 1.368 | 422 | 39 | 2.089 | 1.694 | 45 | 17 | 0.210 | 0.384 | 126 | 18 | 0.859 | 0.714 |
| Lepidoptera (A) | 1 | 1 | 0.006 | 0.015 | 3 | 2 | 0.095 | 0.051 | | | | | | | | |
| Lepidoptera (L) | | | | | 5 | 4 | 0.095 | 0.073 | 3 | 3 | 0.147 | 0.057 | | | | |
| Orthoptera | 2 | 2 | 0.093 | 0.047 | 3 | 3 | 0.028 | 0.041 | 33 | 27 | 4.157 | 0.820 | 38 | 26 | 2.112 | 0.703 |
| Phasmida | 1 | 1 | 0.105 | 0.036 | | | | | | | | | | | | |
| Gasteropoda | | | | | | | | | | | | | 1 | 1 | 0.003 | 0.014 |
| Plant Material | 20 | 20 | 0.778 | 0.439 | 19 | 19 | 0.408 | 0.325 | 15 | 15 | 1.646 | 0.374 | 13 | 13 | 0.591 | 0.262 |
| Totals | 353 | 92 | 4.717 | | 576 | 109 | 3.458 | | 222 | 106 | 9.985 | 3 | 312 | 100 | 6.574 | 3 |

and 0.439 for males, and 1.694, 0.616, and 0.325 for females, respectively (Table 2).

We recorded 11 dietary categories for the lizard population of El Enzuelado (Table 1), with insects (72.7%) being the most important prey category, followed by arachnids, gastropods, and plant material, 9.09% each (Tables 1, 2). The dietary categories of Coleoptera (A), Orthoptera, Hymenoptera, and plant material showed the highest value

of ViI, as well as the greatest number of consumed prey (Table 1), and the same dietary categories also were the most important throughout the sampling period (Fig. 1b). When analyzing the diet by sex, males consumed eight prey categories, and females 10 (Table 2). With respect to males, the prey in the categories of Coleoptera (A), Orthoptera, Hymenoptera, and plant material showed the greater values of ViI, with 1.046, 0.820, 0.338, and 0.374, respec-

tively. Alternatively, females consumed prey from the same categories as males, but the importance of order varied; with the most important prey being Coleoptera (A; 1.082), Hymenoptera (0.714), Orthoptera (0.703), and plant material (0.262; Table 2).

Dietary composition by season

Dietary composition varied between seasons in each population. There was a higher prey number in the dry season (October–May) than in the wet season (June–September; Table 3 and Appendix 2) for both populations. A total of 13 diet categories were reported for La Manzana during the dry season, where Hymenoptera, Coleoptera (A), and plant material showed the highest values of ViI (Table 3 and Appendix 2). Only seven dietary categories were re-

corded during the wet season, with Hymenoptera, Coleoptera (A), and plant material showing the highest values of ViI (Table 3 and Appendix 2). With respect to the population from El Enzuelado, a total of 10 dietary categories were registered during the dry season, where Coleoptera (A), Orthoptera and Hymenoptera had the highest values of ViI (Table 3 and Appendix 2); while a total of eight diet categories were recorded during the wet season, being Coleoptera (A), Orthoptera, Hymenoptera and Hemiptera, the categories with the highest values of ViI (Table 3 and Appendix 2).

When the values of ViI of prey categories were analyzed by population, season, and sex, it was revealed that Hymenoptera, Coleoptera (A), and plant material were the dietary categories with the highest values of ViI for both males and females from La Manzana, and for both seasons (Table 3). ViI, however, varied for the population of El En-

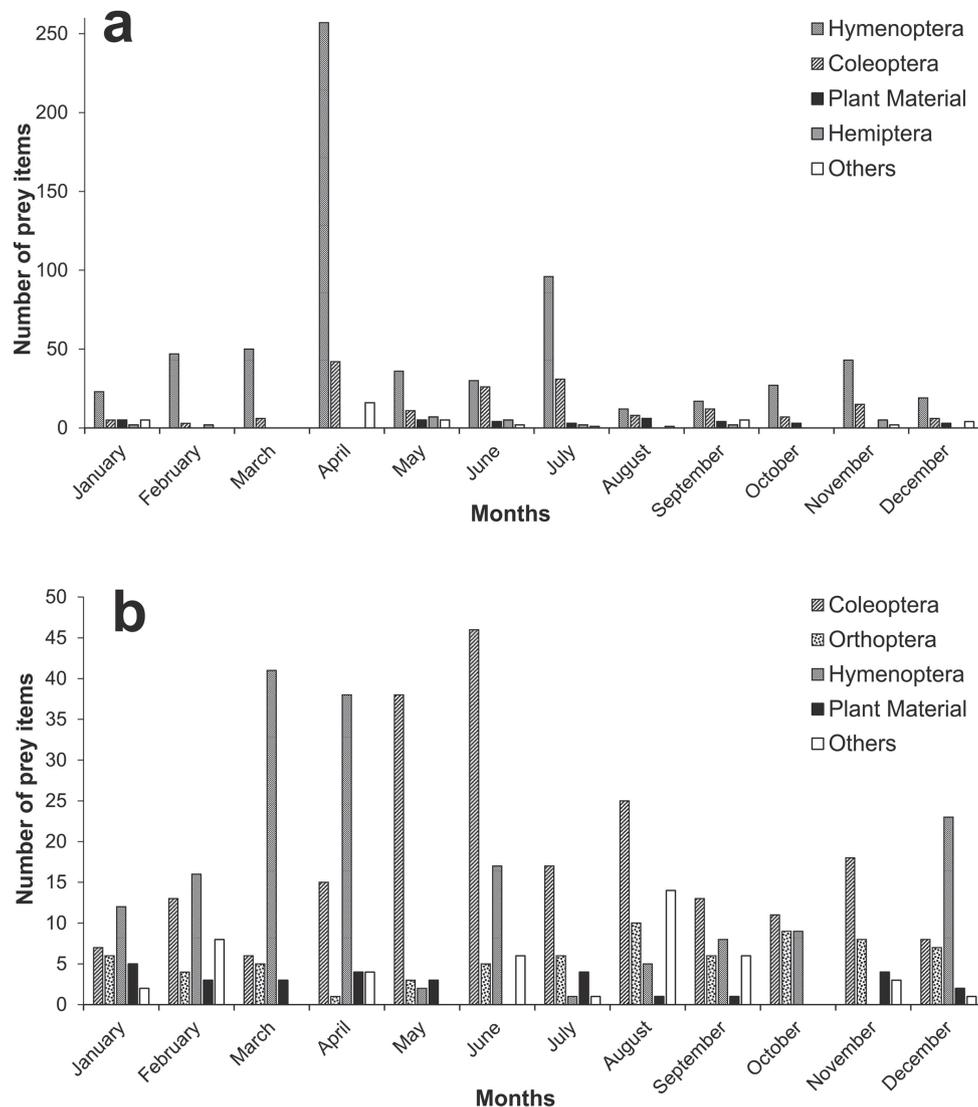


Figure 1. Abundance of prey items of the principal diet categories throughout the year in La Manzana (a) and El Enzuelado (b). The remaining categories with low value of importance shown in Table 1 are lumped into the category termed “Others.”

Table 3. Value of feeding importance (ViI) of males and female from La Manzana and El Enzuelado by seasons (Dry and Rainy). A = adult, L = larvae.

| Prey Categories | La Manzana | | | | El Enzuelado | | | |
|-----------------|------------|--------------|----------|------------|--------------|--------------|----------|------------|
| | Rainy-Male | Rainy-Female | Dry-Male | Dry-Female | Rainy-Male | Rainy-Female | Dry-Male | Dry-Female |
| Araneae | | | | 0.041 | 0.103 | 0.101 | 0.023 | 0.022 |
| Coleoptera (A) | 1.122 | 0.840 | 0.584 | 0.497 | 1.431 | 1.174 | 0.867 | 1.040 |
| Coleoptera (L) | | | | 0.039 | 0.099 | | 0.023 | 0.087 |
| Dermaptera | | | 0.022 | | | | | 0.026 |
| Diptera | | | 0.021 | 0.019 | | | | |
| Hemiptera | 0.042 | 0.180 | 0.252 | 0.099 | 0.469 | 0.223 | 0.164 | 0.021 |
| Homoptera | | | 0.079 | 0.019 | | | | 0.020 |
| Hymenoptera | 1.103 | 1.198 | 1.484 | 1.978 | 0.264 | 0.446 | 0.479 | 0.843 |
| Lepidoptera (A) | 0.045 | 0.037 | | 0.059 | | | | |
| Lepidoptera (L) | 0.148 | 0.068 | 0.027 | 0.075 | | | 0.050 | |
| Orthoptera | 0.044 | | 0.052 | 0.070 | 0.504 | 0.866 | 0.920 | 0.622 |
| Phasmida | | | 0.057 | | | | | |
| Gasteropoda | | | | | | 0.040 | | |
| Plant Material | 0.495 | 0.679 | 0.423 | 0.104 | 0.130 | 0.148 | 0.474 | 0.319 |

enzuelado, since in addition to the prey categories previously mentioned for La Manzana, also Orthoptera and Hemiptera showed high values of ViI (Table 3).

Breadth and overlap of food niche

Diet niche breadth was lower at La Manzana ($B_A = 0.07$) than El Enzuelado ($B_A = 0.24$). When each population was

analyzed by sex, season and sex/season the lizards from La Manzana showed the lowest value compared to the lizards from El Enzuelado (Fig. 2).

Diet niche overlap between populations was high ($O_{jk} = 0.77$). There were high overlapping values at La Manzana between sexes ($O_{jk} = 0.998$) and between seasons ($O_{jk} = 0.957$). Diet overlap between sexes also were similarly high for both the wet ($O_{jk} = 0.964$) and dry ($O_{jk} = 0.997$) seasons. A similar pattern occurred in El Enzuelado, with high val-

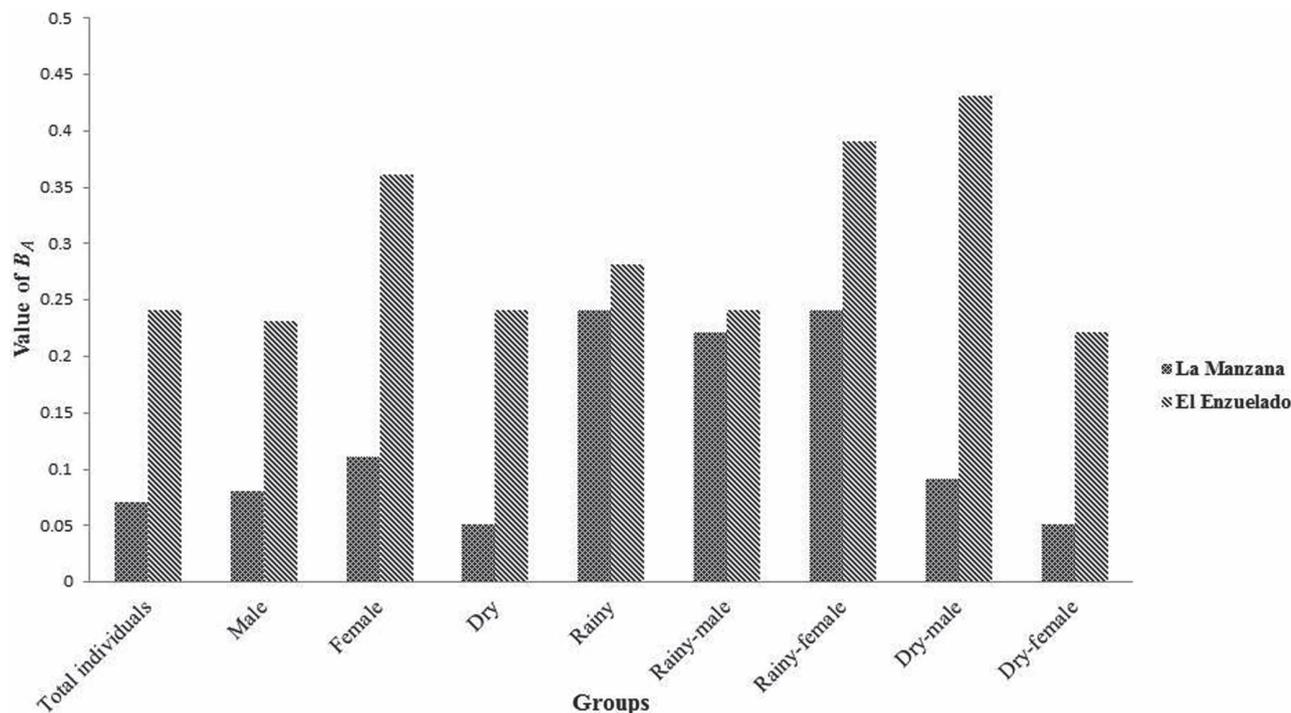


Figure 2. Diet niche breadth by population (La Manzana and El Enzuelado), sex, season, and sex/season.

ues of diet overlap between sexes ($O_{jk} = 0.917$), seasons ($O_{jk} = 0.839$), and between sexes by season (wet, $O_{jk} = 0.929$; dry, $O_{jk} = 0.94$).

Variation in stomach content volume, prey number and correlation analysis

The MANOVA test showed significant differences with respect to diet between localities (Wilks' lambda = 0.918, $F_{2,135} = 6.05$, $P = 0.003$) and between sexes (Wilks' lambda = 0.949, $F_{2,135} = 3.66$, $P = 0.028$). However, with respect to the number of stomach prey, significant differences were observed only between localities ($F_1 = 5.8$, $P = 0.026$). Lizards from La Manzana consumed a higher number of prey items ($\bar{x} = 12.5 \pm 2$) than lizards from El Enzuelado ($\bar{x} = 7 \pm 0.5$). However, significant differences were not observed between seasons (Wilks' lambda = 0.996, $F_{2,135} = 0.23$, $P = 0.78$), localities/sexes (Wilks' lambda = 0.998, $F_{2,135} = 0.16$, $P = 0.84$), localities/seasons (Wilks' lambda = 0.98, $F_{2,135} = 1.13$, $P = 0.32$), sexes/seasons (Wilks' lambda = 0.99, $F_{2,135} = 0.55$, $P = 0.57$) or localities/sexes/seasons (Wilks' lambda = 0.97, $F_{2,135} = 2.07$, $P = 0.12$).

There were significant differences in stomach content volume during the different stages of the reproductive period in females for both populations ($F_{2,70} = 13.4$, $P < 0.001$). Females had a high stomach content volume during postpartum ($\bar{x} = 5,811.22 \text{ mm}^3$, La Manzana; $\bar{x} = 4,696.37 \text{ mm}^3$, El Enzuelado), followed by vitellogenesis ($\bar{x} = 2,160.27 \text{ mm}^3$, La Manzana; $\bar{x} = 3,220.97 \text{ mm}^3$, El Enzuelado), and embryonic development ($\bar{x} = 1,157.68 \text{ mm}^3$, La Manzana; $\bar{x} = 2,496.74 \text{ mm}^3$, El Enzuelado). However, there were no differences between populations ($F_{1,70} = 0.65$, $P = 0.42$).

A correlation analysis showed a relationship between SVL and stomach content volume of lizards from La Manzana ($r = 0.29$, $P = 0.01$), but not between SVL and total prey number ($r = -0.11$, $P = 0.32$). A similar pattern occurred with lizards from El Enzuelado, where SVL was correlated with stomach content volume ($r = 0.26$, $P = 0.02$), but not with total prey number ($r = -0.11$, $P = 0.32$). When analyzed by sex in La Manzana there were no observed relationships between SVL and stomach contents volume for males ($r = 0.027$, $P = 0.13$), females ($r = 0.26$, $P = 0.10$), or with total number of prey (males, $r = -0.05$, $P = 0.78$; females, $r = -0.07$, $P = 0.063$). A similar pattern occurred at El Enzuelado, where SVL was not correlated with stomach content volume in males ($r = 0.25$, $P = 0.13$) or females ($r = 0.25$, $P = 0.13$), and there was no correlation with total prey number (males, $r = 0.14$, $P = 0.39$; females, $r = 0.01$, $P = 0.93$). Finally, a positive correlation was found only between JL and volume of complete prey for lizards from El Enzuelado ($r = 0.45$, $P = 0.02$).

Discussion

Our results regarding the diet of both populations of *Sceloporus minor* indicated that this species is omnivorous. The

highest proportion of prey categories was represented by insects; however, plant material was always part of the diet of lizards from both populations (Table 1). Dominance of insects in the diet of *S. minor* is similar to that of other species in the genus, such as *S. grammicus* WIEGMANN, 1828 (LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010), *S. jarrovii* COPE, 1875 (GADSDEN et al. 2011), *S. torquatus* WIEGMANN, 1828 (FERIA-ORTÍZ et al. 2001), among others; and also similar to that of species in other genera [*Eutropis multifasciata* KUHL, 1820 (NGO et al. 2014); *Anolis* (= *Norops*) *nebulosus* WIEGMANN, 1834 (HERNÁNDEZ-SALINAS et al. 2016); *Xenosaurus mendozai* NIETO-MONTES DE OCA et al. 2013 (ZAMORA-ABREGO & ORTEGA-LEÓN 2016); *Tropidurus torquatus* WIED-NEUWIED, 1820 (SIQUEIRA et al. 2013)]. Insects in the diet of lizards of small size should provide the best nutrients for growth, development, and daily activities (GADSDEN et al. 2011, ZAMORA-ABREGO & ORTEGA-LEÓN 2016), contrary to medium-sized species or large-sized species that generally feed on plant or other type of animal material (PIANKA & VITT 2003).

The most consumed groups by females and males from both populations were Hymenoptera, Coleoptera (adults), Orthoptera, Hemiptera, and plant material. This pattern is similar to those reported for its congeneric species, including *S. mucronatus* COPE, 1885 (MÉNDEZ-DE LA CRUZ et al. 1992), *S. poinsetti* BAIRD & GIRARD, 1852 (BALLINGER 1981), or related species, such as *S. jarrovii* (GADSDEN et al. 2011, LEACHÉ et al. 2016). With regard to *S. jarrovii*, Hymenoptera (ants), Coleoptera and Isoptera were the main prey categories consumed (MÉNDEZ-DE LA CRUZ et al. 1992; GADSDEN et al. 2011). However, in the populations we studied, Isoptera was not part of the diet of *S. minor*; suggesting that this prey group does not inhabit these environments or if it does, it is probably not abundant enough to be part of the diet of these lizards, or simply these lizards did not consume this type of prey.

Plant material was consumed with high frequency by *S. minor*, a pattern similar to that of other lizard species such as *S. mucronatus* (MÉNDEZ-DE LA CRUZ et al. 1992) or *S. torquatus* (FERIA-ORTÍZ et al. 2001). Our results showed that a high percentage of individuals from La Manzana (55%) and El Enzuelado (39%) consumed a high proportion of plant material, but the males ate a higher percentage than females. These results have been explained in other lizard species in three ways, (i) plant material provides a significant amount of water in dry environments (MÉNDEZ-DE LA CRUZ et al. 1992, SAZIMA et al. 2005, SERRANO-CARDOZO et al. 2008), (ii) consumption of plant material is an additional source of food when insect abundance decreases in the environment (GREENE 1982, BÚRQUEZ et al. 1986), and (iii) consumption of plant material enhances the digestive process of these individuals (BÚRQUEZ et al. 1986).

The composition of the diet between populations was similar; and this pattern also was maintained between sexes and seasons. The number of consumed prey categories and their abundance was higher in the dry season than the wet season. This result was similar to those found in oth-

er lizard species, such as *E. multifasciata* (NGO et al. 2015), *A. ocellatus* COPE, 1879 (JANZEN & SCHOENER 1968), and *A. nebulosus* (HERNÁNDEZ-SALINAS et al. 2016), but different to those reported in *S. torquatus* (FERIA-ORTÍZ et al. 2001) and *X. mendozai* (ZAMORA-ABREGO & ORTEGA-LEÓN 2016). Similarities or differences could be explained by characteristics of the environments these lizards inhabit, such as precipitation and temperature, which regulate diversity and abundance of insects (food), and, ultimately, the dietary composition of lizards (LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010, HERNÁNDEZ-SALINAS et al. 2016, ZAMORA-ABREGO & ORTEGA-LEÓN 2016). Seasonal variation occurred in lizards from both populations (Fig. 1). In La Manzana, the frequency of Hymenoptera decreased during the wet season, but the opposite pattern was observed for Coleoptera. In El Enzuelado, the consumption of Coleoptera increased during the wet season, but Hymenoptera and Coleoptera were more consumed than Coleoptera during the dry season (Fig. 1). This pattern has been reported in other species of the genus *Sceloporus* (BROOKS & MITCHELL 1989, SERRANO-CARDOZO et al. 2008, GADSDEN et al. 2011). For example, SERRANO-CARDOZO et al. (2008) and GADSDEN et al. (2011) noticed seasonal changes in diet according to variation in precipitation. The latter variable triggered the increasing abundance of Hymenoptera, Isoptera, or Coleoptera, with these prey orders in turn reflected in the dietary composition of lizards (BALLINGER & BALLINGER 1979, ZAMORA-ABREGO & ORTEGA-LEÓN 2016).

A similar dietary composition between sexes and populations showed low niche breadth values, but a high niche overlap. These data indicated a specialist diet, because although food availability in the environment was not assessed, our numbers showed that there exists a preference for a few prey categories. Lizards from La Manzana consumed a lower number of prey categories (Hymenoptera, Coleoptera and plant material) than lizards from El Enzuelado (Hymenoptera, Coleoptera, Orthoptera and plant material). Consumption of these prey types by lizards from both populations could be explained by the presence of the former all year round; this way lizards can obtain the high nutritional values that they need for their activities, such as growth, tissue repair, and reproduction (LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010, CRUZ-ÉLIZALDE et al. 2014).

Food variation could be affected by environmental factors, such as precipitation (BALLINGER & BALLINGER 1979), whereas body size (NGO et al. 2014), as well as dimension of the mandibular structure (GADSDEN et al. 2011, NGO et al. 2015), will determine the size and type of prey consumed. Differences found in stomach content volume between populations and positive correlations between prey size and lizard jaw dimensions (only the population of El Enzuelado) could be related to morphological variation of males and females from both populations, as occur in other populations of this species (RAMÍREZ-BAUTISTA et al. 2014, GARCÍA-ROSALES et al. 2017). Likewise, morphological variation (size) could influence the feeding be-

havior of both populations, because individuals from La Manzana with a smaller SVL (see RAMÍREZ-BAUTISTA et al. 2014, GARCÍA-ROSALES et al. 2017) consumed a higher prey number than those from El Enzuelado with larger SVL (see RAMÍREZ-BAUTISTA et al. 2014, GARCÍA-ROSALES et al. 2017), suggesting that the lizards from La Manzana ate a larger amount of small prey than do lizards from El Enzuelado, which in turn ate fewer prey but with a larger size. This pattern was similar to that seen in other lizard species (*Aspidoscelis sacki* WIEGMANN, 1834 [ALDAPE-LÓPEZ et al. 2009]; *Eutropis multifasciata* [NGO et al. 2015]).

Food is a source of energy that influences reproduction (BALLINGER & BALLINGER 1979, LÓPEZ-JURI et al. 2015). Variation in food intake was found when comparing stomach content volume of females with different stages of reproductive cycle (vitellogenesis, embryonic development and post-partum; RAMÍREZ-BAUTISTA et al. 2014); females from both populations showed a greater stomach content volume during post-partum. In this stage, fat body mass is smaller (March–April) and increases at the beginning of the vitellogenic period (July–November). Fat body mass reaches its maximum size and remains constant until embryonic development (November–April; RAMÍREZ-BAUTISTA et al. 2014). In the latter period, there is a considerable decrease of fat body mass, which coincides with the smallest size of stomach content for both populations. This pattern has been reported in other species in the genus, such as *S. mucronatus* (MÉNDEZ-DE LA CRUZ et al. 1992), *S. torquatus* (FERIA-ORTÍZ et al. 2001), and *S. grammicus* (LEYTE-MANRIQUE & RAMÍREZ-BAUTISTA 2010), as well as in other genera, such as *Liolaemus crepuscularis* ABDALA & DÍAZ-GÓMEZ, 2006 (SEMHAN et al. 2013) and *Tupinambis rufescens* GÜNTHER, 1871 (LÓPEZ-JURI et al. 2015). The fact that small food content volumes were reported during gestation could be explained by the limited space being allocated mostly for the pregnancy related process (MÉNDEZ-DE LA CRUZ et al. 1992), when appetite is inhibited by high production of progesterone (CREWS & GARRICK 1980), and also, it is in this period when the foraging activity decreases (FERIA-ORTÍZ et al. 2001, GADSDEN et al. 2011). The post-partum stage (April) coincides with high insect abundance (spring), since this is the stage when females begin both the feeding activity (BALLINGER & BALLINGER 1979) and the storage of fat body mass for the next reproductive period (RAMÍREZ-BAUTISTA et al. 2008, 2014).

In conclusion, our results showed that *S. minor* has an omnivorous diet composed primarily of insects and plant material. This species, however, consumes more frequently certain types of prey; in both populations, sexes, and seasons, the lizards showed a high preference for prey items found in a few categories. Also, our results showed that the volume of stomach content in females varied significantly through the three stages of the reproductive cycle, vitellogenesis, embryonic development, and post-reproductive period, having a smaller stomach volume when embryos were present. This study increases the knowledge on food ecology of *S. minor* at both the species and population level. It also provides information on the effect of food (ener-

gy) on the female reproductive period throughout the year. As has been previously noticed (STEPHENSON 2010, RAMÍREZ-BAUTISTA et al. 2014, GARCÍA-ROSALES et al. 2017), there are different morphs (colour patterns) in the males of these populations, which differ in various morphological and behavioral attributes (STEPHENSON 2010). Therefore, it is necessary to carry out ecological studies contemplating different years, populations, age class, sex, and morphs to explain variations in the diet at both intra- and interpopulational levels (STEPHENSON & RAMÍREZ-BAUTISTA 2012, GARCÍA-ROSALES et al. 2017).

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Appendix 1

Number of vouchers of the individuals used in this work.

| Locality | Sex | Voucher |
|--------------|--------|---|
| La Manzana | Male | ZIMABR 1♂, ZIMABR 6♂, ZIMABR 7♂, ZIMMAY 9♂, ZIMMAY 10♂, ZIMMAY 12♂, ZIMJUN 14♂, ZIMJUN 15♂, ZIMJUN 16♂, ZIMJUL 20♂, ZIMJUL 21♂, ZIMJUL 25♂, ZIMAGO 27♂, ZIMAGO 29♂, ZIMAGO 31♂, ZIMSEP 33♂, ZIMSEP 35♂, ZIMSEP 37♂, ZIMOCT 38♂, ZIMOCT 40♂, ZIMNOV 47♂, ZIMDIC 53♂, ZIMDIC 54♂, ZIMENE 57♂, ZIMENE 59♂, ZIMENE 61♂, ZIMFEB 63♂, ZIMFEB 64♂, ZIMFEB 67♂, ZIMMZO 68♂, ZIMMZO 69♂, and ZIMMZO 71♂ |
| La Manzana | Female | ZIMABR 2♀, ZIMABR 3♀, ZIMABR 4♀, ZIMABR 5♀, ZIMMAY 8♀, ZIMMAY 11♀, ZIMMAY 13♀, ZIMJUN 17♀, ZIMJUN 18♀, ZIMJUN 19♀, ZIMJUL 22♀, ZIMJUL 23♀, ZIMJUL 24♀, ZIMAGO 26♀, ZIMAGO 28♀, ZIMAGO 30♀, ZIMSEP 32♀, ZIMSEP 34♀, ZIMSEP 36♀, ZIMOCT 39♀, ZIMOCT 41♀, ZIMOCT 42♀, ZIMNOV 43♀, ZIMNOV 46♀, ZIMNOV 48♀, ZIMNOV 49♀, ZIMDIC 50♀, ZIMDIC 51♀, ZIMDIC 52♀, ZIMDIC 55♀, ZIMENE 56♀, ZIMENE 58♀, ZIMENE 60♀, ZIMFEB 62♀, ZIMFEB 65♀, ZIMFEB 66♀, ZIMMZO 70♀, ZIMMZO 72♀, and ZIMMZO 73♀ |
| El Enzuelado | Male | MEZTABR 2♂, MEZTABR 3♂, MEZTABR 6♂, MEZTMAY 7♂, MEZTMAY 9♂, MEZTMAY 11♂, MEZTJUN 15♂, MEZTJUN 18♂, MEZTJUN 19♂, MEZTJUL 21♂, MEZTJUL 22♂, MEZTJUL 25♂, MEZTAGO 26♂, MEZTAGO 29♂, MEZTAGO 30♂, MEZTAGO 32♂, MEZTSEP 34♂, MEZTSEP 36♂, MEZTSEP 38♂, MEZTOCT 41♂, MEZTOCT 42♂, MEZTOCT 43♂, MEZTNOV 45♂, MEZTNOV 47♂, MEZTNOV 49♂, MEZTDIC 51♂, MEZTDIC 52♂, MEZTDIC 54♂, MEZTENE 58♂, MEZTENE 59♂, MEZTFEB 63♂, MEZTFEB 66♂, MEZTFEB 67♂, MEZTMZO 72♂, MEZTMZO 73♂, and MEZTMZO 74♂ |
| El Enzuelado | Female | MEZTABR 1♀, MEZTABR 4♀, MEZTABR 5♀, MEZTMAY 8♀, MEZTMAY 10♀, MEZTMAY 12♀, MEZTMAY 13♀, MEZTJUN 14♀, MEZTJUN 16♀, MEZTJUN 17♀, MEZTJUL 20♀, MEZTJUL 23♀, MEZTJUL 24♀, MEZTAGO 27♀, MEZTAGO 28♀, MEZTAGO 31♀, MEZTSEP 33♀, MEZTSEP 35♀, MEZTSEP 37♀, MEZTOCT 39♀, MEZTOCT 40♀, MEZTOCT 44♀, MEZTNOV 46♀, MEZTNOV 48♀, MEZTNOV 50♀, MEZTDIC 53♀, MEZTDIC 55♀, MEZTDIC 56♀, MEZTENE 57♀, MEZTENE 61♀, MEZTENE 62♀, MEZTFEB 64♀, MEZTFEB 65♀, MEZTFEB 68♀, MEZTMZO 69♀, MEZTMZO 70♀, and MEZTMZO 71♀ |

Appendix 2

Dietary composition of *Sceloporus minor* from La Manzana and El Enzuelado by seasons (Dry [October–May] and Rainy [June–September]). N = number of items, F = frequency of occurrence, W = weight (g) of prey category, and ViI = Value of feeding importance. A = adult, L = larvae.

| Prey Categories | La Manzana | | | | | | | | El Enzuelado | | | | | | | |
|-----------------|------------|-----|-------|-------|-------|----|-------|-------|--------------|-----|--------|-------|-------|----|-------|-------|
| | Dry | | | | Rainy | | | | Dry | | | | Rainy | | | |
| | N | F | W | ViI | N | F | W | ViI | N | F | W | ViI | N | F | W | ViI |
| Araneae | 2 | 2 | 0.008 | 0.021 | | | | | 2 | 2 | 0.011 | 0.022 | 4 | 4 | 0.104 | 0.102 |
| Coleoptera (A) | 95 | 30 | 0.767 | 0.546 | 77 | 20 | 1.431 | 0.994 | 118 | 35 | 4.230 | 0.944 | 101 | 23 | 1.742 | 1.297 |
| Coleoptera (L) | 2 | 1 | 0.037 | 0.019 | | | | | 2 | 2 | 0.313 | 0.046 | | | | |
| Dermaptera | 1 | 1 | 0.003 | 0.010 | | | | | 1 | 1 | 0.026 | 0.013 | | | | |
| Diptera | 2 | 2 | 0.001 | 0.020 | | | | | | | | | | | | |
| Hemiptera | 16 | 10 | 0.355 | 0.178 | 9 | 7 | 0.012 | 0.124 | 9 | 7 | 0.084 | 0.087 | 22 | 11 | 0.325 | 0.348 |
| Homoptera | 8 | 4 | 0.005 | 0.047 | | | | | 1 | 1 | <0.001 | 0.011 | | | | |
| Hymenoptera | 502 | 45 | 2.932 | 1.717 | 155 | 24 | 0.882 | 1.153 | 140 | 25 | 0.823 | 0.666 | 31 | 10 | 0.246 | 0.360 |
| Lepidoptera (A) | 2 | 1 | 0.082 | 0.028 | 2 | 2 | 0.019 | 0.039 | | | | | | | | |
| Lepidoptera (L) | 5 | 3 | 0.084 | 0.049 | 6 | 3 | 0.148 | 0.107 | 2 | 2 | 0.032 | 0.024 | 1 | 1 | 0.115 | 0.049 |
| Orthoptera | 4 | 4 | 0.117 | 0.062 | 1 | 1 | 0.004 | 0.017 | 44 | 32 | 5.233 | 0.783 | 27 | 20 | 1.035 | 0.683 |
| Phasmida | 1 | 1 | 0.105 | 0.031 | | | | | | | | | | | | |
| Gasteropoda | | | | | | | | | | | | | 1 | 1 | 0.003 | 0.019 |
| Plant Material | 16 | 16 | 0.585 | 0.273 | 23 | 23 | 0.600 | 0.566 | 23 | 23 | 2.060 | 0.405 | 5 | 5 | 0.177 | 0.140 |
| Totals | 656 | 120 | 5.080 | | 273 | 80 | 3.096 | | 342 | 130 | 12.811 | | 192 | 75 | 3.748 | |