








Sex and seasonal variation in the diet of the Mountain Horned Lizard (*Phrynosoma orbiculare*)

Variación sexual y estacional en la dieta del Camaleón de Montaña (*Phrynosoma orbiculare*)

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- Received: 08/May/2024
- Accepted: 01/Abr/2025
- Online Publishing: 16/05/2025

Citation: Rojas-Hernández U, Pérez-Pérez A, Gómez-Benítez A, Granados-González G, Sherbrooke W, Suárez-Varón G, Hernández-Gallegos O. 2025. Sex and seasonal variation in the diet of the Mountain Horned Lizard (*Phrynosoma orbiculare*). *Caldasia* 47:e112305. doi: <https://doi.org/10.15446/caldasia.v47.112305>

ABSTRACT

Food acquisition is fundamental in animals. Some dietary studies of *Phrynosoma* have shown a strong intake of ants. This study analyzes sexual and seasonal variations in diet characteristics of 59 adults of *Phrynosoma orbiculare* captured in the State of Mexico, Mexico, analyzed through stomach flushing. This population is strongly myrmecophagous within the genus *Phrynosoma* and the most myrmecophagous within the Tapaja clade. There are sexual and seasonal variations in ant consumption, and a generalized linear model showed differences in the diet for both factors. The results of this study were compared with other studies on the diet of the species and within the genus, an important aspect in planning for the conservation and recovery of this and other *Phrynosoma* species.

Keywords: Diet, Seasonal differences, Sexual differences, Myrmecophagy, Phrynosomatidae.

RESUMEN

La obtención de alimento es fundamental en animales. Algunos estudios hechos sobre la dieta de *Phrynosoma* han mostrado un elevado consumo de hormigas. Este estudio analiza la variación sexual y estacional en las características alimenticias de 59 adultos de *Phrynosoma orbiculare* que fueron capturados en el Estado de México, México, analizadas a través de lavado estomacal. La población estudiada es altamente mirmecófaga dentro del género *Phrynosoma* y la más mirmecófaga dentro del clado

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Tapaja. Existe variación sexual y estacional en el consumo de hormigas, un modelo lineal generalizado indicó que existen diferencias en la dieta para ambos factores. Los resultados de este estudio fueron comparados con otros trabajos sobre la dieta en la especie y dentro del género, un aspecto importante para el desarrollo de planes de conservación y recuperación de ésta y otras especies de *Phrynosoma*.

Palabras clave: Dieta, Diferencias estacionales, Diferencias sexuales, Mirmecofagia, Phrynosomatidae.

INTRODUCTION

Food is one of the fundamental factors for the survival and reproduction of animals. Various biotic and abiotic factors determine the potential of organisms to obtain certain types of prey (Vitt and Caldwell 2014). Therefore, variation in the composition of the diet can be attributed to differences between sexes, ontogenetic stages, and/or seasonal aspects of their lives (Cappellari *et al.* 2007, Verrastro and Ely 2015). Sexual variations in diet can influence several aspects, for example, they can decrease competition both qualitatively and quantitatively due to morphological differences. These variations also allow for adjustments to meet energy and nutritional needs (allowing females to improve the quantity and quality of eggs/embryos). Additionally, sexual variations in diet can enhance the survival of the sexes during winter (Munger 1984, Verrastro and Ely 2015, Cocilio *et al.* 2016, Ramakrishnan *et al.* 2018). Some lizard species, such as *Ameivula ocellifera* (Spix, 1825), *Sceloporus torquatus* (Wiegmann, 1828), and *S. grammicus* (Wiegmann, 1828) do not exhibit sex related feeding differences, or these are minimal (Feria-Ortiz *et al.* 2001, Leyte-Manrique and Ramírez-Bautista 2010, Santana *et al.* 2010). In contrast, in other species such as *Ptyodactylus guttatus* (Heyden, 1827) the differences between sexes are substantial, related mainly to morphological differences in head size (Perry and Brandeis 1992).

Seasonal variations in habitat structure may modify the abundance and diversity of prey available for some species, thus reducing the ability of organisms to specialize (Verrastro and Ely 2015, Gainsbury and Meiri 2017). For example, in *Sitana ponticeriana* (Cuvier, 1829) and *Liolaemus occipitalis* (Boulenger, 1885) there are seasonal differences in prey preferences and in prey abundances due to seasonal climatic changes that affect food availability

(Pal *et al.* 2007, Verrastro and Ely 2015). In contrast, Ferreira *et al.* (2017) found no seasonal changes in the diets of six equatorial lizard species.

The 17 species of horned lizards, genus *Phrynosoma* (Wiegmann, 1828), have been classified into four clades: Tapaja, Anota, Brevicauda, and Doliosaurus (Leaché and Linkem 2015). Various studies on diets of *Phrynosoma* have shown nutritional preference for arthropods, mainly ants, beetles, and orthopterans (Pianka and Parker 1975). The degree of myrmecophagy varies among different clades. Within the Anota clade, ant diet consumption may be above 90 % (90.3 – 97.3 %), while within Tapaja myrmecophagy is lower (67.5 – 85.8 %) (Pianka and Parker 1975). Currently, there is no known species whose diet is 100 % myrmecophagous, as occurs within the Australian Thorny Devil *Moloch horridus* (Gray, 1841) (Withers and Dickman 1995, Pianka *et al.* 1998), a species exhibiting many convergent adaptations with horned lizards (Sherbrooke 2003). To date, few dietary studies of *Phrynosoma* emphasize the influence of sexual dimorphism, ontogeny, and seasonal environmental changes on diets of horned lizards (Powell and Russell 1984, Lahti and Beck 2008, Newbold and MacMahon 2009, Lahti 2010).

The Mountain Horned Lizard, *Phrynosoma orbiculare* (Linnaeus, 1758), is endemic to Mexico and has a wide geographical distribution (Bryson *et al.* 2012), at elevations ranging between 1500 and 3400 m, inhabiting pine-oak forests and semi-arid scrub areas (Méndez-de la Cruz *et al.* 2003). The mating season occurs during summer, females remain pregnant for more than seven months and birth occurs during spring (Hernández-Hernández *et al.* 2025, Gómez-Benitez *et al.* 2021a). As with other species of the genus (Sherbrooke 2003), *P. orbiculare* is considered a sit-and-wait forager and, according to Pianka and

Parker (1975), it mainly consumes ants. However, Pianka and Parker (1975) combined different populations in their review from different elevations and vegetation types. This can result in significant dietary results not necessarily universal to a particular species (Refsnider *et al.* 2019). For example, in other species of *Phrynosoma* it has been recorded that the incidence and abundance of different ant species, influence the species of ants consumed (Suárez *et al.* 2000, Newbold and MacMahon 2009).

Phrynosoma orbiculare is considered threatened according to Mexican law NOM-059-SEMARNAT-2010 (SEMARNAT 2010). Moreover, under the Environmental Vulnerability Score (EVS), *P. orbiculare* has a score of twelve points, thus designating it a species of medium vulnerability (Wilson *et al.* 2013), and least concern by the IUCN Red List.

The current study addresses the diet and variation related to sex and season in a single population of *P. orbiculare* located in the State of Mexico, Mexico.

MATERIALS AND METHODS

The *P. orbiculare* population studied is found in the Parque de la Ciencia Sierra Morelos (PCSM), Toluca, State of Mexico (19°18'41.1" North, 99°41'34" Western at ~2700 m elevation). This region exhibits a temperate-humid climate with variations in precipitation during rainy (June-September) and dry season (October-May); it is a temperate forest with predominant vegetation conformed for pines and cedars (Gobierno del Estado de México 2013). Within the area of study there are different species of clump-forming grasses that serve as refuges for *P. orbiculare*. Recreational and agricultural activities are carried out within and around the park. There are other species of reptiles and amphibians in the study site, however it is not known if these share any dietary overlap with *P. orbiculare*.

Between 2016 and 2018, sampling was carried out during spring (April-June), summer (July-September) and fall (October-December). No sampling was done in winter since there is a significant decrease in lizard activity due to dormancy (Gómez-Benitez *et al.* 2021a). Adults were considered to have SVL \geq 65 mm for males, the minimum size at which femoral pore secretion was observed (Oviedo-Hernández 2024), and SVL \geq 66 mm for females, the minimum size at which a gravid female has been recorded

(Suárez-Rodríguez *et al.* 2018). The individuals were captured and sexed by the presence of post-cloacal scales in males (Sherbrooke 2003). Snout-to-vent length (SVL) and tail length (TL) were taken with a digital vernier caliper (precision 0.01 mm). Body weight was obtained with a Pesola® spring scale (precision 0.5 g), and locations were determined with a Garmin Etrex Vista GPS (\pm 4 m precision) to release the organisms in the same place where they were collected.

Captured individuals were placed in cloth bags, with the collect permit SGPA/DGVS/002491/18 granted by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), and transferred to the Herpetology Laboratory of the Facultad de Ciencias, Universidad Autónoma del Estado de México, where stomach flushing technique was applied as a method that has demonstrated not cause harm to individuals (Legler 1977, Refsnider *et al.* 2019). A 3.5 cm long feeding tube (a plastic tube to provide nutrition), with a diameter of 2.7 mm, was connected to 5 ml syringe, and this was used to orally inject 3 ml of tap water into the stomach of each lizard. Following collection of flushed materials, the lizards were kept under observation, provided with water and food *ad libitum*, and their healthy recovery was verified prior to release at their capture sites.

Stomach flushing samples were fixed in 70 % ethyl alcohol for later identification to the lowest taxonomic level possible, using taxonomic keys (McGavin 2000) and a stereoscopic microscope. Identified prey were counted and their width and length were recorded for volume determination (shape was assumed as an ellipsoid) using the equation: $V = (4/3)\pi(L/2)(W/2)^2$ (Feria-Ortiz *et al.* 2001).

An importance value (*VI*) for prey was obtained according to the relative abundance ($RA = N^{ij}$, calculated as the number of prey consumed in a category divided by the total number of prey consumption), relative volume ($RV = V^{ij}$, as the volume of prey consumed in a category divided by the total volume of prey consumption), and incidence ($IP = F^{ij}$, as the number of stomach contents that includes a prey category divided by the total number of stomachs analyzed) for each of the identified prey categories (Gadsden and Palacios-Orona 2000, Leyte-Manrique and Ramírez-Bautista 2010): $VI = V^{ij} + N^{ij} + F^{ij}$. Standardized Levin's indexes were calculated to determine by sex and/or season, if the lizards were specialists or generalists, with the following equation: $(B' = \frac{(\frac{1}{\sum P_i^2}) - 1}{n-1})$, where P_i represents the *RA* value

for each prey category. Values close to zero corresponded to a specialist and values close to one to a generalist. In order to make an inference regarding sex, Pianka's similarity index (Krebs 1999) was applied ($O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$), where P_{ij} is the RA value for each prey category for males, and P_{ik} is the RA value for each prey category for females. Like Standardized Levin's index, it uses two reference values, where those values close to one corresponded to a high niche overlap, and values close to zero to low overlap. The normality was verified with Kolmogorov-Smirnov test, and Levene's test was performed to assess differences in the variance of prey volume between sex and seasons. In addition, according to the nature of the data and in order to compare and to analyze an effect in diet by sex, season and the interaction sex*season on prey categories, a Generalized Linear Models (GLMs) with Poisson distribution and log as linking function was performed with twelve prey categories (see Table 1) as dependent variables, sex and season as factors, in the program Jamovi (The Jamovi Project 2022, v. 2.3). Homoscedasticity of the data was verified through visual examination of residuals and QQ plots (Zuur et al. 2010). When a test revealed a significant difference, we performed a Bonferroni post-hoc test.

Table 1. Prey categories that make up the diet of *Phrynosoma orbiculare* in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. The values of volume (RV), abundance (RA) and incidence of prey (IP) obtained for the calculation of the importance value (VI) are shown for each determined category. The highlighted values correspond to the most common prey categories.

Prey category	RV	RA	IP	VI
Hymenoptera	62.08	91.4	93.6	65.16
Coleoptera	19.71	3.51	46.77	14.75
Opiliones	0.08	0.07	1.61	0.29
Araneae	1.01	0.83	14.52	2.79
Isopoda	13.55	3.10	40.32	11.59
Myriapoda	0.02	0.07	1.61	0.27
Dermoptera	0.10	0.07	1.61	0.30
Hemiptera	1.26	0.62	12.90	2.56
Diptera	0.10	0.07	1.61	0.30
Lepidoptera	0.56	0.07	3.23	0.69
Orthoptera	1.45	0.07	1.61	0.75
No ID	0.08	0.14	3.23	0.56
Total	100	100	-	100

Additionally, an analysis of covariance (ANCOVA) was performed where the dependent variables were the metric characteristics (length, width and volume of prey) as well as the number of preys consumed (by sex), using sex and

season as factors, and, as a covariate, the SVL of each individual. Moreover, it was determined, through a Student's t-test, if there was sexual size dimorphism in SVL. Analyses were carried out with the Statgraphics Centurion XVIII package, and performed with alpha of 0.05.

RESULTS

A total of 59 individuals (27 males and 32 females) were captured during three seasons: spring ($n = 16$), summer ($n = 36$) and autumn ($n = 7$). The SVL ($\bar{x} \pm SD$) of the males was 76.0 ± 5 mm (range = 68 - 85 mm) and that of the females was 81.1 ± 5 mm (range = 66 - 95 mm), where the females were significantly larger ($t = -3.75, p = 0.0004$).

Population analysis

A total of 1451 prey, were identified in eleven orders and one unidentified category. The Hymenoptera (although two bees were observed, just ants (Formicidae) were considered for this category) had the highest RA (91.4 %; 1326 prey), and it was present in 93.6 % of the stomachs analyzed, followed by Coleoptera and Isopoda (Table 1). Despite that the rest of the prey categories were below 1 %, Hemiptera and Araneae were found in 12.9 % and 14.52 % of the total stomachs analyzed; Standardized Levin's index was close to 0 ($B' = 0.01$). Additionally, skin molts of *P. orbiculare* were observed in two of the 59 stomach samples analyzed.

Sex and seasonal analyses

The relative abundance of Hymenoptera in males was (92.79 %, 759 prey) and in females (89.57 %, 567 prey), thus being the category of prey most widely consumed for both sexes. Additionally, a minimal variation was obtained between sexes regarding the consumption of Coleoptera and Isopoda; five of the twelve prey categories registered for the population were present in the diet of males, while females had at least one prey in each category (Table 2). Despite this, the B' for males (M) and females (F) was close to 0 ($M = 0.01; F = 0.01$), while Pianka's similarity index was close to 1 ($O_{jk} = 0.99$). The GLMs reveal a significant difference in ant consumption between sexes ($X^2 = 5.88, p = 0.015$), males consumed more ants than females (post hoc Bonferroni test: $z = 2.58, p = 0.01$). Ant consumption varies by season ($X^2 = 403.92, p < 0.001$), in spring, lizards consumed more ants than in summer and autumn (post hoc Bonferroni test: $z = 17.95, p < 0.001$ and $z = 10.35, p < 0.001$). Interaction season*sex was significant

($X^2 = 116.61, p < 0.001$, Fig. 1). In general terms, males and females consume a greater number of ants during spring and fewer in autumn, but in summer males consume more ants than females. The rest of prey categories analyzed with the GLMs did not show significant differences between sexes and seasons ($p > 0.05$, results not showed).

Table 2. Dietary characterization of males and females in *Phrynosoma orbiculare* in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. The volume (RV), abundance (RA) and importance value (VI) of the different prey categories are shown; the highlighted values correspond to the most common prey categories.

Prey category	Males			Females		
	RV	RA	VI	RV	RA	VI
Hymenoptera	73.81	92.79	69.51	50.74	89.57	60.99
Coleoptera	11.41	3.42	13.55	27.73	3.63	16.23
Opiliones	0.00	0.00	0.00	0.15	0.16	0.55
Araneae	0.52	0.49	1.95	1.49	1.26	3.58
Isopoda	13.64	2.81	12.47	13.46	3.48	10.98
Myriapoda	0.00	0.00	0.00	0.05	0.16	0.51
Dermaptera	0.00	0.00	0.00	0.20	0.16	0.56
Hemiptera	0.62	0.49	2.52	1.88	0.79	2.67
Diptera	0.00	0.00	0.00	0.20	0.16	0.56
Lepidoptera	0.00	0.00	0.00	1.10	0.16	0.86
Orthoptera	0.00	0.00	0.00	2.85	0.16	1.45
No ID	0.00	0.00	0.00	0.16	0.32	1.05
Total	100	100	100	100	100	100

During the analyzed seasons, the relative abundance of consumed Hymenoptera decreased from spring to autumn, 94.3 % in spring, 90.0 % in summer and 77.1 % in autumn. In addition, a seasonal increase in relative abun-

dance was observed in the two next most abundant prey categories, Coleoptera and Isopoda, during the periods from spring through autumn. Coleoptera increased from 2.5 % in spring to 4.8 % in autumn, while isopods increased from 1.9 % to 13.3 % (Fig. 2). Isopod volume was higher (32.9 %) during the fall, differing greatly from spring (12.7 %) and summer (10.4 %). The remaining prey categories varied across seasons when abundance was significantly less or even null (Table 3). However, the Standardized Levin's index (B') by seasons detected that the niche width increased as the seasons progressed (spring = 0.01; summer = 0.02; autumn = 0.05). Similarly, Levene's analysis showed that there is no statistically significant difference in the variance of prey volume between seasons ($F = 3.02, df = 56, p = 0.056$). There were no differences in volume variance between sexes ($F = 0.77, p = 0.051$). Sex ($df = 1$) and seasonal ($df = 2$) comparisons indicated non-significant differences in prey size (length: $F = 1.04, p > 0.05$; $F = 0.17, p > 0.05$; width: $F = 0.07, p > 0.05$; $F = 2.34, p > 0.05$ and volume: $F = 2.43, p > 0.05$; $F = 0.70, p > 0.05$, respectively) and abundance of prey consumed by sex ($F = 0.64, p > 0.05$).

DISCUSSION

The results indicated that the population of *P. orbiculare* in the PCSM is highly myrmecophagous. Together Hymenoptera, Coleoptera and Isopoda make up more than 95 % of this lizard's diet. Nine other orders, with minimal abundance, complete the food spectrum of *P. orbiculare* in the study population.

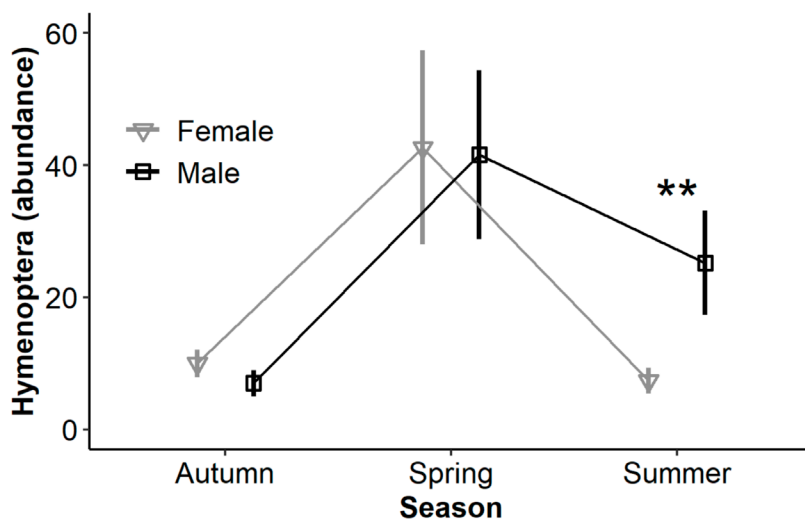


Figure 1. Relative abundance of Hymenoptera consumption by sex and season in *Phrynosoma orbiculare*. Asterisks indicate significant differences between sexes in summer.

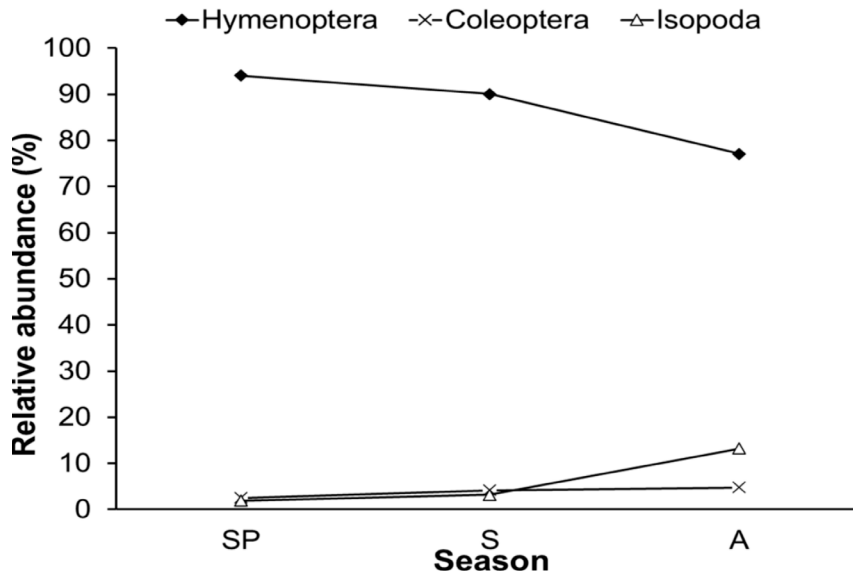


Figure 2. Seasonal variation in the consumption of the three most representative prey categories in *Phrynosoma orbiculare* diet in the Parque de la Ciencia Sierra Morelos. SP = spring, S = summer, and A = autumn.

It has been reported that the diets of *Phrynosoma* species are strongly based on ants, although beetles and other arthropods have been noted. However, there is variation regarding the percentage of ants that are consumed by each species (Pianka and Parker 1975). Our results indicated that 91.4 % of total prey consumed by *P. orbiculare* from the PCSM are ants, making it a highly myrmecophagous and specialized population (Standardized Levin's index close to 0). According to previous reports, within the Tapaja clade, *P. ditmarsii* (Stejneger, 1906) was the species with the highest degree of myrmecophagy (85.8 %), followed by other populations of *P. douglasii* (Bell, 1829) (81 %), *P. orbiculare* (67.5 %), and *P. hernandesi* (Girard, 1858) (41 %) (Pianka and Parker 1975, Meyers *et al.* 2018). In species of the Anota clade (*P. mcallii* (Hallowell, 1852), *P. solare* (Gray, 1845) and *P. coronatum* (Blainville, 1835)) ant consumption is above 90 % of the diet (Pianka and Parker 1975). Currently, the high degree of myrmecophagy obtained in the *P. orbiculare* population of the PCSM is the highest reported within the Tapaja. Our results indicate a higher degree of myrmecophagy for the species than the reported by Pianka and Parker (1975), where they included data from different populations. In the same way, our population can be considered as having a high degree of myrmecophagy in the genus along with *P. cornutum* (Harlan, 1825) (99.95 %) (Eifler *et al.* 2012), *P. mcallii* (97.2 %), and *P. solare* (90.3 %) (Pianka and Parker 1975).

The genus *Phrynosoma* shares a series of characteristics that differentiate it from other species within the family Phrynosomatidae: highly cryptic coloration, flattened and broadly-rounded body, presence of cranial spines, large stomach, slow movements, sit-and-wait foraging, large clutch/litter size, wide abdominal cavity surrounded by laterally extending fringe scales, and ant-based diet (Suárez-Rodríguez *et al.* 2018). The myrmecophagous or specialist diet varies between species or clades within the genus, as well as between populations. Species with reduced dietary incorporation of ants exhibit more robust cranial morphology, and dentition (Meyers *et al.* 2018). These characteristics within the Tapaja are not-reduced, as is currently found in other more myrmecophagous clades. They remain myrmecophagous but have a greater capacity and preference for consuming hard-bodied invertebrates that require jaw-crushing capture and ingestion, compared to members of other *Phrynosoma* clades, which are more limited to using hyolingual tongue capture of ants (Schwenk 2000, Lahti 2010, Meyers *et al.* 2018). However, given the high proportion of formicids consumed by *P. orbiculare* in this population, it differs from the feeding trend observed in other *Phrynosoma* species, which show a wide variation in ant consumption ranging from 11 % to 89 %, similar to what is seen in lizards considered generalists (Pianka and Parker 1975; Meyers *et al.* 2018). Since ants are an apparently highly predictable resource in the study area, given the size,

Table 3. Prey identified from the stomach contents of *Phrynosoma orbiculare* during the sampling seasons analyzed in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico; the volume (RV), abundance (RA), and importance value (VI) for each of the most common identified prey categories are highlighted.

Prey category	Spring			Summer			Autumn		
	RV	RA	VI	RV	RA	VI	RV	RA	VI
Hymenoptera	71.13	94.27	68.47	57.15	90.03	64.02	43.72	77.11	52.56
Coleoptera	13.50	2.51	12.84	29.63	4.45	18.62	0.87	4.82	7.16
Opiliones	0.17	0.14	0.94	0	0	0	0	0	0
Araneae	0.69	0.28	1.99	1.43	1.38	3.50	0.52	1.20	2.33
Isopoda	12.70	1.96	10.72	10.35	3.07	10.03	32.88	13.25	24.15
Miriapoda	0	0	0	0.05	0.15	0.50	0	0	0
Dermaptera	0.22	0.14	0.95	0	0	0	0	0	0
Hemiptera	1.58	0.70	4.09	1.21	0.61	2.32	0	0	0
Diptera	0	0	0	0	0	0	1.04	1.20	2.50
Lepidoptera	0	0	0	0	0	0	5.84	1.20	4.10
Orthoptera	0	0	0	0	0	0	15.14	1.20	7.20
No ID	0	0	0	0.18	0.31	1.02	0	0	0
Total	100	100	100	100	100	100	100	100	100

distribution and activity of the ant hills, myrmecophagy here may maximize feeding rewards (Newbold and MacMahon 2009) despite apparent phylogenetic/morphological divergences. Additionally, although other prey categories are available, a conserved ant diet could occur to obtain formic acid to use blood-squirting, a widespread defense strategy in *Phrynosoma* (Gómez-Benitez *et al.* 2021b).

The presence of skin molts in lizard stomach contents can have ecological (reduction of external parasites), nutritional, survival and other effects. This behavior has only been recorded in three species of *Phrynosoma* (*P. cornutum*, *P. modestum* (Girard, 1852) and *P. platyrhinus* (Girard, 1852): all in the Doliosaurus clade) (Mitchell *et al.* 2006). To our knowledge, this is the first record of skin molt ingestion in *P. orbiculare* and in the Tapaja clade.

Although the use of habitat that is equally preferred by the two sexes in the PCSM (Martínez-Nova 2019), according

to our results, the sex, season and the interaction sex*season have an effect in the ant consumption of *P. orbiculare*, where in summer, males consume a greater amount of Hymenoptera than females, season associated with reproductive activity and the energetic demands in search of mating; while spring is the season with the highest level of myrmecophagy. In other species such as *P. hernandesi* and *P. douglasii* males tend to consume ant prey at a higher percentage of diet than females (M = 92.6 % and F = 81.7 %, M = 77.1 % and F = 75.5 %, respectively) (Lahti and Beck 2008, Lahti 2010). Moreover, within the Tapaja clade, Powell and Russell (1984) observed that sex-related differences in the diet of *P. douglasii* are related to the food niche of each sex; conversely, in *P. douglasii*, beetles are more abundant in the diet of females, whereas in *P. hernandesi*, males show a higher affinity for this type of prey compared to females (Lahti and Beck 2008, Lahti 2010). Our data resemble those obtained in *P. douglasii*, where females tend to consume more Coleoptera than

males (Table 2), but males present a higher percentage in ant consumption than females. Even in *P. cornutum* (Anota clade), sex-related feeding differences were observed due to the size, availability and abundance of prey consumed (Ramakrishnan *et al.* 2018). Variations in environmental conditions affect the prey availability of a species, that is, seasonal fluctuations modify the diversity of prey available, reducing the ability of the predator to specialize towards certain prey categories (Gainsbury and Meiri 2017). The high abundances of ants that apparently made them advantageous prey, but it is possible that the increased incidence of rainfall during the summer at the PCSM promotes an increase in the number of other resources or prey categories available for *P. orbiculare*, such as coleopterans and isopods and females required other sources of energy prior to the gestation period. But it is possible also that this variation in myrmecophagy is related to the population dynamics of ants, since it has been recorded that some ant species in central Mexico and North America have bimodal surface activity and that they decrease or cancel such activity towards winter (Sanders 1972, Ríos-Casanova *et al.* 2014).

Phrynosoma douglasii and *P. platyrhinos* exhibit more pronounced seasonal variations in diet (Lahti and Beck 2008, Newbold and MacMahon 2009) than the population of *P. orbiculare* analyzed in the present study. In *P. douglasii*, hymenopteran prey was low in numbers from spring into summer but increased in autumn, and in *P. platyrhinos* the proportion of ants consumed increases throughout the year. In contrast, in both species the abundance of consumed coleopterans in the diet decreased towards autumn (Lahti and Beck 2008, Newbold and MacMahon 2009).

Previous studies have reported that sex differences in size can affect the metric characteristics of prey and influence the exploited food niche, particularly for females, which may provide energy resources during the mating season (summer), vitellogenesis, and/or gestation (Powell and Russell 1984). In this sense, our covariance analysis indicated that there are no significant differences in prey size between seasons or sex in *P. orbiculare*, despite the presence of sexual size dimorphism in the population. The similarity in prey size between sexes could have more to do with available prey sizes rather than prey selection by the lizards. If there is limited variation in prey size, we

wouldn't expect to necessarily see a difference in prey size consumed. A current study of prey availability may resolve this issue.

Although it is generally known that the diet in *Phrynosoma* is based in ants, little is known about the existence of variation in the consumption of ants and other prey, and whether this variation is a consequence of the seasonality that changes the habitat structure, which must modify the abundance and diversity of available prey, and as part of the necessary requirements for reproduction. In this way, the diet of the *P. orbiculare* population in the PCSM is highly myrmecophagous. In terms of sex and season there is always a tendency to consumption of Hymenoptera (ants). Sex sharing of the resources available in the population's habitat results in a wide overlap of niche that is also seasonal, despite there being a slight variation regarding the abundance of the prey categories consumed during the seasons. The high consumption of Hymenoptera is present throughout. As in other works (Pianka and Parker 1975, Powell and Russell 1984, Lahti and Beck 2008, Lahti 2010, Leyte-Manrique and Ramírez-Bautista 2010, Ramakrishnan *et al.* 2018) diet is a vital need of the species and studies may be useful for understanding ecosystem functionality, the importance value of species to food webs, and the relevance for implementation of conservation plans for habitat protection and selection in the future.

AUTHOR'S CONTRIBUTIONS

URH investigation, writing-early versions, methodology, data curation, review. APP field work, methodology, investigation. AGB field work, data analysis, investigation, review. GGG field work, writing-early versions, investigation, review. WCS visualization, methodology, review. GSV field work, investigation, data analysis, writing-original draft, review and editing. OHG conceptualization, supervision, investigation, field work, writing-original draft, review and editing.

ACKNOWLEDGEMENTS

We thank the students of the Herpetology Laboratory (Ana Esthela López Moreno, Orlando Suárez Rodríguez, Gabriel Andrade Soto, Daniel Sánchez Manjarrez, Gerardo Salas

Mercado and María Fernanda Pérez Arriaga) of the Facultad de Ciencias, Universidad Autónoma del Estado de México, for their assistance in the field. CEPANAF granted permission to carry out the study in the PCSM and SEMARNAT gave permission (Office SGPA/DGVS/002491/18 and permission FAUT-0074) to collect the animals. We thank to Programa Investigadoras e Investigadores COMECYT Edomex por la cátedra ESYCA2023- 141617 a GS-V. This work was supported by the Universidad Autónoma del Estado de México under the grant project 4310/2017/CI.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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