Herpetology Notes, volume 15: 523-532 (2022) (published online on 24 July 2022)

Food in the city: the urbanised diets of *Rhinella diptycha* (Anura: Bufonidae), *Hemidactylus mabouia* (Squamata: Gekkonidae), and *Tropidurus torquatus* (Squamata: Tropiduridae) in Pilar, Paraguay

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Abstract. In this study we investigated the urbanised diets of *Rhinella diptycha*, *Hemidactylus mabouia*, and *Tropidurus torquatus* in Pilar, Paraguay. To retrieve stomach contents, we dissected the faecal matter of juvenile *R. diptycha* (*n* = 43), *H. mabouia* (*n* = 128) and *T. torquatus* (*n* = 50) and stomach flushed adult *R. diptycha* (*n* = 85). The three most abundant orders of prey by volume for each of the study species were *R. diptycha*: Coleoptera (41.14%), Formicidae (27.9%), Hemiptera (3.85%); *H. mabouia*: Orthoptera (29%), Coleoptera (11.66%), Hemiptera (6.31%), and *T. torquatus*: Coleoptera (38.36%), Formicidae (14.34%), Orthoptera (13.23%). We found dietary overlap between the invasive *H. mabouia* and native *T. torquatus*, suggesting the possibility of detrimental intraguild competition for the native species. Furthermore, we believe that these species adaptations to an urbanised lifestyle was the primary driver to their diet composition.

Keywords. Diet, faecal analysis, food web, herpetofauna, South America, stomach flushing, urbanisation

Introduction

Understanding a species diet composition is an integral component in learning about their life history. Species' diet corresponds directly to various aspects of their ecology, including habitat preference (Machovsky-Capuska et al., 2018; de Almeida-Rocha et al., 2020), predators (Ward-Fear et al., 2020) and pathogens (Valtonen et al., 2010). When comparing two species diet breadths, it is possible to distinguish if they are in competition and to what degree they overlap (Sutherland, 2011; Mollov et al., 2012). Species that compete for the same prey items may negatively affect each other resulting in decreased fitness (White and Fleming, 2021); this is especially important when comparing invasive and native species diets (Kalb et al., 2018; Ghazi, 2020). Additionally, diet compositions can differ between populations within the same species, due to different habitats and stressors changing prey availability (Murray et al., 2015; Robbins et al., 2019; Santana et al., 2019).

Urbanisation is a major external pressure that can influence a species diet composition (Baxter-Gilbert et al., 2020; Peneaux et al., 2021; Gámez et al., 2022). Previous studies have shown some species in anthropogenic environments to consume less nutritious diets (Larson et al., 2020; Peneaux et al., 2021) and smaller meals (Wolfe et al., 2018); while other species have adapted well (Guiry and Buckley, 2018; Saufi et al., 2020). Most studies focused on animal diets in urbanised settings are on mammals (Guiry and Buckley, 2018; Larson et al., 2020; Tucker et al., 2021) and bird species (Saufi et al., 2020; Peneaux et al., 2021), therefore it is critical to study other taxa to understand how their diets might differ from rural populations.

Herpetofauna diets are especially important to study, as they are typically in the centre of a trophic food chain (Schoener et al., 2002; Aresco et al., 2015) and widespread (Das and Van Dijk, 2013; Jestrzemski and Schuetz, 2015; O'Donnell et al., 2017). Herpetofauna have also been able to adapt and coexist in anthropogenic locations, such as cities and farms (Banville and Bateman, 2012;

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Balakrishna et al., 2016; Santana et al., 2019). Although many studies have focused on herpetofauna diets, most of them were conducted in pristine habitats, resulting in a gap in our understanding of potential anthropogenic effects that may contribute to large declines in species populations (Balakrishna et al., 2016; Wolfe et al., 2018; Santana et al., 2019). Furthermore, many species of herpetofauna are imperilled, with as many as 42% of known amphibian species (International Union for the Conservation of Nature [IUCN] Species Survival Commission [SSC] Amphibian Specialist Group, 2017; Le et al., 2018) and 19% of known reptilian species to be considered endangered (Lesbarrères et al., 2014). With global temperatures continuing to rise (Schwartz, 2018), and humans continuing to modify natural landscapes (Huang et al., 2007; Nowakowski et al., 2018), many threatened species could go extinct, and least-concerned species may become endangered (Silvano and Segalla, 2005; Nori et al., 2018; Andrade-Díaz et al., 2019). As urbanisation in Paraguay continues to increase (Canese de Estigarribia et al., 2019), herpetofauna diets may become restricted (Cacciali et al., 2015).

Paraguay is home to 276 species of known herpetofauna including 189 reptiles (Cacciali et al., 2016) and 87 amphibians (Cabral et al., 2020). Although Paraguayan cities have high herpetofauna diversity (Motte et al., 2009), Paraguay has a poor representation in herpetological research, which could be detrimental to our understanding of endemic species and regionally distinct populations (Huang et al., 2007; Andrade-Díaz et al., 2019; Cabral et al., 2020). As human activity continues to transition Paraguayan forests into agricultural fields and urbanised landscapes, displaced reptile and amphibian species must adapt to city environments (Cacciali et al., 2015; Santana et al., 2019). Therefore, it is important to investigate the diets of herpetofauna species that already coexist in these anthropogenic habitats (Balakrishna et al., 2016; Santana et al., 2019). A combination of emerging stressors such as extreme climatic events from droughts to floods and urbanisation in Pilar can result in increased pressure on herpetofauna (Anderson et al., 1993). Dietary analysis is a key technique to better understand the overall health of these populations.

We studied the diet composition of the three most abundant of herpetofauna in Pilar, Paraguay: *Hemidactylus maboiua* (Moreau de Jonnès, 1818), *Rhinella diptycha* (Cope, 1862), and *Tropidurus torquatus* (Wied-Neuwied, 1820) (Fig. 1). Our goals were to: 1) identify diets of our focal species and 2) identify any distinct differences in their diets compared to previous studies conducted in more rural landscapes.

Materials and Methods

Study site. The city of Pilar (26.8634°S, 58.2919°W) is in southwestern Paraguay and situated to the east of the Rio Paraguay. Twelve 1-km long transects were

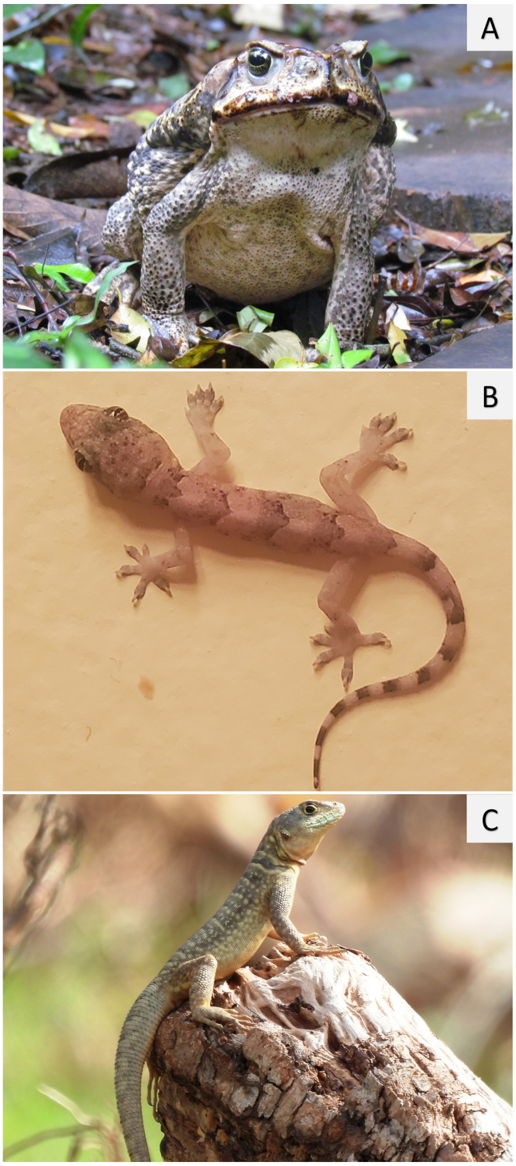

Figure 1. This studies herpetofauna species. (A) An adult *Rhinella diptycha.* (B) An adult *Hemidactylus mabouia*. (C) An adult *Tropidurus torquatus*. Photos by João Menezes (A), Joshua Sands (B), and Wagner Fiorentino (C).

randomly selected along the sidewalks in the western half of the city and a thirteenth 1-km long transect was chosen along the coast of the Arroyo Ñeembucú. These transects were labelled "night transects" and were used to catch the most abundant nocturnal herpetofauna in Pilar. In addition, two locations were selected for data collection where we found populations of *T. torquatus*; these locations were labelled "selected locations" (See Mackenzie and Vladmirova, 2021 study site section for further description; Fig. 2).

Data collection. We collected specimens of *Rhinella diptycha, Hemidactylus mabouia* and *Tropidurus torquatus* from 16 November 2019 to 6 March 2020. A single 1-km long night transect was randomly chosen and surveyed at 21:45–22:45 h. Each night transect was surveyed for three nights, giving a combined total of 39 nights searched. Each selected location was surveyed a total of 23 times, making a combined total of 46 searches. For every captured individual we recorded the location, transect number, date, time, temperature,

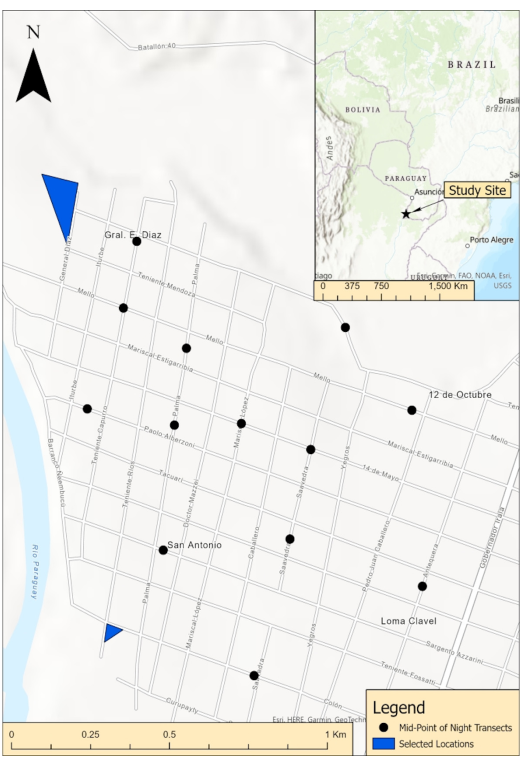

Figure 2. Study site displaying 13 night transects and two selected locations for all herpetofauna captures in Pilar, Paraguay. Maps were created in ArcGIS Pro, background basemaps were retrieved from Esri (Esri, 2021, 2022).

species and relative age (juvenile or adult) of the animal. All individuals were then brought to the lab at Fundación Para La Tierra for stomach content analysis (see acknowledgements for relevant research permits).

All captured individuals had their snout to vent length (SVL) measured to the nearest 1 mm, and were toe clipped for identification (Ursprung et al., 2011; Comas et al., 2020). Adult *R. diptycha* were stomach flushed to retrieve intact non-digested prey items. The following methodology and ethical considerations were adapted from Solé et al. (2005); all equipment was sterilised before use. The individual was carefully immobilised without the use of anaesthetics. Silicon tubing (1 cm in diameter) attached to a syringe with spring water entered through the oesophagus until the end of tubing reached their stomach. We slowly pushed spring water out of the syringe into the adult *R. diptycha's* stomach to push stomach contents out. This procedure was repeated, until only clear water was excreted; stomach contents were stored in 70% ethanol. After all adult *R. diptycha* had been stomach flushed, they were immediately released to their point of capture.

We did not find success in stomach flushing smaller bodied herpetofauna like previous studies (Gambale et al., 2020), so to prevent injury from silicon tubing *R. diptycha* with smaller oesophagus's (SVL of < 6 cm), all *H. mabouia*, and *T. torquatus* were used for faecal analysis. The following methodology and ethical considerations were adapted from Powers et al. (2018). Individuals were placed in separate jars and checked every 12 hours, any faeces present would be removed and preserved. Spring water was poured into juvenile *R. diptycha* containers, and cotton balls soaked in spring water were placed in *H. mabouia* and *T. torquatus* containers. After 48 hours, individuals were released at their capture site.

Dietary analysis. Stomach contents were placed under a stereo microscope, with attached Amscope software and MU1003 camera and were identified to the lowest taxonomic category possible, typically order. Invertebrate prey remains were sorted to order/family, rocks and plant material were counted and separated and items that could not be classified as unidentified. To estimate the volume of prey types we measured the width and length of each pile with digital callipers from the AmScope software and input these measurements into the ellipsoid volume formula (Bonfiglio et al., 2006; Hidalgo-Ruz et al., 2012).

Results

Among the captured herpetofauna (n = 332), we collected stomach contents from 311 individuals, stomach flush (n=43) and faeces (n=268). Temperatures ranged from 25.0–31.2 °C in night transects and from 28.6–41.0 °C in selected locations. Within the three study species, we observed 16 different invertebrate prey types (1 phylum, 1 subclass, 1 informal group, 11 orders and 2 families), as well as plant and unidentified categories (Table 1).

We obtained stomach contents from 128 *R. diptycha*, 43 adults, and 85 juveniles. *Rhinella diptycha* primarily ingested Coleoptera (41.14%), Formicidae (27.79%), and Hemiptera (3.85%). *Rhinella diptycha* was the only species to ingest prey from Mantodea, Chilopoda, and Pulmonata. Out of the three study species *R. diptycha* consumed the most plant material, close to 7.0% of its obtained diet (Table 1). Furthermore, on average, adult *R. diptycha* ingested two times more plant matter in their diet than juvenile *R. diptycha*. All captured juvenile *R. diptycha* predated on Formicidae, consisting of close to half of their diet, and incorporated four times more Formicidae in their diet than adult *R. diptycha*. Adults of *R. diptycha* had a more diverse diet (Table 2). Their SVL measurements ranged from 1.80–17.5 cm, with an average length of 13.83 ± 0.29 cm for adults, and an average of 3.53 ± 0.11 cm for juveniles.

We collected stomach contents from 133 *H. mabouia*: 94 adults, and 39 juveniles. The majority of *H. mabouia*'s diet was Orthoptera (29%), Coleoptera (11.66%), and Hemiptera (6.31%). *Hemidactylus mabouia* was the only species to not consume any plant material (Table 1). Across all study species and ages, only adult *H. mabouia* ingested prey in the order Neuroptera and the family Termitoidae. The *Hemidactylus mabouia*diets were very similar among juveniles and adults; apart from adults consuming and incorporating two times more Diptera in their diet. Adults were almost three times more likely to ingest Acari, while juveniles on average ingested more

Table 1. Prey items found in each of the studied species. Prey items were categorised to lowest taxonomic group possible (usually order). Number of individuals that ingested that prey (n_i), total prey count consumed (n_p), and percentage of prey consumed by volume (prey volume / total volume = V% in mm^3).

Prey type	***Rhinella diptycha*** n_i = 128			***Hemidactylus mabouia*** n_i = 133			***Tropidurus torquatus*** n_i = 50		
	n_i	n_p	V%	n_i	n_p	V%	n_i	n_p	V%
Acari	1	1	0.00	7	8	0.00	0	0	0.00
Araneae	4	6	0.03	4	7	0.09	1	1	0.01
Chilopoda	1	1	0.175	0	0	0.00	0	0	0.00
Coleoptera	120	1007	41.14	77	113	11.66	47	249	38.36
Diptera	73	306	0.98	76	360	6.17	27	177	2.87
Formicidae	121	13,279	27.79	39	87	1.31	32	886	14.34
Hemiptera	58	103	3.85	76	230	6.31	27	77	2.79
Lepidoptera	1	3	0.10	2	3	0.11	4	4	0.80
Mantodea	1	1	0.00	0	0	0.00	0	0	0.00
Nematodes	0	0	0.00	0	0	0.00	1	2	0.02
Neuroptera	0	0	0.00	1	3	0.08	0	0	0.00
Odonata	0	0	0.00	0	0	0.00	2	2	0.31
Orthoptera	43	89	2.24	113	141	29.00	26	41	13.23
Plant	103	293	6.89	0	0	0.00	6	18	0.06
Pulmonata	2	2	0.33	0	0	0.00	0	0	0.00
Termitoidae	0	0	0.00	7	8	2.21	0	0	0.00
Trichoptera	4	2	0.02	1	1	0.07	0	0	0.00
Unknown	108	N/A	16.48	124	N/A	42.98	48	N/A	27.21

Table 2. Compares the diets of adult and juvenile of the studied species. Prey items were categorised to lowest taxonomic group possible (usually order). Number of individuals that ingested that prey (n_i), percentage of individuals that ingested prey within each group (*N*%), and total volume as a percentage of prey consumed within each group (prey volume / total volume = *V*% in mm^3).

Prey type	Adult *R. diptycha* $n_i = 43$		Juvenile *R. diptycha* $n_i = 85$		Adult *H. mabouia* $n_i = 94$		Juvenile *H. mabouia* $n_i = 39$		Adult *T. torquatus* $n_i = 32$		Juvenile *T. torquatus* $n_i = 18$	
	N%	*V*%	*N*%	*V*%	*N*%	*V*%	*N*%	*V*%	*N*%	*V*%	*N*%	*V*%
Acari	0.00	0.00	1.18	6.20×10^{-5}	6.38	2.60×10^{-4}	2.56	3.14×10^{-3}	0.00	0.00	0.00	0.00
Araneae	6.98	0.06	1.18	1.60×10^{-3}	4.26	0.10	0.00	0.00	3.13	0.01	0.00	0.00
Chilopoda	2.33	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	93.02	50.56	94.12	31.72	63.83	11.95	43.59	8.02	98.75	38.01	94.44	41.69
Diptera	34.88	0.36	68.24	1.70	65.96	6.43	35.90	3.14	75.00	2.60	83.33	5.40
Formicidae	83.72	10.99	100	45.35	32.98	1.33	20.51	0.97	62.50	15.05	66.67	7.57
Hemiptera	44.19	5.55	45.88	1.85	62.77	5.84	43.59	11.77	56.25	2.70	50.00	3.67
Lepidoptera	2.33	0.17	0.00	0.00	1.06	0.08	2.56	0.51	9.38	0.88	0.00	0.00
Mantodea	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nematodes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	3.13	0.02	0.00	0.00
Neuroptera	0.00	0.00	0.00	0.00	1.06	0.08	0.00	0.0	0.00	0.00	0.00	0.00
Odonata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	0.35	0.00	0.00
Orthoptera	46.51	3.35	27.06	0.94	85.11	28.59	84.62	33.03	59.38	13.90	38.89	6.78
Plant	81.40	8.86	80.00	4.57	0.00	0.00	0.00	0.00	18.75	0.06	0.00	0.00
Pulmonata	2.33	0.61	1.18	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Termitoidae	0.00	0.00	0.00	0.00	5.52	2.40	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	4.65	0.04	2.35	2.5×10^{-3}	1.06	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Unknown	79.07	19.09	87.06	13.87	95.74	42.91	87.18	42.58	96.88	26.41	94.44	34.90

than twice the amount of Hemiptera (Table 2). Their SVL's ranged from 1.9–7.0 cm, with an average length of 5.72 ± 0.07 cm for adults, and an average of 2.86 ± 0.08 cm for juveniles.

We collected stomach contents from 50 *T. torquatus*, 32 adults and 18 juveniles. The bulk of *T. torquatus* diet consisted of Coleoptera (38.36%), Formicidae (14.34%), and Orthoptera (13.23%). Adult *T. torquatus* were the only group to have ingested Nematodes and Odonata. In addition, adult *T. torquatus* consumed plant material, while juveniles did not. Further, adult *T. torquatus* ingested more than double the volume of Orthoptera than juveniles. All but one juvenile *T. torquatus* ingested Coleoptera making it close to half of their diet composition (Table 2). Their SVL's ranged from 4.1–12.3 cm, with an average length of 9.25 ± 0.16 cm for adults, and an average of 5.13 ± 0.09 cm for juveniles.

Discussion

Coleoptera, Orthoptera and Formicidae were the most consumed prey across all three species. Combined these prey items were close to 60% of the total ingested volume. Since all three species are considered generalists due to their sit and wait foraging patterns (Bonfiglio et al., 2006; Batista et al., 2011; Drago et al., 2020), high abundance of Coleoptera, Orthoptera and Formicidae in their diets could reflect high abundances in Pilar. Additionally, Coleoptera and Formicidae can be difficult to digest due to unpalatable substances such as quinones and formic acid. Thus, to meet energy requirements, a predator would need to consume large quantities of prey (Hirai and Matsui, 2002; Batista et al., 2011). Surprisingly, we found much higher proportions of plant matter in *R. diptycha's* diet compared to the other species. We also observed lower volumes of Araneae and Diptera across all species than previously reported (Fialho et al., 2000; Bonfiglio, 2007; Batista et al., 2011). Furthermore, two nematodes were present in an adult *T. torquatus* faeces, which are consumed by ant predation (Pereira et al., 2012).

Our findings are well supported by previous studies that investigated the diets of *T. torquatus* despite differences in their diet extraction methodologies. (Fialho et al., 2000; Siqueira et al. 2013; Drago et al., 2020). Drago et al. (2020) observed anthropogenic disturbance to impact diet composition after comparing the diets of *T. torquatus* in Rio de Janeiro to an Atlantic Forest population. The diet compositions of both their urban and rural populations were very similar to ours. Additionally, plant consumption has been reported to be a substantial dietary item in *T. torquatus* populations found in rural sites; flowers and fruits (2–58%) (Fialho et al., 2000; Siqueira et al., 2013). We observed only six individuals to ingest fruit, which contributed to a low volumetric percentage when compared to *T. tropidurus* diets at other sites (Fialho et al., 2000; Siqueira et al., 2013). This could imply that *T. torquatus* might be more selective when optimal prey choices such as fruits and flowers are present, but as a generalist can adapt to the most abundant prey (Siqueira et al., 2013; Drago et al., 2020).

Our results support previous literature that documents *R. diptycha* as an obligate generalist, thus its diet varies greatly by location (Batista et al., 2011; Severgnini et al., 2020; Silva-Alves et al., 2020). Most studies researching *R. diptycha* and other *Rhinella* species note that their diet is primarily comprised of arthropods, specifically Formicidae and Coleoptera, regardless of locality (Sabagh and Carvalho-e-Silva, 2008; Duré et al., 2009; Bastista et al., 2011; Maragano and Souza, 2011). Batista et al. (2011), collected stomach contents from 18 *R. diptycha* at a farm in southwestern Brazil, they reported the major prey items were insect larva, Coleoptera, and Hymenoptera. We identified insect larva into their taxonomic orders or as unidentified if digested, however, we did not observe a large quantity of insect larva in either juvenile or adult *R. diptycha* in our study. Batista et al. (2011) may have observed a much higher quantity of insect larva than we found due to site habitat differences (Mahan and Johnson, 2007; Santana et al., 2019; Roselle et al., 2020). Other studies have documented *R. diptycha* to ingest berries, crabs, and lizards (Oda and Landgraf, 2012; Severgnini et al., 2020; Silva-Alves et al., 2020). However, unlike previous studies we did not find any regionally distinct prey items. We found a large abundance of plant material in *R. diptycha* stomach contents including berries, which could be through accidental consumption or deliberate to grind invertebrate exoskeletons (Anderson et al., 1999).

We found *H. maboiua* diet composition to be substantially different when compared to previous studies. It has been well observed that *H. maboiua* predates Arcanae and Blattodea in large quantities across its South American range (Ramies and Fraguas, 2003; Bonfiglio, 2007; Rocha and Anjos, 2007; Iturriaga and Marrero, 2013). Although we found *H. maboiua* to ingest both Blattodea and Araneae, their percent volumes were minuscule compared to previous studies (Bonfiglio, 2007; Rocha and Anjos, 2007; Iturriaga and Marrero, 2013). Additionally, the Blattodea we found *H. mabouia* to ingest were identified to the infraorder Termitoidae, while the Blattodea Rocha and Anjos (2007) observed were identified to the Blattidae family. Although Blattidae and Temitoidae are within the same order, they are ecologically and morphologically distinct from each other, and thus would represent different prey items (Schal et al., 1984; Bignell and Eggleton, 2000). Rocha and Anjos (2007), examined 291 *H. maboiua* at a farm in Southeastern Brazil and identified 21 arthropod orders, while we only found 11. These differences in diets could be attributed to Pilar being more urbanised, which could have decreased arthropod biodiversity (Magura et al., 2010; Bang and Faeth, 2011; Van Nuland and Whitlow, 2014). Additionally, we used faecal analysis rather than dissection to extract their diets, potentially influencing these results (Hódar et al., 2006; Rocha and Anjos, 2007; Crovetto et al., 2012).

Due to dietary overlap within the study species, there could be potential competition between *H. mabouia* and *T. torquatus*. *Hemdactylus mabouia* is an invasive nocturnal gecko species from Africa and has quickly established itself in urban settings (Rodder et al., 2008). *Tropidurus torquatus* is a native heliophilos lizard species, which is abundant in cities (Fialho et al., 2000). Although both lizard species have different life histories, we found the bulk of their diets to be very similar. Furthermore, when searching for *T. torquatus* populations in Pilar, we only found two relatively small populations, while *H. mabouia* was ubiquitous throughout. *Hemadactylus mabouia* has been shown to outcompete native gecko species that fulfil similar niches throughout the Americas (Short and Petren, 2011; Hughes et al., 2015). Based on low abundances of *T. torquatus* in Pilar and high dietary overlap of the abundant *H. mabouia*, *H. mabouia* might be replacing *T. torquatus* in urban settings. Invasive species replacement can have dire consequences to ecosystem functions (Radford et al., 2020; González-Sánchez et al., 2021; Piquet and López-Darias, 2021). If *H. mabouia* replaces *T. torquatus,* the impact could negatively affect the food web, and other ecosystem services (Pietczak et al., 2013; Cortéz-Gómez et al., 2015; Hughes et al., 2015). Further studies are necessary to test whether *H. mabouia* is outcompeting *T. torquatus* and causing their populations to decline.

We conclude that all three of the study species are generalist opportunistic predators that adapt effectively in an urbanised setting. We suspect the different prey items observed compared to other studies is attributed to their relative abundance in Pilar. Furthermore, it has been strongly debated within the scientific community as to which diet extraction methodology is most suitable (Caputo and Vogt, 2008; Pérez-Mellado et al., 2011; Luiselli et al., 2011; Akmentins and Gastón, 2020). To best assess which methodology is most optimal, we believe more studies (e.g., Crovetto et al., 2012) should compare faecal analysis and stomach flushing within the same individuals.

Acknowledgments. The authors would like to thank Fundación Para La Tierra for use of laboratory facilities and equipment as well as general assistance. We also thank the residents of the city of Pilar for access to study sites. We also would like to thank Michelle VanCompernolle, Madeleine Hiscock, and Brogan L. Pett for their support in the study, and the latter for comments on the manuscript. We also thank two anonymous reviewers whose comments greatly enhanced the manuscript. Permits (process n. 219719) for this research were provided by the Ministerio del Ambiente y Desarrollo (MADES) and ethical aspects of the research were sanctioned by the same organisation and Fundación Para La Tierra. The research complied with all local laws.

References

Akmentins, M.S., Gastón, M.S. (2020): Feeding habits of the threatened aquatic andean frog *Telmatobius rubigo* (Anura: Telmatobiidae). Amphibian and Reptile Conservation **14**(3): 162–168.

Anderson, J.R., Santos, N.F.R., Diaz, H.F. (1993): An analysis of flooding in the Paraná/Paraguay river basin. The Word Bank Latin America and the Caribbean Technical Department Environment Division. LATEN Dissemination Note **5**: 1–68.

Andrade-Díaz, M.S., Sarquis, J.A., Loiselle, B.A., Giraudo, A.R., Díaz-Gómez, J.M. (2019): Expansion of the agricultural frontier in the largest South American dry forest: identifying priority conservation areas for snakes before everything is lost. PLoS ONE **14**(9): 1–23.

Aresco, M.J., Travis, J., MacRae, P.S.D. (2015): Trophic interactions of turtles in a north Florida lake food web: prevalence of omnivory. Copeia **103**(2): 343–356.

Balakrishna, S., Batabyal, A., Thaker, M. (2016): Dining in the city: dietary shifts in indian rock agamas across an urban-rural landscape. Journal of Herpetology **50**(3): 423–428.

Bang, C., Faeth, S.H. (2011): Variation in arthropod communities in response to urbanization: seven years of arthropod monitoring in a desert city. Landscape and Urban Planning **103**(3-4): 383–399.

Banville, M.J., Bateman, H.L. (2012): Urban and wildland herpetofauna communities and riparian microhabitats along the Salt River, Arizona. Urban Ecosystems **15**(2): 473–488.

Batista, R.C., De-Carvalho, C.B., de Freitas, E.B., Franco, S.C., Batista, C.C., Coelho, et al. (2011): Diet of *Rhinella schneideri* (Werner, 1894) (Anura: Bufonidae) in the Cerrado, Central Brazil. Herpetology Notes **4**: 17–21.

Baxter-Gilbert, J., Riley, J.L., Frère, C.H., Whiting, M.J. (2020): Shrinking into the big city: influence of genetic and environmental factors on urban dragon lizard morphology and performance capacity. Urban Ecosystems **24**: 661–674.

Bignell, D.E., Eggleton, P. (2000): Termites in Ecosystems. In Termites: Evolution, Sociality, Symbioses, Ecology, p. 363–387. Abe, T., Bignell, D.E., Higashi, M. Eds., Dordrecht, Netherlands, Springer.

Bonfiglio, F., Balestrin, R.L., Cappellari, L.H. (2006): Diet of *Hemidactylus mabouia* (Sauria, Gekkonidae) in urban area of southern Brazil. Biociencias **14**(2): 107–111.

Cabral, H., Casagranda, M.D., Brusquetti, F., Netto, F., Ferreira, V., Lavilla, E. (2020): Multiscale endemism analysis for amphibians of Paraguay. Herpetological Journal **30**(1): 35–46.

Cacciali, P., Cabral, H., Yanosky, A.A. (2015): Conservation implications of protected areas' coverage for Paraguay's reptiles. Parks **21**(2): 101–119.

Cacciali, P., Scott, N.J., Luz, A., Ortíz, A., Fitzgerald, L.A., Smith, P. (2016): The reptiles of Paraguay: literature, distribution, and an annotated taxonomic checklist. Museum of Southwestern Biology Special Publications **11**: 1–373.

Canese de Estigarribia, M.I.C., Espínola, C.M.V., Sagüi, N.J., Díaz, G.A.I., Pignata, R.M., Gauto, N.A.V., et al. (2019): Popular urbanization in Asuncion, Paraguay. Revista INVI **34**(95): 9–42.

Caputo, F.P., Vogt, R.C. (2008): Stomach flushing vs. fecal analysis: the example of *Phrynops rufipes* (Testudines: Chelidae). Copeia **2**: 301–305.

Comas, M., Reguera, S., Zamora-Camacho, F.J., Moreno-Rueda, G. (2020): Age structure of a lizard along an elevational gradient reveals nonlinear lifespan patterns with altitude. Current Zoology **66**(4): 373–382.

Cortéz-Gómez, M.A.M., Ruiz-Agudelo, C.A., Valencia-Aguilar, A., Ladle, R.J. (2015): Ecological functions of neotropical amphibians and reptiles: a review. Universitas Scientiarum **20**(2): 229–245.

Crovetto, F., Romano, A., Salvidio, S. (2012): Comparison of two non-lethal methods for dietary studies in terrestrial salamanders. Wildlife Research **39**(3): 266–270.

Das, I., van Dijk, P.P. (2013): Species richness and endemicity of the herpetofauna of south and southeast Asia. Raffles Bulletin of Zoology **29**: 269–277.

de Almeida-Rocha, J.M., Peres, C.A., Monsalvo, J.A.B., Oliveira, L.D.C. (2020): Habitat determinants of golden-headed lion tamarin (*Leontopithecus chrysomelas*) occupancy of cacao agroforests: gloomy conservation prospects for management intensification. American Journal of Primatology **82**(9): 1–15.

Drago, M.C., Kato, M.M., Koster, R., Vrcibradic, D. (2020): How does habitat anthropization influence lizard diets? An analysis comparing two populations of *Tropidurus torquatus* (Iguania). Journal of Herpetology **54**(2): 144–150.

Duré, I.M., Kehr, I.A., Schaefer, F.E. (2009): Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. Phyllomedusa **8**(1): 27–39.

Esri (2021): World topographic basemap. Available at https://www.arcgis.com/home/item.html?id=30e5fe3149c34df1ba922e6f5bbf808f Accessed on 10 May 2022.

Esri (2022): Terrain with labels basemap. Available at https://www.arcgis.com/home/item.html?id=a52ab98763904006aa382d90e906fddAccessed on 10 May 2022.

Fialho, R.F., Rocha, C.F.D., Vrcibradic, D. (2000): Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. Journal of Herpetology **34**(2): 325–330.

Gambale, P.G., da Silva, M.R., Oda, F.H., Bastos, R.P. (2020): Diet and trophic niche of two sympatric *Physalaemus* species in central Brazil. South American Journal of Herpetology **17**(1): 63–70.

Gámez, S., Potts, A., Mills, K.L., Allen, A.A., Holman, A., Randon, P.M., Linson, O., Harris, N.Y. (2022): Downtown diet: a globel meta-analysis of increased urbanization on the diets of vertebrate predators. Proceedings of the Royal Society B **289**: 20212487.

Ghazi, A.H. (2020): Dietary competition between the local shrimp *Metapenaeus affinis* and the invasive *Macrobrachium nipponense* shrimp southern Iraq. EurAsian Journal of BioSciences **14**: 4769–4776.

González-Sánchez, V.H., Johnson, J.D., González-Solís, D., Allison Fucsko, L., Wilson, L.D. (2021): A review of the introduced herpetofauna of Mexico and Central America with comments on the effects of invasive species and biosecurity methodology. ZooKeys **1022**: 79–154.

Guiry, E., Buckley, M. (2018): Urban rats have less variable, higher protien diets. Proceedings of the Royal Society B **285**: 20181441.

Hidalgo-Ruz, V., Gutow, L., Thompson, R.C., Thiel, M. (2012): Microplastics in the marine environment: A review of the methods used for identification and quantification. Environmental Science and Technology **46**(6): 3060–3075.

Hirai, T., Matsui, M. (2002): Society for the study of amphibians and reptiles feeding ecology of *Bufo japonicus formosus* from the montane region of Kyoto, Japan. Journal of Herpetology **36**(4): 719–723.

Hódar, J.A., Pleguezuelos, J.M., Villafranca, C., Fernández-Cardenete, J.R. (2006): Foraging mode of the Moorish gecko *Tarentola mauritanica* in an arid environment: inferences from abiotic setting, prey availability and dietary composition. Journal of Arid Environments **65**(1): 83–93.

Huang, C., Kim, S., Altstatt, A., Townshend, J.R.G., Davis, P., Song, K., et al. (2007): Rapid loss of Paraguay's atlantic forest and the status of protected areas - a landsat assessment. Remote Sensing of Environment **106**(4): 460–466.

Hughes, D.F., Meshaka, W.E., Van Buurt, G. (2015): The superior colonizing gecko *Hemidactylus mabouia* on Curaçao: Conservation implications for the native gecko *Phyllodactylus martini*. Journal of Herpetology **49**(1): 60–63.

International Union for the Conservation of Nature (IUCN), Species Survival Commission (SSC) Amphibian Specialist Group. (2017): Available at https://www.iucn.org/commissions/ssc-groups/amphibians-reptiles/amphibian. Accessed on 10 March 2021.

Iturriaga, M., Marrero, R. (2013): Feeding ecology of the tropical house gecko *Hemidactylus mabouia* (Sauria: Gekkonidae) during the dry season in Havana, Cuba. Herpetology Notes **6**: 11–17.

Jestrzemski, D., Schuetz, S. (2015): Arthropods as predators of herpetofauna in the Chu Mom Ray National Park, Vietnam. Asian Journal of Conservation Biology **5**(1): 3–15.

Kalb, D.M., Bowman, J.L., DeYoung, R.W. (2018): Dietary resource use and competition between white-tailed deer and introduced sika deer. Wildlife Research **45**(5): 457–472.

Larson, R.N., Brown, J.L., Karels, T., Riley, S.P.D. (2020): Effects of urbanization on resource use and individual specialization in coyotes (*Canis latrans*) in southern California. PLoS ONE **15**(2): e0228881.

Le, D.T.T., Rowley, J.J.L., Tran, D.T.A., Vo, T.N., Hoang, H.D. (2018): Diet composition and overlap in a montane frog community in Vietnam. Herpetological Conservation and Biology **13**(1): 205–215.

Lesbarrères, D., Ashpole, S.L., Bishop, C.A., Blouin-Demers, G., Brooks, R.J., Echaubard, P., et al., (2014): Conservation of herpetofauna in northern landscapes: threats and challenges from a Canadian perspective. Biological Conservation **170**: 48–55.

Luiselli, L., Akani, G.C., Ebere, N., Pérez-Mellado, V. (2011): Stomach flushing affects survival/emigration in wild lizards: a study case with rainbow lizards (*Agama agama*) in Nigeria. Amphibia-Reptilia **32**(2): 253–260.

Machovsky-Capuska, G.E., Miller, M.G.R., Silva, F.R.O., Amiot, C., Stockin, K.A., Senior, A.M., et al. (2018): The nutritional nexus: linking niche, habitat variability and prey composition in a generalist marine predator. Journal of Animal Ecology **87**(5): 1286–1298.

Mackenzie, C.M., Vladimirova, V. (2021): Preliminary study and first evidence of presence of microplastics in terrestrial herpetofauna from southwestern Paraguay. Studies on Neotropical Fauna and Environment 1–9.

Magura, T., Lövei, G.L., Tóthmérész, B. (2010): Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? Global Ecology and Biogeography **19**(1): 16–26.

Mahan, D.R., Johnson, J.R. (2007): Diet of the gray treefrog (*Hyla versicolor*) in relation to foraging site location. Journal of Herpetology **41**(1): 16–23.

Maragano, P.F., Souza L F. (2011): Diet of *Rhinella scitula* (Anura, Bufonidae) in the Cerrado, Brazil: the importance of seasons and body size. Revista Mexicana de Biodiversidad **82**(3): 879–886.

Mollov, I., Boyadzhiev, P., Donev, A. (2012): Trophic niche breadth and niche overlap between two lacertid lizards (Reptilia: Lacertidae) from south Bulgaria. Acta Zoologica Bulgarica **4**: 129–136.

Motte, M., Núñez, K., Cacciali, P., Brusquetti, F., Scott, N., Aquino, A.L. (2009): Categorización del estado de conservación de los Anfibios y Reptiles de Paraguay. Cuadernos de Herpetología **23**(1): 5–18.

Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S., St. Clair, C.C. (2015): Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. Ecography **38**(12): 1235–1242.

Nori, J., Leynaud, G.C., Volante, J., Abdala, C.S., Scrocchi, G.J., Rodríguez-Soto, C., Pressey, R.L., Loyola, R. (2018): Reptile species persistence under climate change and direct human threats in north-western Argentina. Environmental Conservation **45**(1): 83–89.

Nowakowski, A.J., Frishkoff, L.O., Thompson, M.E., Smith, T.M., Todd, B.D. (2018): Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. Proceedings of the National Academy of Sciences of the United States of America **115**(15): E3453–E3462.

Oda, F.H., Landgraf, G.O. (2012): An unusual case of scavenging behavior in *Rhinella schneideri* in the upper Paraná River basin, Brazil. Boletín de la Asociación Herpetológica Española **23**(1): 57–59.

O'Donnell, C.F.J., Weston, K.A., Monks, J.M. (2017): Impacts of introduced mammalian predators on New Zealand's alpine fauna. New Zealand Journal of Ecology **41**(1): 1–22.

Peneaux, C., Grainger, R., Lermitea, F., Machovsky-Capuska, G.E., Gastond, T., Griffind, A.S. (2021): Detrimental effecs of urbanization on the diet, health, and signal coloration of an ecologically successful alien bird. Science of the Total Environement **796**: 148828.

Pérez-Mellado, V., Pérez-Cembranos, A., Garrido, M., Luiselli, L., Corti, C. (2011): Using faecal samples in lizard dietary studies. Amphibia-Reptilia **32**(1): 1–7.

Pereira, F.B., Sousa, B.M., De Souza Lima, S. (2012): Helminth community structure of *Tropidurus torquatus* (Squamata: Tropiduridae) in a rocky outcrop area of Minas Gerais state, southeastern Brazil. Journal of Parasitology **98**(1): 6–10.

Pietczak, C., Steindorf de Arruda, J.L., Cechin, S.Z. (2013): Frugivory and seed dispersal by *Tropidurus torquatus* (Squamata: Tropiduridae) in southern Brazil. Herpetological Journal **23**: 75–79.

Piquet, J.C., López-Darias, M. (2021): Invasive snake causes massive reduction of all endemic herpetofauna on Gran Canaria. Proceedings of the Royal Society B **288**: 20211939.

Powers, S.D., McTernan, M.R., Powers, D.R., Anderson, R.A. (2018): Energetic consequences for a northern, range-edge lizard population. Copeia **106**(3): 468–476.

Radford, I.J., Woolley, L.E., Dickman, C.R., Corey, B., Trembath, D., Fairman, R. (2020): Invasive anuran driven trophic cascade: an alternative hypothesis for recent critical weight range mammal collapses across northern Australia. Biological Invasions **22**: 1967–1982.

Ramies, E.N., Fraguas, G.M. (2003): Tropical house gecko (*Hemidactylus mabouia*) predation on brown spiders (*Loxosceles intermedia*). Journal of Venomous Animals and Toxins including Tropical Diseases **10**(2): 185–190.

Robins, C.W., Kertson, B.N., Faulkner, J.R., Wirsing, A.J. (2019): Effects of urbanization on cougar foraging ecology along the wildland–urban western Washington. Ecosphere **10**(3): e02605.

Rocha, C.F.D., Anjos, L.A. (2007): Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. Brazilian Journal of Biology **67**(3): 485–491.

Rodder, D., Solé, M., Bohme, W. (2008): Predicting the potential distributions of two alien invasive housegeckos (Gekkonidae: *Hemidactylus frenatus, Hemidactylus mabouia*). North-Western Journal of Zoology **4**(2): 236–246.

Roselle, J., Gersava, D., Abad, R.G., Camino, F.A., Responte, M.A., John, M., et al. (2020): Native and invasive alien anuran species in urbanized areas in Davao City, Philippines, with preliminary study of feeding biology. Biological Diversity and Conservation **13**(1): 1–8.

Sabagh, T.L., Carvalho-e-Silva, T.P. (2008): Feeding overlap in two sympatric of sympatric species of species of *Rhinella* (Anura: Bufonidae) of the Atlantic Rain Forest. Revista Brasileira de Zoologia **25**(2): 247–253.

Santana, D.J., Ferreira, V.G., Crestani, G.N., Neves, M.O. (2019): Diet of the Rufous Frog *Leptodactylus fuscus* (Anura, Leptodactylidae) from two contrasting environments. Herpetozoa **32**(1): 1–6.

Saufi, S., Ravindran, S., Hamid, N.H., Abidin, C.M.R.Z., Ahmad, H., Ahmad, A.H., Salim, H. (2020): Diet composition of introduced barn owls (*Tyto alba javanica*) in urban area in comparison with agriculture settings. Journal of Urban Ecology **6**(1): 1–8.

Schal, C., Gautier, J.Y., Bell, W.J. (1984): Behavioural ecology of cockroaches. Biological Reviews **59**(2): 209–254.

Schoener, T.W., Spiller, D.A., Losos, J.B. (2002): Predation on a common *Anolis* lizard: Can the food-web effects of a devastating predator be reversed? Ecological Monographs **72**(3): 383–407.

Schwartz, S.E. (2018): Unrealized global temperature increase: implications of current uncertainties. Journal of Geophysical Research: Atmospheres **123**(7): 3462–3482.

Severgnini, M.R., Moroti, M. de T., Pedrozo, M., Ceron, K., Santana, D.J. (2020): Acerola fruit: an unusual food item for the cururu toad *Rhinella diptycha* (Cope, 1862) (Anura: Bufonidae). Herpetology Notes **12**: 7–10.

Short, K.H., Petren, K. (2011): Rapid species displacement during the invasion of Florida by the tropical house gecko *Hemidactylus mabouia*. Biological Invasions **14**(6): 1177–1186.

Silva-Alves, V.D., Canale, G.R., da Costa, T.M., Muniz, C.C., Dos Santos Filho, M., da Silva, D.J. (2020): Record of the crabs *Poppiana argentiniana* (Rathbun, 1905) and *Valdivia camerani* (Nobili, 1896) in the diet of *Rhinella diptycha* (Cope, 1862) (Anura: Bufonidae), in the pantanal mato-grossense, Brazil. Herpetology Notes **13**: 309–312.

Silvano, D.L., Segalla, M.V. (2005): Conservation of Brazilian Amphibians. Conservation Biology **19**(3): 653–658.

Siqueira, C.C., Kiefer, M.C., Van Sluys, M., Rocha, C.F.D. (2013): Variation in the diet of the lizard *Tropidurus torquatus* along its coastal range in Brazil. Biota Neotropica **13**(3): 93–101.

Solé, M., Beckmann, O., Pelz, B., Kwet, A., Engels, W. (2005): Stomach-flushing for diet analysis in Anurans: An improved protocol evaluated in a case study in Araucaria forests, southern Brazil. Studies on Neotropical Fauna and Environment **40**(1): 23–28.

Sutherland, D.R. (2011): Dietary niche overlap and size partitioning in sympatric varanid lizards. Herpetologica **67**(2): 42–49.

Tucker, M.A., Santini, L., Carbone, C., Mueller, T. (2021):

Mammal population densities at a global scale are higher in human-modified areas. Ecography **44**(1): 1–13.
Ursprung, E., Ringler, M., Jehle, R., Hödl, W. (2011): Toe regeneration in the neotropical frog *Allobates femoralis*. Herpetological Journal **21**(1): 83–86.
Valtonen, E.T., Marcogliese, D.J., Julkunen, M. (2010): Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. Oecologia **162**(1): 139–152.
Van Nuland, M.E., Whitlow, W.L. (2014): Temporal effects on biodiversity and composition of arthropod communities along an urban–rural gradient. Urban Ecosystems **17**(4): 1047–1060.
Ward-Fear, G., Shine, R., Brown, G.P. (2020): Within-population variation in dietary traits: implications for vulnerability and impact of imperiled keystone predators. Ecosphere **11**(10): e03136.
White, J.L., Fleming, P.A. (2021): Potential for dietary competition between the threatened black-flanked rock wallaby and sympatric western grey kangaroo. Journal of the Australian Mammal Society **44**(2): 243–255.
Wolfe, A.K., Bateman, P.W., Fleming, P.A. (2018): Does urbanization influence the diet of a large snake? Current Zoology **64**(3): 311–318.

Accepted by Fabrício Hiroiuki Oda