Dietary Competition Between *Hemidactylus mabouia* (Sauria: Gekkonidae) and a Native Anuran in Pilar, Paraguay

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Abstract.—In the Americas, the invasive Tropical House Gecko (*Hemidactylus mabouia*) is ubiquitous in urban environments, but its potential threats to native species are understudied. To evaluate the risk of dietary competition, we conducted dietary composition and niche analyses from fecal samples obtained from *H. mabouia* and native Anurans encountered during standardized visual surveys in the city of Pilar, Paraguay. We collected data on *H. mabouia*, native Rococo Toads (*Rhinella diptycha*), and four frog species; however, we removed the frog data from analysis due to small total sample size (n = 10). Our results indicate considerable dietary differences across the lifecycle of *H. mabouia*. Adults had more specialized diets consisting largely of Coleoptera. Juveniles had more generalist diets consisting largely of Hemiptera. *Rhinella diptycha* were more specialized feeders than *H. mabouia*, primarily consuming Coleoptera. We encountered approximately two-thirds of *H. mabouia* and *R. diptycha* in artificially lighted habitats. Specimens found in artificially lighted habitats had marginally higher diet breadth, suggesting exploitation of lighted habitats for dietary gain. A high dietary niche overlap between *H. mabouia* and *R. diptycha* suggests the potential for direct and/or indirect competition, depending on the use of shared niches. We found a high niche overlap between juvenile *H. mabouia* and *R. diptycha*, highlighting the importance of evaluating the influence of life stage when assessing the impacts invasive species. We also incidentally documented microplastics in the feces of all taxonomic groups, providing, to our knowledge, the earliest record of microplastic ingestion by terrestrial herpetofauna in South America..

Key Words.—diet; invasive species; interspecific competition; niche breadth; niche overlap; Paraguay; *Rhinella diptycha*; urban

Introduction

Invasive species have detrimental impacts on native biodiversity and natural environments all over the world. If a non-native species is introduced and it becomes invasive, the balance in an ecosystem can be disrupted, resulting in potential interspecific competition with native species and trophic niche divergence (Tran et al. 2015). A divergence in the trophic niche can facilitate successful integration of a non-native species into an ecosystem (e.g., Jackson and Britton 2014). When resources are not fully exploited within an ecosystem, vacant niches can be occupied by these newly introduced species, and this increases the risk of their becoming invasive by reducing interspecific competitive pressure with native species and enabling coexistence (Shea and Chesson 2002; Jackson and Britton 2014). When interspecific competition does occur, it can result in temporal shifts within the niche as a mechanism to avoid interspecific conflict (Harrington et al. 2009; McCauley et al. 2012). When two species

compete for a shared resource, the outcome may be coexistence or one species may outcompete the other, with the latter potentially leading to population reductions and displacements or even extirpation of remanent natives (Leger and Espeland 2010). Reduced competition and the ability to coexist is promoted when there is a considerable divergence in niche occupation and little interaction within other niches (Hardin 1960; Koutsidi et al. 2020).

Native to Africa, the Tropical House Gecko (*Hemidactylus mabouia*) is a species of gecko that has successfully colonized much of Central and South America since the 19th Century (de Albuquerque et al. 2013). These opportunistic and generalist insectivores typically predate on Diptera, Lepidoptera, and non-flying Arthropoda (Iturriaga and Marrero 2013; Drüke and Rödder 2017) and have also been known to cannibalize other geckos (Bonfiglio et al. 2006). Additionally, *Hemidactylus* species are highly adaptable, which allows them to exploit a wide range of environments including well-lighted urban niches that

many native species avoid (e.g., Zozaya et al. 2015). Nevertheless, this ability to exploit the urban niche and the generalist feeding behaviors of *Hemidactylus* can result in resource competition with the native herpetofauna (Rocha and Anjos 2007). Native lizard populations have already faced population declines in the Pacific Islands as a result of the depletion of food resources from a *Hemidactylus* species (Petren and Case 1996) and evidence of interspecific competition has been observed in Barbados, where *H. mabouia* and the Barbados Leaf-toed Gecko (*Phyllodactylus pulcher*) compete for food resources and diurnal refuge sites (Williams et al. 2016).

Although competition between invasive *Hemidactylus* species and native lacertilians has been observed (Harfmann Short and Petren 2012; Williams et al. 2016), it is less clear whether they have negatively impacted other groups of native herpetofauna found in the same environments. Native Anurans, such as the Warty Snouted Tree Frog (*Scinax acuminatus*; Anura: Hylidae) and the Rococo Toad (*Rhinella diptycha*; Anura: Bufonidae), are often found alongside the introduced *H. mabouia* in damp spaces of buildings throughout urban environments in many parts of South and Central America (Smith, P. 2006. Warty Snouted Tree Frog *Scinax acuminatus* CHACO. Fauna Paraguay. Available from http://www.faunaparaguay.com/scinaxacuminatus.html [Accessed 27 September 2018]). Other Anuran genera, such as *Leptodactylus* (Anura: Leptodactylidae) and *Hypsiboas* and *Dendropsophus* (Anura: Hylidae), are also found in the urban environment, attracted to urban water bodies. Similar to *H. mabouia*, *Scinax*, *Hypsiboas*, and *Dendropsophus* tend to be more arboreal genera, in contrast to the ground dwelling *Rhinella* and *Leptodactylus* (Teixeira and Vrcibradic 2003; Moravec et al. 2008; Sabagh et al. 2010). There is still, however, opportunity for overlap in trophic niche as all species are known to optimize artificially lighted urban habitats (e.g., Perry and Fisher 2006; Perry et al. 2008; Martín et al. 2018), which are known to have an increased relative abundance of invertebrates (Bruce-White and Shardlow 2011; Davies et al. 2012; de Medeiros et al. 2017; Komine et al. 2020). Exploitation of shared trophic resources and artificially lighted habitats could impact the local abundance of prey species, resulting in indirect competition for these resources (Prasad 2022).

Additionally, species of the *Scinax* and *Rhinella* genera have similar generalist and opportunistic feeding habits to *H. mabouia* (de Carvalho Batista et al. 2011). Over half of the dietary composition of *Scinax* species are insects, with the most frequently consumed food source being Diptera (32% of food items) and the remainder of their diet largely consisting of Arachnida, Gastropoda, and Clitellata species (Kittel and Solé 2015). Similarities can be seen in the dietary composition of *Hypsiboas* and *Dendropsophus*, with Dipterans, Aranae, Lepidopterans, Hemipterans, Homopterans, and Coleopterans representing valuable prey items in their dietary composition (López et al. 2009; Castro et al. 2016; Leivas et al. 2018). *Rhinella* is a genus of toad native to the Neotropical region found in both urban and rural environments with diets consisting of Formicidae, Coleoptera, and various insect larvae (de Carvalho Batista et al. 2011). Coleopterans also represent a considerable part of the dietary composition of *Leptodactylus*, as do Orthopterans and Hemipterans (Ceron et al. 2018). Similarities in trophic preference can be seen between *H. mabouia*, and native Anurans, like *Scinax, Hypsiboas, Dendropsophus, Leptodactylus,* and *Rhinella* species (e.g., de Carvalho Batista et al. 2011; Iturriaga and Marrero 2013; Kittel and Solé 2015).

Similarities in trophic preferences such as those described above may lead to trophic niche overlap, in which species share resources, and potential indirect competition. When species exhibit high niche overlap, this raises the potential for multiple types of interactions. For example, competition and exclusion may occur (Giménez Gómez et al. 2018; Pascual-Rico et al. 2020). Alternatively, species that experience strong interactions within a single niche may be able to coexist by having limited interactions in other niches (Koutsidi et al. 2020). In contrast, low niche overlap can suggest sustainable co-existence due to limited interaction (Koutsidi et al. 2020; Yang and Hui 2020).

The observed dietary similarities described above are especially concerning given that increases in species introductions during the Anthropocene has led to considerable amphibian diversity loss, with 16% of species in decline due to invasive species (Nunes et al. 2019). This underscores the importance of evaluating the ecological impacts of *H. mabouia* invasions on the native Anurans in South America. Therefore, our aim is to evaluate the potential for interspecific competition between *H. mabouia* and native Anurans in an urban environment. As such, we conducted a dietary analysis of urban-dwelling *H. mabouia* and *R. diptycha* and four species of frog within Hylidae and Leptodactylidae (Butter Frog, *Leptodactylus letrans*, Warty Snouted Treefrog, *Scinax acuminatus*, Polka Dot Treefrog, *Hypsiboas punctatus*, and Dwarf Treefrog, *Dendropsophus nanus*).

Materials and Methods

Study area.—Pilar, the capital city of the Ñeembucú Department in southwest Paraguay, is situated alongside the Rio Paraguay and Arroyo Ñeembucú and is surrounded by a large expanse of wetland habitats. Despite being an urban environment, Pilar supports a wide range of herpetofauna. Invasive *H. mabouia* are

found predominantly within the city limits, whereas *R. diptycha*, *S. acuminatus*, and other native anurans are found throughout the city, congregating by the edge of the river and in isolated artificial pockets of water within buildings. The study area included three transects in the inner-city area and one transect on the boardwalk along the riverbank, called the *Costanera*. Each of the four transects was 1 km in length, representing typical levels of urbanization for Pilar, and had no overlap to ensure that a large area of the city was covered. We selected transects based on accessibility by foot and proximity to the research center, located in the North of Pilar. Inner-city transects covered a 0.38 km^2 area and consisted mostly of human-made surfaces on the outside of buildings with some vegetated areas. The *Costanera* transect followed the boardwalk along the edge of the river and consisted mostly of paved and vegetated areas.

Data collection.—We collected *H. mabouia* and native Anurans through Visual-Encounter Surveys between August and November 2018 (Davis et al. 2020). Each survey night, we surveyed one of the four transects for 1 h of extensive active searching on all surfaces between 2000 and 2300 (Bonfiglio et al. 2007). Each transect was repeated five times, resulting in 20 total survey nights. The inner-city transect consisted mostly of pavement, vegetation, and the outsides of properties, whereas the *Costanera* transect included pavement, riverbank, vegetation, and the boardwalk wall. When possible, we collected specimens by hand. For specimens that were out of reach, we used a 60 cm diameter butterfly net on a 150 cm pole for capture and a second 150 cm pole to guide the individual towards the net entrance. Once a specimen was caught, we paused the 1 h timer to allow for data collection.

For each captured individual, we measured and recorded the snout-vent length (SVL), distance from refuge site, lighting conditions, ambient temperature, and ambient humidity. We categorized lighting conditions as lighted (lit), partially lit, and unlit. We defined lighted conditions as being fully illuminated by an artificial light source in immediate proximity, partially lighted conditions as having low levels of illumination from an artificial light source located within close proximity, and unlighted conditions as having no artificial light source. A refuge site was defined as any hiding space a specimen could use to evade capture, for example roof rafters or a wall crevice. We visually estimated distance from refuge site into two groups: < 0.5 m from a refuge site and > 0.5 m from a refuge site.

We transported captured *H. mabouia* and frog specimens from the field to the laboratory in separate numbered glass jars and transported captured toad specimens in separate numbered cotton bags. We securely placed specimens in a cool box for safe transportation. We kept all captured specimens in separate containers for 24 h to allow sufficient time for defecation to occur and to avoid mixing up fecal samples. We maintained *H. mabouia* and Hylid species in large jars with air holes in the lids for airflow and we included a wet cotton ball for water. Due to their larger size, we housed *R. diptycha* and Leptodactylid species in glass terrariums and lidded buckets with a petri dish of water. We stored all enclosures containing specimens indoors, in a room with minimal disturbance (such as noises from walking), and under a large bedsheet to minimize stress to these nocturnal species. After 24 h, we examined each enclosure, collected any feces, and released all specimens back at their sites of capture.

Data collection.—To dissect fecal samples, we used 70% ethanol and a SZMT2 stereo-microscope (AmScope, Irvine, California, USA). We identified, counted, and measured digested material using the digital calipers on the AmScope computer software with an AmScope MU1003 microscope camera. We identified food items to the taxonomic level of Order, except for Hymenoptera, in which Formicidae was distinguished from all other Hymenoptera. Additionally, we recorded and measured the presence of plant material and inorganic food items, such as plastic and fine sediment. We calculated the volume of wings using length, width, and an average wing depth of 0.02 mm. For all other food items, we measured the lengths and widths to calculate the volume of each food item using the ellipsoid formula:

$$Volume = \frac{\pi \cdot Length \cdot Width^2}{6}$$

For each fecal sample, we calculated the total volume of each prey type by summing the volumes of individual food items belonging to the same prey type (e.g., Formicidae). For *R. diptycha* (previous known as *R. schneideri;* Lavilla and Brusquetti 2018), given the larger volume of fecal matter produced, we only analyzed one quarter of each sample (by volume), and multiplied the resulting food item volumes by four for analysis.

Using the volumetric calculations, we calculated the proportion of diet represented by each prey items (> 5% of total prey consumed) for *H. mabouia*, Hylidae, Leptodactylidae, and *R. diptycha*. To calculate volumetric proportion of diet for each taxon, we summed the total volume of each prey item that we then divided by the total volume of all the prey items consumed. We also calculated the volumetric proportion of diet for juvenile (SVL < 3.5 cm) and adult *H. mabouia* separately (https://animaldiversity.org/accounts/ Hemidactylus_mabouia/). To determine how similar the

usage of shared resources is between different species within a niche, we calculated Levins' Niche Breadth (B; Levins 1968) as:

$$B = \frac{1}{\sum p_i^2}$$

where p_i is volumetric proportion of items in the diet of food category i. We calculated B for the following groups: (1) *R. diptycha*; (2) Frogs (*Leptodactylus letrans*, *Scinax acuminatus*, *Hypsiboas punctatus*, and *Dendropsophus nanus*); (3) Juvenile *H. mabouia*; (4) Adult *H. mabouia*; and (5) All *H. mabouia* age groups. To take into consideration the number of different prey items consumed by each species group, we standardized niche breadth values (Hurlbert 1978):

$$B_A = \frac{B-1}{n-1}$$

where B_A is the Standardized B and n is the number of prey types used by the species group of interest. Standardized values range from 0 to 1, with higher values indicating more generalized feeding behaviors. To better understand the factors impacting the niche breadth of invasive *H. mabouia* in Pilar, we calculated B measures for *H. mabouia* based on distance from refuge site (> vs. ≤ 0.50 m), and lighting conditions (unlit vs. lit or partially lit).

Whereas niche breadth indicates how specialized or generalized a species is within a certain environment, it does not indicate whether the potential for competition exists between different taxa. For this reason, we used the Pianka index (Pianka 1986) to determine the niche overlap and diet uniformity between invasive *Hemidactylus* and native Anurans. The Pianka index is calculated as:

$$O_{jk} = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 P_{ik}^2}}$$

where O_{jk} indicates the Pianka Niche Overlap between species group j and k, P_{ij} is the proportion that food item i is of the total food items used by species j, and P_{ik} is the proportion that food item i is of the total food items used by species k. Values range from 0 to 1, with lower numbers indicating fewer shared dietary items and a value of 1 indicating complete dietary overlap.

We analyzed all our data with MATLAB R2020a (MathWorks, Inc. 1996). We performed Fisher's Exact Tests to evaluate differences between taxa groups in their exploitation of the urban lighted environment (α = 0.05). We also used a Wilcoxon Rank Sum Test to evaluate differences in distances from hiding spaces between taxa groups (α = 0.05).

RESULTS

Survey results.—We captured 196 specimens during 20 visual encounter surveys across a four-month survey period.; however, the sample size of captured frog specimens was too small to be considered for further analysis (n = 10 specimens across four species). Ambient temperature ranged from 17.3° C to 30.6° C with an average ambient temperature of 26.6° ± 2.7° C. Of the captured *H. mabouia*, we encountered 72% in lit or partially lit habitats. No significant relationship (Fisher's Exact Test, $P > 0.05$) was found between *H. mabouia* and *R. diptycha* (69%) preference for lit or unlit habitats. We encountered R. diptycha further from refuge sites than H. mabouia ($P = 0.0098$, df = 54, Z = 2.5813), but no significant relationships were found between other taxa groupings.

Of the 121 *H. mabouia* captured, 38 provided fecal samples (31.4%) within the 24-h waiting period. Of these individuals, 24 were adults and 11 were juveniles (Lennox 2017, *op. cit.*). We did not measure SVL for three *H. mabouia* individuals, which we consequently omitted from the analyses for adult and juvenile groupings but included in all other analyses. Of the 49 collected *R. diptycha* specimens, 20 provided fecal samples (40.8%) and had an average SVL of 12.8 ± 1.5 cm (range, 8.4–14.3 cm).

Dietary results.—Fecal samples from *H. mabouia* had a volumetric mean of 24.9 mm³ (± 24.6 mm³), and samples from *R. diptycha* had a volumetric mean of 4,915 mm³ (± 5,050 mm³). *Hemidactylus mabouia* consumed 11 prey types, with nearly half of their diet consisting of Coleoptera (43.7%; Fig. 1), whereas Hemiptera (28.4%), Formicidae (10.0%), Blattodea (6.2%), and Diptera (5.5%) also occurred at high proportions (Table 1). There was considerable variation between juvenile and adult dietary composition. Juveniles consumed seven prey types dominated by Hemiptera (43.6%) and Formicide (32.6%), whereas adults consumed 10 prey types dominated by Coleoptera (47.2%) and Hemiptera (26.7%). *Rhinella diptycha* consumed seven prey types, but two thirds of their diet was composed of Coleoptera (63.6%), with smaller proportions of Formicidae (13.4%), Diptera (5.9%), and Hemiptera (5.7%). Of the frog species, *D. nanus* (n = 1) predominantly consumed Hempitera (73.4%) and Diptera (26.1%), *H. punctatus* (n = 2) predominantly consumed Orthoptera (79.5%) and Formicadae (20.5%), *S. acuminatus* (n = 6) predominantly consumed Coleoptera (38%) and Aranae (32%), and *L. letrans* (n = 1) predominantly consumed Formicadae (43%; Table 2).

In addition to food items, we found microplastics (Fig. 1) in 18 *H. mabouia* samples (47.4%), four of
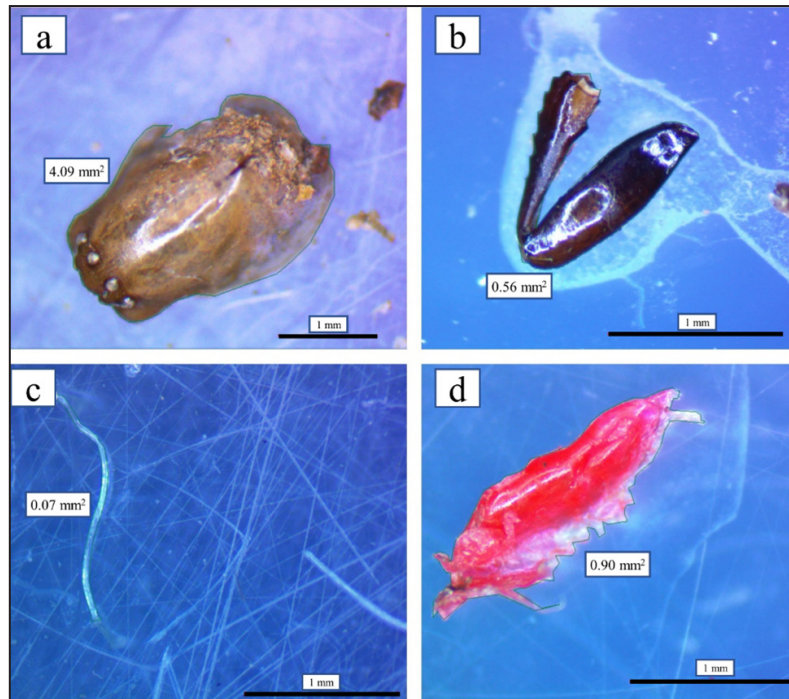
FIGURE 1. Examples of fecal sample content including (a) an Araneae head (4.09 mm^2) from a frog sample, (b) A beetle tibia and femur (0.56 mm^2) from a gecko sample, (c) a microplastic fiber (0.07 mm^2) from a toad sample, and (d) a microplastic fragment (0.90 mm^2) from a gecko sample. (Photographed by Madeleine Hiscock).

which were from juveniles and 14 from adults, three frog samples (30%), and three *R. diptycha* samples (15%). *Hemidactylus mabouia* consumed microplastics significantly more often than native *R. diptycha* (Fisher's Exact Test, $P = 0.021$), and individual *H. mabouia* consumed, on average, more pieces of microplastics than native *R. diptycha* ($W = 507.5$, df $= 56$, $P = 0.015$). Levin's Niche Breadth ranged from 0.171 to 0.381, with *R. diptycha* having the lowest niche breadth. Juvenile *H. mabouia* had a larger niche breadth than adults (Table 3). *Hemidactylus mabouia* individuals encountered in a fully or partially lit habitat had a marginally higher niche breadth, than specimens encountered in unlit conditions (Table 4). *Hemidactylus mabouia* individuals captured < 0.5 m from the nearest refuge had a higher niche breadth (Table 5). Pianka index values indicated a relatively low niche overlap between juvenile *H. mabouia* and *R. diptycha* (0.380) compared with the higher niche overlap observed between adult *H. mabouia* and *R. diptycha* (Table 3). We found a moderate niche overlap between adult and juvenile *H. mabouia* specimens (0.642). When analyzed by lighting condition, the amount of niche overlap was substantial between *R. diptycha* and *H. mabouia* caught in both lit (0.749) and unlit (0.969) conditions (Table 4). When analyzed by distance caught from the nearest refuge site, there was considerable niche overlap between *R. diptycha* and *H. mabouia* caught both < 0.5 m (0.788) and > 0.5 m (0.922) from the nearest refuge site (Table 5).

DISCUSSION

We found that niche overlap may be occurring between invasive *H. mabouia* and native *R. diptycha* and that ontogenetic shifts in the diet of *H. mabouia* may lead to increased interspecific competition with native species as they mature. Invasive species put pressure on the native biodiversity and can alter niche and resource partitioning. Therefore, it is critical to improve understanding of such interactions to inform conservation and management practices.

The dietary composition of *H. mabouia* found in Pilar, Paraguay (dominated by Coleoptera, Hemiptera and Formicidae) was considerably different from similar studies, where Blattodea, Diptera, Araneae, and Hemiptera are the highest consumed groups (e.g., Bonfiglio et al. 2006; de Albuquerque et al. 2013). These differences highlight the opportunistic feeding behavior and adaptability of *H. mabouia* and reflect both the methods used and the microhabitat in which specimens were found (Zamprogno and Teixeira 1998).

Juvenile *H. mabouia* had a larger diet niche breadth than adult individuals, suggesting juveniles exploit a larger range of prey types, becoming more specialized feeders with age. Similarly, Iturriaga and Marrero (2013) found juveniles consumed an overall greater variety of prey than adults, but only consumed a few food items at high volumes. Concordantly, we found nearly a third of the juvenile diet consisted of Formicidae. This may

TABLE 1. Volumetric proportions (V%) of prey items consumed by herpetofauna in Pilar, Paraguay, listed by the number and life stage of species: Hm = the Tropical House Gecko, *Hemidactylus mabouia*, and Rd = the Rococo Toad, *Rhinella diptycha*. The term n (%) = the number of individuals of a group and the proportion of the total group that consumed that prey item.

Prey Item Group	11 Juvenile Hm V%	11 Juvenile Hm n (%)	24 Adult Hm V%	24 Adult Hm n (%)	38 Adult/Juvenile Hm V%	38 Adult/Juvenile Hm n (%)	20 Rd V%	20 Rd n (%)
Araenae	1.3	1 (9.1)	1.3	3 (12.5)	2.3	5 (13.2)	<0.1	4 (20.0)
Blattodea	—	—	6.8	2 (8.3)	6.2	2 (5.3)	3.7	1 (5.0)
Coleoptera	11.4	3 (27.3)	47.2	7 (29.2)	43.7	10 (26.3)	63.6	19 (95.0)
Diptera	3.8	5 (45.4)	5.7	12 (50.0)	5.5	18 (47.4)	5.9	1 (5.0)
Formicidae	32.6	1 (9.1)	8.4	5 (20.8)	10.0	6 (15.8)	13.4	20 (100)
Hemiptera	43.6	6 (54.5)	26.7	12 (50.0)	28.4	19 (50.0)	5.7	6 (30.0)
Hymenoptera	2.8	1 (9.1)	<0.1	—	0.2	2 (5.3)	—	—
Lepidoptera	—	—	0.6	1 (4.2)	0.6	2 (5.3)	—	—
Neuroptera	—	—	2.6	1 (4.2)	2.4	1 (2.6)	—	—
Orthoptera	—	—	<0.1	1 (4.2)	<0.1	1 (2.6)	<0.1	1 (5.0)
Pseudoscorpiones	4.5	2 (18.2)	—	—	0.3	2 (5.3)	—	—
Microplastics	<0.1	4 (36.4)	<0.1	14 (58.3)	<0.1	18 (47.4)	<0.1	3 (15.0)
Fine Sediment	0.1	2 (18.2)	0.1	5 (20.8)	0.2	7 (18.4)	7.2	10 (50.0)
Plant Material	—	—	0.5	1 (4.2)	0.5	1 (2.6)	0.5	14 (70.0)

TABLE 2. Volumetric proportions (V%) of prey items consumed by Hylidae/Leptodactylidae in Pilar, Paraguay. Abbreviations are n = total number of individuals and n (%) = the number (n) of individuals of a species and proportion (%) of the individuals of that species that consumed that prey item.

Prey Item Group	Dwarf Treefrog (*Dendropsophus nanus*) (n = 1) V%	Dwarf Treefrog (*Dendropsophus nanus*) (n = 1) n (%)	Polka-dot Treefrog (*Hypsiboas punctatus*) (n = 2) V%	Polka-dot Treefrog (*Hypsiboas punctatus*) (n = 2) n (%)	Warty Snouted Ttreefrog (*Scinax acuminatus*) (n = 6) V%	Warty Snouted Ttreefrog (*Scinax acuminatus*) (n = 6) n (%)	Butter Frog (*Leptodactylus letrans*) (n = 1) V%	Butter Frog (*Leptodactylus letrans*) (n = 1) n (%)
Araenae	—	—	—	—	32.3	2 (33.3)	—	—
Blattodea	—	—	—	—	—	—	—	—
Coleoptera	—	—	—	—	38.0	1 (16.7)	—	—
Diptera	26.1	1 (100.0)	—	—	—	—	—	—
Formicidae	—	—	20.5	2 (100.0)	16.1	5 (83.3)	43.0	1 (100.0)
Hemiptera	73.4	1 (100.0)	—	—	—	—	—	—
Hymenoptera	—	—	—	—	7.53	1 (16.7)	—	—
Lepidoptera	—	—	—	—	—	—	—	—
Neuroptera	—	—	—	—	—	—	—	—
Orthoptera	0.529	1 (100.0)	79.5	1 (50.0)	5.30	1 (16.7)	—	—
Pseudoscorpiones	—	—	—	—	—	—	—	—
Microplastics	—	—	0.002	1 (50)	0.001	1 (16.7)	0.044	1 (100.0)
Fine Sediment	—	—	—	—	0.741	5 (83.3)	9.41	1 (100.0)
Plant Material	—	—	—	—	—	—	47.6	1 (100.0)

TABLE 3. Results from the Levins' Niche Breadth (LNB) and Pianka Niche Overlap (PNO) applied to the Tropical House Gecko (*Hemidactylus mabouia*) and the Rococo Toad (*Rhinella diptycha*) showing the sample size (n) of each group. The abbreviation BA = Levin's Standardized Niche Breadth.

	LNB	PNO	
Groups (n)	B_A	*H. mabouia* (juveniles)	*R. diptycha*
H. mabouia – adults and juveniles (38)	0.241	—	0.890
H. mabouia – adults (24)	0.243	0.642	0.912
H. mabouia – juveniles (11)	0.362	—	0.380
R. diptycha (20)	0.171	—	—

TABLE 4. Results from the Levins' Niche Breadth (LNB) and Pianka Niche Overlap (PNO) applied to the Tropical House Gecko (*Hemidactylus mabouia*) and the Rococo Toad (*Rhinella diptycha*), and Lit (fully illuminated by an artificial light source) and Unlit (not illuminated artificial light source) niche conditions. The abbreviation BA = Levin's Standardized Niche Breadth.

	PNO		LNB	
	H. mabouia		B_A	
Species (n)	Lit	Unlit	Lit	Unlit
H. mabouia (38)	—	—	0.261	0.235
Lit (24)	—	0.782	—	—
R. diptycha (20)	0.749	0.969	—	—

be an adaptive mechanism ensuring survival during high-predation-risk growth periods by minimizing foraging time while increasing nutritional and energetic gains and exposure to new foods (Durtsche 2000). Moreover, ontogenetic shifts in head morphology and bite capacity greatly influence patterns in resource use and ontogenetic shifts in diet (Lima and Moreira 1993; Duellman and Trueb 1994), suggesting adult individuals have the bite capacity necessary to predate on larger and therefore fewer invertebrates with harder chitin such as Coleoptera (Herrel et al. 2001; Sagonas et al. 2014). Furthermore, smaller SVL, and biomechanical structures, such as the tongue, jaw, and gaping capacity, limit maximum prey size and proportions of prey types ingested (Strüssman et al. 1984; Lima and Moreira 1993; Pough et al. 2003).

Rhinella diptycha had the smallest diet breadth, indicating a relatively more specialized feeding behavior that exploits fewer prey types than *H. mabouia*, contradicting previous research (e.g., de Carvalho Batista et al. 2011; Lavilla and Brusquetti 2018). Large amounts of Coleoptera and Formicidae were consumed by the urban *R. diptycha* of this study, which may be due to high availability of these taxa in the survey area but could also suggest low competition for this food resource (Clarke 1974), as well as reflect the ground dwelling nature of *R. diptycha* and restricted access to flying invertebrates. We observed a marginally higher niche breadth for *H. mabouia* found in lit and partially lit habitats when compared to the niche breadth of individuals found in unlit habitats, which may be attributed to the increased relative abundance of invertebrates in artificially lit habitats (Davies et al. 2012; Komine et al. 2020). We encountered over two-thirds of all specimens in artificially lit microhabitats, suggesting urban *R. diptycha* and *H. mabouia* in Pilar may be using artificial light sources for increased predation success (Ineich 2010; Komine et al. 2020).

We found microfibers within the fecal pellets of all three taxonomic groups, providing the first and earliest record of microplastic ingestion by terrestrial herpetofauna in South America, and to our knowledge, the second record globally of microplastic ingestion in terrestrial reptiles (see Lu et al. 2020). Our finding has since led to additional research into microplastic ingestion by South American herpetofauna completed at the same research station from November 2019 to March 2020 (see Mackenzie and Vladimirova 2021). Recent studies on ingestion by Anurans highlight impaired intestinal passage, uptake of nutrients, and growth, causing morphological abnormalities, decreased physical fitness, and increased mortality (Boyero et al. 2020; da Costa Araújo et al. 2020). In our study, ingestion could be a result of bioaccumulation in the food web, or through accidental ingestion during predation or geophagy (Sokol 1971; Hui 2004). Nevertheless, some of the microplastic consumption could be a result of contamination during the dissection process, and further studies should control for these factors.

Adult *H. mabouia* had a very high niche overlap with *R. diptycha*, suggesting the two species are using shared resources with either the potential for interspecific competition to occur (Giménez Gómez et al. 2018; Pascual-Rico et al. 2020) or with competition already occurring within the trophic niche but with the partitioning of resources in other niches, which permits

TABLE 5. Results from the Levins' Niche Breadth and Pianka Niche Overlap applied to the different groups of species and niche conditions. The headings < 0.5 m and > 0. 5m refer to the distance from the nearest refuge space a gecko was found. The abbreviation BA = Levin's Standardized Niche Breadth.

	PNO		LNB	
	H. mabouia		B_A	
Species (n)	< 0.5 m	> 0.5 m	< 0.5 m	> 0.5 m
H. mabouia (38)			0.346	0.209
< 0.5m (16)	—	0.777	—	—
R. diptycha (20)	0.788	0.922	—	—

a current coexistence within the trophic niche (Koutsidi et al. 2020). This potentially is due to different spatial niches, morphological differences, and/or high levels of shared resource availability. Despite different spatial niches, the current trophic niche overlap between adult *H. mabouia* and *R. diptycha* could have future implications on the local abundance of invertebrate species, leading to indirect competition with native *R. diptycha* for these resources (Robillard et al. 2013; Prasad 2022). This is especially concerning given predicted declines in invertebrates, particularly for Lepidopteran, Hymenopteran, and Coleopteran species and urban invertebrate populations (Sánchez-Bayo and Wyckhueys 2019; Owens et al. 2020), which may exacerbate indirect competition (Robillard et al. 2013; Prasad 2022). The relatively lower niche overlap between *H. mabouia* occupying lit microhabitats and *R. diptycha* (compared with *H. mabouia* in unlit habitats and *R. diptycha*) suggests some resource partitioning has already occurred in this shared microhabitat. It should be considered, however, that fecal analyses hold some degree of bias towards chitinous invertebrates and underrepresent soft-bodied invertebrates, which are essential dietary items for *Rhinella* (Pincheira-Donoso 2008; de Carvalho Batista et al. 2011). Nonetheless, our study indicates a high dietary niche overlap is occurring between adult *H. mabouia* individuals and *R. diptycha* without the presence of soft-bodied prey items.

The relatively low dietary overlap we observed between juvenile *H. mabouia* and *R. diptycha* can be partially explained by differential microhabitat use between *R. diptycha* and *H. mabouia*, and thus the consumption of different invertebrates and food availability (Saenz 1996; Howard et al. 2001). Although juvenile *H. mabouia* and *R. diptycha* typically operate in similar niches closer to the ground (Iturriaga and Marrero 2013), we found juveniles perched, on average, 2 m above the ground, whereas all *R. diptycha* were found at ground level. Morphological differences in head size may further enable resource partitioning between these two groups (e.g., Saenz 1996; de Carvalho Barista et al. 2011). Use of similar niches for even just one part of a the life cycle of a species does not hinder the potential invasion of that native community (Escoriza and Boix 2012). If resources are not partitioned equally between the two taxa groups across all life stages, *R. diptycha* populations could be negatively impacted as they lack adaptive mechanisms needed to withstand changes within a niche, increasing their vulnerability to competition (Diamond and Case 1986; Kats and Ferrer 2003; Bucciarelli et al. 2014).

This study is the first to evaluate interactions between the invasive *H. mabouia* and native *R. diptycha* in Paraguay, and further studies are necessary to assess the full threat this species poses to native herpetofauna.

Ontogenetic shifts in *H. mabouia* diet indicate a lower overlap with *R. diptycha* during their juvenile stage and higher during adulthood, highlighting the importance of evaluating the influence of life stage when determining the impact of invasive species on new ecosystems. If competition is occurring between invasive and native species, it is essential action be taken to maintain a healthy balance within the ecosystem and prevent future population declines of native Anurans.

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