**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 remnant 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. Fauna Paraguary. 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 Vreibradic 2003; Moravec et al. 2008; Sabaghi 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; Martin 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, Araneae, 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 nanaus).

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 km² 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 M1003 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:

\[
\text{Volume} = \frac{\pi \cdot \text{Length} \cdot \text{Width}^2}{6}
\]

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) \( R. \) dipticha; (2) Frogs (Leptodactylus letrans, Scinax acuminatus, Hyspiboa 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. \( \leq \) 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:

\[
O_{jk} = \frac{\sum p_i g_i p_{jk} k}{\sqrt{\sum p_i^2 g_i \sum p_{jk}^2}}
\]

where \( O_{jk} \) indicates the Pianka Niche Overlap between species group \( j \) and \( k \), \( p_i \) is the proportion that food item \( i \) is of the total food items used by species \( j \), and \( P_{jk} \) 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 \( (\alpha = 0.05) \). We also used a Wilcoxon Rank Sum Test to evaluate differences in distances from hiding spaces between taxa groups \( (\alpha = 0.05) \).

### 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 \( R. \) dipticha (69%) preference for lit or unlit habitats. We encountered \( R. \) dipticha 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 \( R. \) dipticha 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 \( R. \) dipticha 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 Formicidae (32.6%), whereas adults consumed 10 prey types dominated by Coleoptera (47.2%) and Hemiptera (26.7%). Rhinella dipticha 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 Hemiptera (73.4%) and Diptera (26.1%), \( H. \) punctatus \( (n = 2) \) predominantly consumed Orthoptera (79.5%) and Formicidae (20.5%), \( S. \) acuminatus \( (n = 6) \) predominantly consumed Coleoptera (38%) and Araneae (32%), and \( L. \) letrans \( (n = 1) \) predominantly consumed Formicidae (43%; Table 2).

In addition to food items, we found microplastics (Fig. 1) in 18 \( H. \) mabouia samples (47.4%), four of
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...
Hiscock et al.—Dietary competition between a gecko and an anuran.

### 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.

<table>
<thead>
<tr>
<th>Prey Item Group</th>
<th>11 Juvenile Hm</th>
<th>24 Adult Hm</th>
<th>38 Adult/Juvenile Hm</th>
<th>20 Rd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araenae</td>
<td>1.3 1 (9.1)</td>
<td>1.3 3 (12.5)</td>
<td>2.3 5 (13.2)</td>
<td>&lt;0.1 4 (20.0)</td>
</tr>
<tr>
<td>Blattodea</td>
<td>— —</td>
<td>6.8 2 (8.3)</td>
<td>6.2 2 (5.3)</td>
<td>3.7 1 (5.0)</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>11.4 3 (27.3)</td>
<td>47.2 7 (29.2)</td>
<td>43.7 10 (26.3)</td>
<td>63.6 19 (95.0)</td>
</tr>
<tr>
<td>Diptera</td>
<td>3.8 5 (45.4)</td>
<td>5.7 12 (50.0)</td>
<td>5.5 18 (47.4)</td>
<td>5.9 1 (5.0)</td>
</tr>
<tr>
<td>Formicidae</td>
<td>32.6 1 (9.1)</td>
<td>8.4 5 (20.8)</td>
<td>10.0 6 (15.8)</td>
<td>13.4 20 (100.0)</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>43.6 6 (54.5)</td>
<td>26.7 12 (50.0)</td>
<td>28.4 19 (50.0)</td>
<td>5.7 6 (30.0)</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>2.8 1 (9.1)</td>
<td>&lt;0.1 —</td>
<td>0.2 2 (5.3)</td>
<td>— —</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>— —</td>
<td>0.6 1 (4.2)</td>
<td>0.6 2 (5.3)</td>
<td>— —</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>— —</td>
<td>2.6 1 (4.2)</td>
<td>2.4 1 (2.6)</td>
<td>— —</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>— —</td>
<td>&lt;0.1 1 (4.2)</td>
<td>&lt;0.1 1 (2.6)</td>
<td>&lt;0.1 1 (5.0)</td>
</tr>
<tr>
<td>Pseudoscorpiones</td>
<td>4.5 2 (18.2)</td>
<td>— —</td>
<td>0.3 2 (5.3)</td>
<td>— —</td>
</tr>
<tr>
<td>Microplastics</td>
<td>&lt;0.1 4 (36.4)</td>
<td>&lt;0.1 14 (58.3)</td>
<td>&lt;0.1 18 (47.4)</td>
<td>&lt;0.1 3 (15.0)</td>
</tr>
<tr>
<td>Fine Sediment</td>
<td>0.1 2 (18.2)</td>
<td>0.1 5 (20.8)</td>
<td>0.2 7 (18.4)</td>
<td>7.2 10 (50.0)</td>
</tr>
<tr>
<td>Plant Material</td>
<td>— —</td>
<td>0.5 1 (4.2)</td>
<td>0.5 1 (2.6)</td>
<td>0.5 14 (70.0)</td>
</tr>
</tbody>
</table>

### 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.

<table>
<thead>
<tr>
<th>Prey Item Group</th>
<th>Dwarf Treefrog (Dendropsophus nanus) (n = 1)</th>
<th>Polka-dot Treefrog (Hypsiboas punctatus) (n = 2)</th>
<th>Warty Snouted Treefrog (Scinax acuminatus) (n = 6)</th>
<th>Butter Frog (Leptodactylus letrans) (n = 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araenae</td>
<td>V% n (%)</td>
<td>V% n (%)</td>
<td>V% n (%)</td>
<td>V% n (%)</td>
</tr>
<tr>
<td>Blattodea</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Diptera</td>
<td>26.1 1 (100.0)</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Formicidae</td>
<td>— —</td>
<td>20.5 2 (100.0)</td>
<td>16.1 5 (83.3)</td>
<td>43.0 1 (100.0)</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>73.4 1 (100.0)</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>— —</td>
<td>— —</td>
<td>7.53 1 (16.7)</td>
<td>— —</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>0.529 1 (100.0)</td>
<td>79.5 1 (50.0)</td>
<td>5.30 1 (16.7)</td>
<td>— —</td>
</tr>
<tr>
<td>Pseudoscorpiones</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
</tr>
<tr>
<td>Microplastics</td>
<td>— —</td>
<td>0.002 1 (50)</td>
<td>0.001 1 (16.7)</td>
<td>0.044 1 (100.0)</td>
</tr>
<tr>
<td>Fine Sediment</td>
<td>— —</td>
<td>— —</td>
<td>0.741 5 (83.3)</td>
<td>9.41 1 (100.0)</td>
</tr>
<tr>
<td>Plant Material</td>
<td>— —</td>
<td>— —</td>
<td>— —</td>
<td>47.6 1 (100.0)</td>
</tr>
</tbody>
</table>
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 (Durstche 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 Brusqueti 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
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 Wyckhuys 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 focal analyses hold some degree of bias towards chitinous invertebrates and underrepresent soft-bodied invertebrates, which are essential dietary items for *Rhinella* (Pinheiro-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 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.

Acknowledgments.—We thank the Ministerio del Ambiente y Desarrollo (MADES) for issuing relevant research permits (No. 219719). We express our gratitude to the members of Para La Tierra, Karina Atkinson and Joseph Sarvary, and the volunteers who assisted with the fieldwork and fecal analysis of this study, including Jack McBride, Patrizia Ugolini, Jorge Ayala, Brogan Pett, Jake Wellian, Phoebe Worley, Harry Pym-Davis, Esteban Velazco, Peter Belo, Silas Van Bekkum, Isaac Shaw, Constantinos Charalambous, and Margaret, and Brett Wohler. We are also grateful for the support from Jim Vafidis from the University of the West of England throughout the research and for his comments on an earlier draft of the manuscript.

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and Phyllodactylus pulcher) for diurnal Trogon rufus. Journal of Herpetological Conservation and Biology


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