

Guilty or innocent? Could the exotic lizard *Hemidactylus mabouia* (Squamata, Gekkonidae) be responsible for the displacement of the native species *Notomabuya frenata* (Squamata, Mabuyidae) in anthropic environments?

Pier Cacciali^{1,2}, Raúl Maneyro³

¹ Guyra Paraguay, Av. Cnel. Carlos Bóveda, Parque Ecológico Capital Verde – Viñas Cué, Asunción, Paraguay

² Instituto de Investigación Biológica del Paraguay, Del Escudo 1607, 1425 Asunción, Paraguay

³ Laboratorio de Herpetología. Facultad de Ciencias. Universidad de la República Uruguay, Montevideo, Uruguay

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Corresponding author: Pier Cacciali (pier_cacciali@yahoo.com)

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Abstract

Hemidactylus mabouia is a gecko species that has successfully colonized southern North, Central, and South America. In Paraguay, there is a commonly held belief that this species has displaced the native skink *Notomabuya frenata* in urban areas. In this study, we compared several ecological features of *N. frenata* and *H. mabouia* to better understand the degree of their niche overlap. A comparative analysis was conducted based on a literature survey and the examination of museum specimens from Asunción (Paraguay). Furthermore, differences in microhabitat use between *H. mabouia* and *N. frenata* were investigated through a review of observational records available on iNaturalist. Our findings indicate that the two species share only a few biological traits, such as an insectivore diet, an ability to adapt to living close to human dwellings, and the use of mimesis as a primary defensive strategy. Both lizards are generalist feeders, although there are notable differences in their frequency of prey consumption. Regarding habitat use, the majority of *N. frenata* specimens were documented on grass or other natural substrates, as well as on trees and shrubs. In the case of *H. mabouia*, the majority of records originate from smooth and brick walls, including metal and glass surfaces. Consequently, there is no evidence to suggest that dietary overlap could induce competition between these species. Therefore, it can be posited that the displacement of the native lizard *N. frenata* is a consequence of human activities that have altered its preferred microhabitat while expanding potential habitat for *H. mabouia*.

Key Words

iNaturalist, invasive species, Paraguay, Reptilia, urban biodiversity

Introduction

Exotic species may constitute a major problem in conservation biology, especially when they become invasive (Lowe et al. 2000). Nevertheless, in some cases, exotic species do not develop invasive capacities and may reach a populational climax without harming local wildlife (Ricciardi and Cohen 2007). In several cases,

exotic invaders have outcompeted native species from ecological niches (Spencer et al. 1991; Holway 1999; Madjidian et al. 2008; Sanders and Suarez 2011). *Hemidactylus mabouia* (Moreau de Jonnés, 1818) is one example of a species that has successfully colonized and invaded southern North, Central, and South America (Ávila-Pires 1995; Fuenmayor et al. 2005; Pinho et al. 2023), most likely due to its broad dietary

range as an opportunistic and generalist species (Rocha and Anjos 2007; Iturriaga and Marrero 2013; Agarwal et al. 2021).

Hemidactylus mabouia probably entered first in South America in northeastern Brazil as early as ~1640 (Agarwal et al. 2021), and the further dispersion was facilitated by human-modified environments (Rocha et al. 2011). It is difficult to pinpoint the exact date of colonization in Paraguay, but the oldest verified record for *H. mabouia* in the country is from 21 January 1983 in the city of Concepción (Baldo et al. 2008; Cacciali and Motte 2009). Since then, the species has successfully colonized Asunción and Ciudad del Este. Nevertheless, the species is more widespread in the country (Cacciali et al. 2016). All records belong to anthropogenic environments, common in human dwellings.

However, Rocha and Anjos (2007) recorded a population of *H. mabouia* in a non-urban environment in thirteen Brazilian states, indicating that the species is encroaching into wild areas. This expansion is a major concern, as the exotic population could potentially spread without constraint. The actual impact of *H. mabouia* on native fauna in Paraguay remains unknown.

In Paraguay, it is widely believed that *H. mabouia* has displaced the native skink lizard *Notomabuya frenata* (Cope, 1862) (Motte et al. 2004; NLT 2007), but there is no rigorous evidence for this claim, only anecdotal. For instance, many residents of Asunción, the capital of Paraguay, informed us that ~30 years ago all houses were inhabited by *N. frenata* (or “Amberé,” as the locals call them), but with the invasion of *H. mabouia*, the original “Amberé” disappeared.

In this study, we compared several ecological features of *N. frenata* and *H. mabouia* to better understand the degree of their niche overlap. We hypothesize that the two species do not compete for resources, mainly due to differences in diel activity and microhabitat use, and therefore *H. mabouia* does not outcompete *N. frenata*. To test this hypothesis, we extracted data from the literature, examined museum specimens, and analyzed records available on an online social network, iNaturalist.

Material and methods

According to Colwell and Futuyama (1971), niche overlap refers to the shared utilization of resources by two or more taxa. However, interspecific competition can be inferred when there is a conflict for the resources trending to the displacement or exclusion of any of such taxa. Thus, to assess the degree of niche overlap between *H. mabouia* and *N. frenata*, we performed a comparison of their biological aspects based on the following literature: Dixon and Soini (1986), Martínez Rivera et al. (2003), Regalado (2003), and Rocha and Anjos (2007) for *H. mabouia*; and Norman (1994), Vrcibradic and Rocha (1998a, b), and Cassel et al. (2012) for *N. fre-*

nata. We followed the PRISMA statement for ecology and evolutionary biology (O’Dea et al. 2021) using a proposed flow diagram by Haddaway et al. (2022) summarized in Suppl. material 1.

One of the key dimensions of the ecological niche that can lead to interspecific competition is the overlap of dietary resources (Duncan et al. 2002; Fabre et al. 2004). We investigated this aspect through an analysis of literature and scientific collections. Information regarding the trophic diversity of *H. mabouia* is based on Rocha and Anjos (2007), while data for *N. frenata* was taken from Vrcibradic and Rocha (1998a). These references were chosen as they both focus on sympatric populations at Valinhos, São Paulo, Brazil, although separated in time by almost a decade. We used percentages because of the differences in sample size. Insect larvae records were not included because of the high rate of quick decomposition.

Extra data from a diet of these two lizard species were taken from specimens from the Museo Nacional de Historia Natural del Paraguay from the same location: Asunción, Paraguay (*Hemidactylus mabouia*, $n = 8$, voucher specimens MNHNP 3129, 3158, 3161-2, 3165, 3814, 3816, 8067; *Notomabuya frenata*, $n = 5$, voucher specimens MNHNP 2921, 2926-7, 3802, 4314). Stomach contents were extracted and analyzed under a stereoscopic microscope to identify prey items to the deepest taxonomic level possible. Literature for stomach content identification is listed in Suppl. material 2.

To assess differences in trophic composition between *H. mabouia* and *N. frenata*, we performed a chi-square test using results from bibliographic data. Rarefaction curves were estimated to compare differences in stomach content richness among dissected individuals. Analyses were performed with the software PAST v. 4.03 (Hammer et al. 2001).

We also examined differences in temporal patterns of *H. mabouia* and *N. frenata* occurrence in Asunción city. This analysis involved studying collection dates (based on MNHNP records) and observations from iNaturalist, an online citizen science-based website, to detect the contemporaneous occurrence of the two species. We chose this digital repository because of its visibility, accessibility, and visualization of data, which makes it a valuable tool for research nowadays (Forti and Szabo 2023; White et al. 2023). We assessed the microhabitat use of both lizards by reviewing records available at iNaturalist and categorizing the microhabitat type as follows: smooth wall, brick wall, wooden wall, tile floor, grass (or other natural ground), bark tree or shrubs, rocky substrate, metal or glass surfaces, and out of habitat (for animals that were deceased, manually handled, or in scientific collections). To eliminate potential latitudinal biases, we used the distribution of *N. frenata* and performed a search for *H. mabouia* within the same range (Lat -6.061683 to -29.280589, Long -65.986297 to -41.32117).

Results

Notomabuya frenata and *H. mabouia* share only a few biological traits, such as diet and defensive behavior (Table 1). Most aspects of those species' lives differ, including diel activity, habitat, reproduction, and communication. As shown in Suppl. material 3, there is a high degree of overlap in the items consumed by both species (at least at the order level) based on literature data. Both lizards are rather generalist feeders, consuming a wide variety of available invertebrates. Nevertheless, Fig. 1 shows a difference in the frequency of prey consumption. *Hemidactylus mabouia* shows a higher number of arachnids in its diet, whereas *N. frenata* ingests a substantial quantity of isopterans. The chi-square test shows a significant difference between items consumed by both predators ($\chi^2 = 92.89$, $DF = 23$, $p < 0.001$).

The analysis of stomach contents of MNHNP specimens from Asunción yielded limited information due to the small sample size and the number of items found. Notably, we discovered inorganic and vegetal substances in the stomachs of *H. mabouia*, including sand, fabric, and remnants of shed skin, presumably from the own lizard (Table 2). None of these items were found in *N. frenata*.

Regarding the items consumed by both species in Asunción, they coincide with the ingestion of spiders, coleopterans, and homopterans (Table 2). The remaining items were not shared by both species (Table 2). Furthermore, there appears to be a difference in the types of species consumed. Rarefaction curves show that dissected specimens of *N. frenata* and *H. mabouia* have a similar dietary structure (Fig. 2). Curves overlap, and the confidence interval for *N. frenata* is entirely encompassed by the confidence interval of *H. mabouia*, meaning that in the city, perhaps with limited resources, the diet coincides.

In terms of recorded dates, *N. frenata* was last recorded in Asunción in 1986 (MNHNP 3802), with two additional records in iNaturalist (3-Feb-1995 and 30-Mar-2017). On the other hand, *H. mabouia* has one voucher record dated in 2016 (MNHNP 12128) and 15 records on iNaturalist (from 21-Nov-2013 to 24-Feb-2022). Based on this fragmented information (these species were not exhaustively sampled), we present the number of records over time in Fig. 3. This figure illustrates that most of the records of *N. frenata* are dated up to 1995 and one in 2017, while the majority of *H. mabouia* records are more recent, and from 2017, the records of this species are notoriously frequent. Notably, there is a significant data gap from 1996 to 2012.

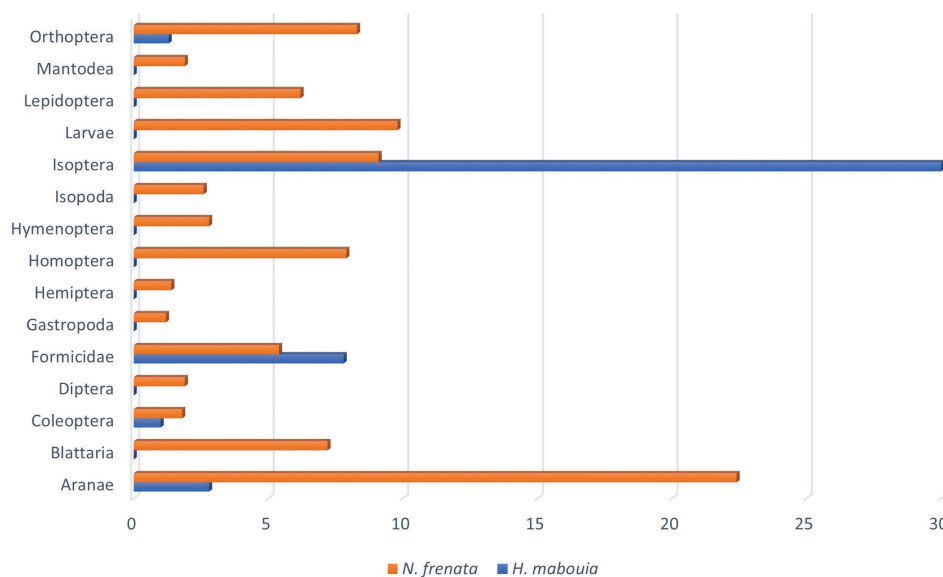


Figure 1. Frequency of prey items (expressed in percentage) consumed by *Notomabuya frenata* and *Hemidactylus mabouia* based on Vrcibradic and Rocha (1998a) and Rocha and Anjos (2007). Only frequencies $\geq 1\%$ are shown. Full graphic available in Suppl. material 3.

Table 1. Biological traits of *Notomabuya frenata* and *Hemidactylus mabouia*. See Methods for bibliographic sources.

	<i>Notomabuya frenata</i>	<i>Hemidactylus mabouia</i>
Diet	Insectivore	Insectivore
Diel activity	Diurnal	Nocturnal, rarely diurnal
Habitat	Wide preferences in natural habitats, as well as in anthropogenic environments	Human dwellings
Microhabitat	Shrubs, logs and planks; climbs by claws; cannot climb smooth surfaces	Houses walls; climbs by lamellae; can climb smooth surfaces
Shelter	Fissures	Any available refugee, even inside electric installations
Reproduction	Ovoviviparous, reproductively active throughout the year	Oviparous, reproductively active throughout the year
Defense	Mimesis, caudal autotomy	Mimesis (including color change), caudal autotomy
Communication	Visual and chemosensory behavior	Acoustic, visual and chemosensory displays

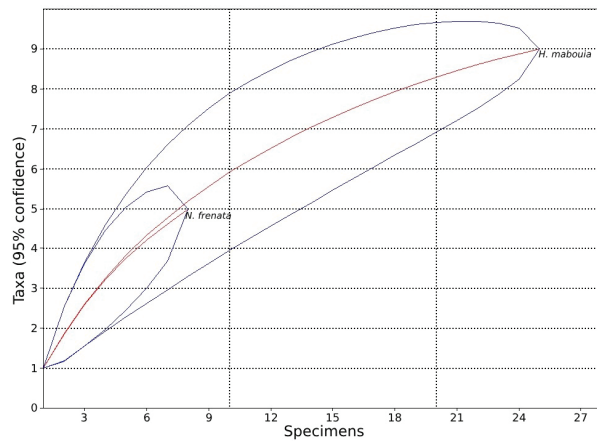


Figure 2. Rarefaction curves showing similar niche amplitude for the species *Notomabuya frenata* and *Hemidactylus mabouia*.

Regarding habitat use, we assessed 126 records with 130 observations of *N. frenata* on iNaturalist (a simple record may contain more than one observation or photograph). For *H. mabouia*, we had a total of 1,761 observations with the classification based on the first 1,000 records. For *N. frenata* and *H. mabouia*, 32 and 209 observations of individuals outside our habitat categories were deleted, leaving 98 and 791 observations, respectively, for comparison. Most specimens of *N. frenata* were documented on grass or natural substrate (30%) or on trees or shrubs (27%) (Fig. 4). Fewer records were observed in human environments such as brick or wooden walls (11% in each case) and tiled floors (9) (Fig. 4). In the case of *H. mabouia*, most of the records come from smooth walls and brick walls (71%), including metal and glass surfaces (3%) that were not used by *N. mabouia* (Fig. 4). A considerably low number of specimens were photographed on tile floors (1%). Comparing habitat use by both species, it is possible to see that wooden walls are the only habitat relatively used with the same frequency (approx. 10%) (Fig. 5).

Table 2. Stomach contents of specimens of *Notomabuya frenata* and *Hemidactylus mabouia* from Asunción (Paraguay). No id. refers to prey items that could not be identified below the major group classification. Lepidoptera marked with * indicate several fragments, probably more than one specimen. Number of specimens (including prey items) in parenthesis. X indicates presence (without quantification).

Major prey group	<i>N. frenata</i> (5)	<i>H. mabouia</i> (8)
Arachnida		
Acari		No id. (1)
Araneae	Salticidae (2)	<i>Kukulcania hibernalis</i> (Filistatidae) (2)
Insecta		
Blattaria		No id. (2)
Coleoptera	No id. (1)	Elateridae (1)
Ephemeroptera		No id. (2)
Dermaptera	<i>Euborellia annulipes</i> (Anisolabididae) (1)	
Diptera		Nematocera (~6) Cyclorrhapha (1)
Homoptera	No id. (1)	No id. (1)
Lepidoptera		No id. (*)
Orthoptera	<i>Gryllodes sigillatus</i> (Gryllidae) (1) No id. (2)	
Psocoptera		Liposcelidae (1)
Others		
Sand		X
Ecdysed lizard skin		X
Fabric		X
Vegetal matter		X

Discussion

Rocha and Anjos (2007) found that even in the wild, when *H. mabouia* shares food resources with native diurnal lizards such as *Tropidurus itambere* Rodrigues, 1987 (Tropiduridae) and *N. frenata*, interspecific competition remains low due to differences in their activity patterns. Additionally, these species have differential preferences in microhabitat use (Van Sluys 1992, 1993; Vrcibradic and Rocha 1998a).

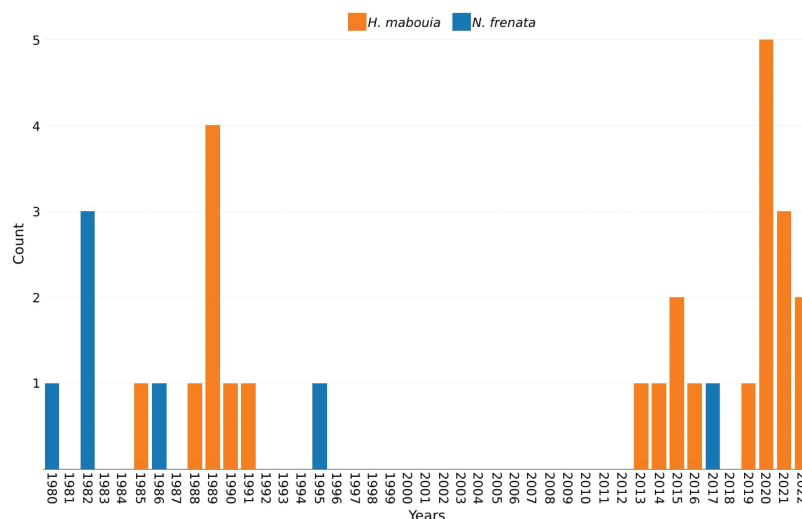


Figure 3. Records of *Hemidactylus mabouia* and *Notomabuya frenata* in Asunción shown by year, based on specimens from the MNHNP and iNaturalist data.

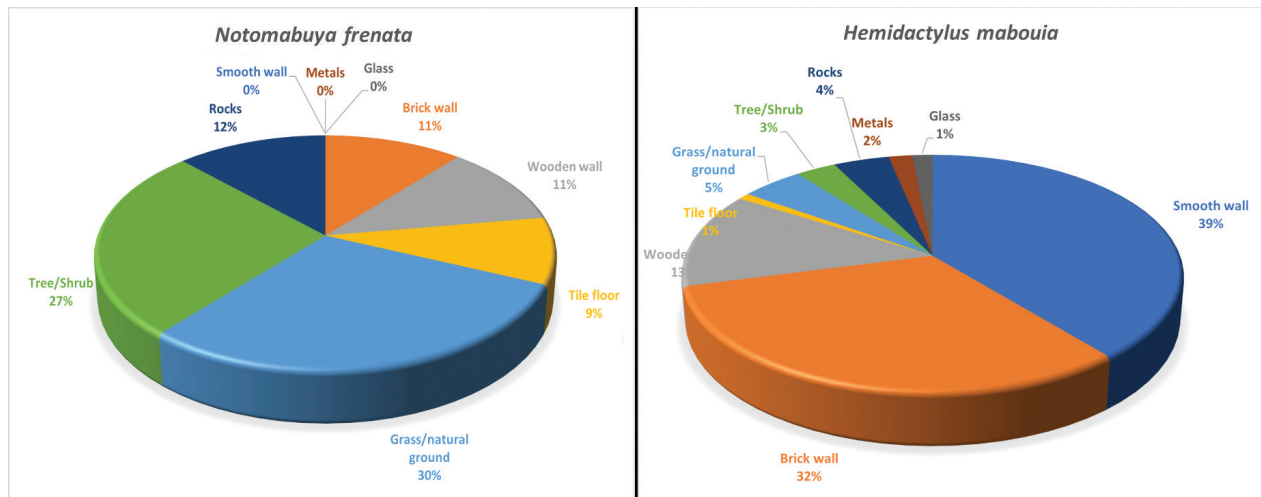


Figure 4. The proportion of microhabitat use by *Notomabuya frenata* (n = 126) and *Hemidactylus mabouia* (n = 1,000) according to records in iNaturalist.

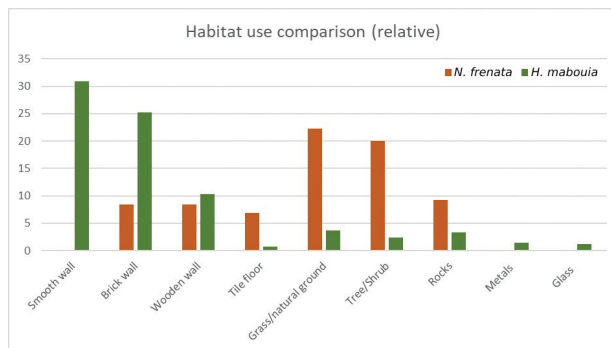


Figure 5. Comparison between the use of habitat in *Notomabuya frenata* and *Hemidactylus mabouia*. Relative values are expressed in percentages.

The use of the same resource by two or more species does not necessarily indicate competition. As Colwell and Futuyma (1971) explain, when a resource is abundant or oversupplied, competition between species may not occur, even if they share the same resource. In the case of the dietary resources for *H. mabouia* and *N. frenata*, the large diversity of insects consumed (Garcete and Molinas 2021) indicates that the species do not compete for this resource. Furthermore, we found significant differences between the dietary composition of *H. mabouia* and *N. frenata* based on bibliographic data. The examination of specimens from the same locality also revealed some differences, even with the limited sample size. As shown in Table 2, *N. frenata* primarily feeds on non-flying insects (e.g., *Euborellia annulipes* (Lucas, 1847)), along with terrestrial and diurnal arthropods (Salticidae and orthopterans). Conversely, the spiders found in the dietary content of *H. mabouia* are nocturnal, typically inhabiting walls. Moreover, the majority of prey items for this lizard consist of flying insects that are often attracted to artificial lights (Elateridae, Ephemeroptera, Diptera, Lepidoptera). We also found synthetic fibers of fabric, probably due to the urban environment. Although ants are a primary food source for many vertebrates, particularly lizards (Cavalcanti et al. 2023), our results show

that they are not a significant component of the diet for *N. frenata* or *H. mabouia*. This suggests that these lizards may rely on other prey items or have adapted to different feeding strategies despite the general importance of ants in many lizards' diets.

In conclusion, there is no evidence that dietary overlap could induce competition between *H. mabouia* and *N. frenata*. In the specific case of Asunción, the diet strongly overlaps, and then prey availability could influence competition. Nevertheless, we argue that if local extinctions of *N. frenata* (mainly in large cities in Paraguay) are related to the invasion of *H. mabouia*, this fact cannot be explained by dietary overlap. Ecological invasions can arise from fitness advantages favoring the invader over the resident species or from niche differences that enable the establishment of the invader even if it may have lower overall fitness (MacDougall et al. 2009). However, many invasions are primarily the result of occupying available niches (Ricciardi and MacIsaac 2011). The latter scenario appears to be the case for *H. mabouia* given that the architectural features of urban development coincide with microhabitats used by this species, which are not suitable for skinks.

Regardless of the presence of *H. mabouia*, *N. frenata* is still commonly found in urban gardens where architectural design allows connections among populations. In areas of the city where *N. mabouia* has already disappeared, there are paved streets, tall and smooth walls, and fewer green areas, which hinder the dispersal of the species and lead to significant isolation of individuals. Therefore, the displacement of the native lizard *N. frenata* is a consequence of human activities, which is not surprising. These same anthropogenic changes that negatively influence *N. frenata* are likely to positively influence human commensal geckos such as *H. mabouia*. Fig. 6 provides an example of city development in an area between the botanical garden and Parque Guasu Metropolitano, two major green areas in Asunción. This figure highlights the expansion of concrete structures and buildings and the loss of gardens, green areas, and unpaved roads.



Figure 6. Development of an area of Asunción between a botanical garden and Parque Guasu Metropolitano, major green areas in Asunción, showing the expansion of concrete structures and buildings. Images obtained in Google Earth Pro 7.3.6. Years 2003 (above) and 2023 (below).

We must clarify that we do not assert that *H. mabouia* is incapable of competing and displacing other species. In fact, in certain areas where *H. mabouia* has been introduced, it has been proven to not only have conquered urban environments but also impact local fauna (Anjos and Rocha 2008). These geckos are highly adaptable and thrive in a variety of environments, from urban areas to natural habitats, and their presence often leads to the displacement of not only native gecko species through direct competition for resources and predation but also to other lizards (Oliveira et al. 2016; Lamb et al. 2021). Additionally, their aggressive behavior and high reproductive rates further exacerbate their impact, making them formidable invasive species that pose a threat to biodiversity and the stability of native ecosystems (Weterings and Vetter 2018; Agarwal et al. 2021).

However, it is worth noting that this exotic lizard is mostly confined to cities in Paraguay (Baldo et al. 2008; Cacciali and Motte 2009; Mackenzie and Vladimirova 2022), and, at least for now, no direct evidence of its possible negative effects on native lizards has been recorded (Cacciali 2024). Hiscock et al. (2023) reported trophic niche overlap, indicating the potential for shared ecological roles, but not necessarily competition, between *H. mabouia* and the common toad, *Rhinella diptycha* (Cope, 1862). An important fact highlighted by Cacciali et al. (2016) is that in the riverine town of Bahía Negra (Alto Paraguay department, northern Paraguay), the largest native Paraguayan gecko, *Phyllopezus przewalskii* Koslowsky, 1895 (12 cm of total length like *H. mabouia*), is found inhabiting

human dwellings where *H. mabouia* is absent. Thus, under the presence of a native species with similar characteristics as the exotic *H. mabouia* (similar body size, diel activity, use of microhabitat), the latter seems to face challenges in colonizing the town (Cacciali et al. 2016). Nevertheless, Norman (2020) reports the existence of *H. mabouia* in the southernmost part of the Paraguayan Chaco and could be even present in areas of Central Chaco (Jacob Unger, pers. com.) where the native gecko *P. przewalskii* is present and deserves a deeper further analysis. Recently, Cacciali (2024) reported the case of local extinction of the endemic species *Phyllopezus heuteri* Cacciali, Lotzkat, Gamble & Köhler, 2018 and the presence of *H. mabouia* instead, but still, it is not clear if the native gecko was first displaced by human activities and then the exotic gecko colonized the area, or if it was an effective case of direct competition.

We provide here the first contribution towards the assessment of competition between a gecko and a skink. This is the first step towards understanding the effect of this exotic lizard in Paraguay. Although financial restrictions are always a major limitation, continuous monitoring is necessary to provide early warning in case of invasion of natural areas by *H. mabouia* in Paraguay and to assess potential competition with other native lizards. To overcome financial constraints, engaging citizen participation through platforms like iNaturalist could be a proactive way to support ongoing monitoring efforts in natural areas. With this respect, it is important to note that species like *H. mabouia* are more frequently recorded in databases, likely because they are easier to observe and photograph, especially when found on walls or near light sources where they feed. This ease of recording may introduce a bias, as more conspicuous species tend to be documented more often. Although this influence on the data cannot be fully mitigated, it should be acknowledged when interpreting the frequency of species in such records. The use of citizen science and platforms like iNaturalist are valuable tools that significantly contribute to the conservation of local biodiversity. These tools facilitate the collection of extensive ecological data, enhance public engagement in scientific research, and support the monitoring and protection of diverse species within their natural habitats.

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Supplementary material 1

Detailed explanation of Methods based on the PRISMA statement

Authors: Pier Cacciali, Raúl Maneyro

Data type: docx

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Link: <https://doi.org/10.3897/herpetozoa.37.e133456.suppl1>

Supplementary material 2

Literature references are used for stomach content identification

Authors: Pier Cacciali, Raúl Maneyro

Data type: docx

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Supplementary material 3

Frequency of prey items consumed by *Notomabuya frenata* and *Hemidactylus mabouia* based on Vrcibradic and Rocha (1998a) and Rocha and Anjos (2007)

Authors: Pier Cacciali, Raúl Maneyro

Data type: docx

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