

ORIGINAL ARTICLE

Food preference for native and invasive prey in the naive lancehead pitviper

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Abstract

The presence of invasive species in the environment can be highly detrimental. The success of these species depends on their interaction with native ones. The prey–predator relationship between invasive and native species can result in biodiversity loss or the introduction of new food items for local predators. Due to its tropical and extensive nature, Brazil is vulnerable to the colonization of invasive species. Snakes are a group of animals that can act as both predators and prey for invasive species. The pitviper *Bothrops jararaca* is an abundant and widely distributed native species on the Brazilian coast. Based on this, we conducted a study on the feeding preferences of naive *B. jararaca* juveniles regarding invasive and native prey. We found that this species exhibits a greater preference for native anurans compared to *Rana catesbeiana*, an invasive amphibian associated with significant environmental impacts. Additionally, the gecko *Hemidactylus mabouia*, a prey that triggered intense predatory responses from the pitviper, reveals that this species, even with a short period of coexistence with *B. jararaca*, has established an intense prey–predator relationship. The negative correlation between prey size and feeding interest, guided solely by olfactory cues, adds a layer of complexity to understanding the feeding choices of *B. jararaca*, providing valuable insights for conservation and environmental management strategies. Abstract in Portuguese is available with online material.

KEYWORDS

amphibians, biological invasion, *Bothrops jararaca*, Brazil, viperidae

1 | INTRODUCTION

The presence of invasive species can lead to significant negative impacts on biodiversity when they establish themselves in new areas (Pimentel, 2014; Salo et al., 2007). For a comprehensive understanding of the effects of introducing invasive species into an ecosystem, it becomes essential to conduct an assessment of the interactions of these species with local predators (Sih et al., 2010).

The naivety of native predators plays a crucial role in the establishment and proliferation of exotic species (Keane &

Crawley, 2002; Shea & Chesson, 2002). Native predator naivety refers to their inability to recognize and/or effectively attack specific prey. Exotic species can benefit from the naivety of a native predator, which facilitates the invasion by these species (Keane & Crawley, 2002).

A group of animals profoundly influenced by naivety are snakes. Although there is some protection of litter by the mother in several snakes (Greene, May, et al., 2002; Stahlschmidt & DeNardo, 2016) these animals lack an elaborate parental care system that involves teaching the young how and what to eat (Waters & Burghardt, 2005).

However, naive newborn snakes respond to olfactory cues from specific prey with high rates of tongue-flicking and predatory attacks (Burghardt, 1993), and these behaviors have a hereditary basis (Brodie & Garland, 1993).

Among several countries in the world, Brazil is a territory prone to and vulnerable to biological invasions due to its vast area, extensive coastline, and climatic conditions conducive to the establishment and persistence of invasive species (Adelino & Lima, 2023). This vast region of South America with high native biodiversity harbors more than 37 invasive vertebrate species (Adelino & Lima, 2023). Three invasive—the African house gecko, *Hemidactylus mabouia* (Moreau De Jonnés, 1818), the rodent *Mus musculus* (Schwartz & Schwartz, 1943), and the American bullfrog, *Rana catesbeiana* (Shaw, 1802) are abundant and have well-established populations in Brazil (Adelino & Lima, 2023; Santos-Pereira & Rocha, 2015; Vanzolini, 1978). These species have caused significant negative impacts on local biodiversity (Adelino & Lima, 2023; Santos-Pereira & Rocha, 2015).

The lancehead pitviper *Bothrops jararaca* (Wied-Neuwied, 1824) has a wide distribution in Brazil and coexists with these invasive species (de Moraes, 2008; Filho et al., 2008). As a juvenile, this snake feeds mainly on anuran amphibians (de Moraes, 2008; Sazima, 1992). Among the most common frogs found in the stomach of this snake are native anurans such as *Physalaemus cuvieri* (Fitzinger, 1826) and *Scinax fuscovarius* (Lutz, 1925) (de Moraes, 2008; Sazima, 1991). Furthermore, both the *M. musculus* mouse and primarily, the African house gecko, *H. mabouia* are prey to *B. jararaca* in the wild (de Moraes, 2008). On the other hand, predation of the American bullfrog has only been observed in captivity (Passos, 2018), although the opposite has been documented in nature, where the American bullfrog predated on *B. jararaca* juveniles (Filho et al., 2008).

Therefore, our research aims to investigate the dietary preferences of naive *B. jararaca* juveniles concerning native and invasive prey, assessing their feeding interest responses to the chemosensory cues of their prey. Given that the co-occurrence time (i.e., the presumed period during which the species maintain a trophic relationship, establishing a predator–prey dynamic) between the *B. jararaca* species and the native prey is longer than with the invasive prey, we hypothesize that the snakes prefer the native prey.

2 | METHODS

2.1 | Animals

We used 24 juveniles *B. jararaca*, aged 10 days, comprising 10 females and 14 males. These specimens were born on February 6, 2023, coming from two distinct litters. The two females that produced the offspring were sourced from the wild, specifically from the highland region of São Paulo State, Brazil (23°32' S 46°38' W), and had been in captivity for 2 months. Following birth, the snakes were individually accommodated in boxes measuring 45 cm in length, 30 cm in width, and 15 cm in height, containing cardboard at the bottom and a water container. All the animals were maintained

in the bioterium of the Laboratory of Ecology and Evolution at the Instituto Butantan, São Paulo, Brazil. The average temperature in the bioterium was maintained around 23°C, following a photoperiod of 12 h of light and 12 h of darkness.

2.2 | Experimental design

To assess the innate feeding preference of *B. jararaca*, we utilized the most abundant natural prey species in its habitat that represent a significant part of its diet (de Moraes, 2008). Among these natural prey items, we evaluated two species of anurans: *S. fuscovarius* and *P. cuvieri*. As for invasive prey species, we included three species that have been previously reported as part of the *B. jararaca* diet: *R. catesbeiana* and the gecko *H. mabouia*, in addition to an endothermic prey, the mouse *M. musculus*.

We investigated food preference using olfactory extracts, employing the tongue-flick attack score (TFAS(R)) proposed by Cooper and Burghardt (1990), albeit with some modifications. This score places greater emphasis on snake bites in response to the stimulus (Cooper & Burghardt, 1990). However, with regard to juvenile *B. jararaca*, an additional behavior carries equal weight to bite. In a particularly high level of interest to the prey, juvenile *B. jararaca* exhibits caudal luring behavior to attract the prey, mimicking a caterpillar (Sazima, 1991). Cooper and Burghardt (1990) described the TFAS method in species of colubrids that engage in active foraging, with biting being the primary behavior indicative of feeding interest. In contrast, *B. jararaca* adopts a "sit-and-wait" hunting strategy (Sazima, 1992). When juveniles of this species encounter potential prey, they initially employ "caudal luring" behavior to attract the prey before striking, a behavior selectively applied only to animals that constitute their prey (Sazima, 1992). Therefore, for *B. jararaca*, caudal attraction behavior is as significant as biting in terms of feeding interest, reflecting an essential aspect of its biology.

To prepare the olfactory extracts, we employed a combination of two extraction techniques (Burghardt, 1993; Cooper, 1998; Greene, Stark, & Mason, 2002; Holding et al., 2016; Mullin et al., 2004; Pernetta et al., 2009; Weaver et al., 2012). All prey were weighed, and their odor was extracted through aqueous extraction. Each killed prey was immersed in distilled water at a concentration of 0.25 g/mL for 4 h. After suspension, sterilized swabs (Global swab Ltda) of 15 cm were impregnated with the odoriferous solution and passed ten times on the dorsal and ventral surfaces of the live prey's body to increase the odor concentration (Figure S1).

To establish controls, we used a swab impregnated with distilled water as a negative control and a swab dipped in a cologne solution at a ratio of 1:10 (Adidas Originals) as a pungency control. The experiments were conducted with the swab inserted into a transparent acrylic block and brought near to the snake. The test began when the swab reached 5 cm from the snake's head, and it exhibited the first tongue-flick movement. All experiment stages were recorded

for 5 min using a camera (HDR-PJ200, Sony) (Figure S1). The order of stimulus presentation was randomized to avoid order effects (Burghardt, 1969). The time between each odor presentation was 1 h and 20 min.

Over 300s, we recorded the number of tongue movements directed at the swab. In the event that the snake was to bite the object or exhibit caudal luring behavior, we also recorded the latency for these behaviors (Burghardt, 1993). These parameters were subsequently transformed into a score of interest/attack with Appropriate Tongue Movements for Repeated Odor Stimuli (TFAS[R]). This index adjusts the value of the response variable upwards when the snake bites the object or exhibits caudal luring, reflecting an increase in the level of predatory interest.

2.3 | Size and co-occurrence time of prey

For the implementation of Principal Component Analysis (PCA) and correlation analyses, we collected data from the literature concerning the average size of the prey and the estimated co-occurrence time between the prey and *B. jararaca*. Due to the lack of studies on the relative abundance of prey species size, we have employed the average size values described for each species. The size data (snout vent length—SVL) and co-occurrence time are as follows: *S. fuscovarius* and *P. cuvieri* (4.3 cm and 3 cm respectively—Haddad et al., 2013) both with an estimated 5 million years (Alencar et al., 2016; Feng et al., 2017); *R. catesbeiana* (8 cm Haddad et al., 2013), introduced in 1935 (Ferreira et al., 2002); *H. mabouia* (5 cm—Iturriaga & Marrero, 2013), introduced between 1600 and 1800 (Dos Anjos & Da Rocha, 2008; Vanzolini, 1978); and *M. musculus* (with a length of 8.28 cm Cory, 1912), introduced in 1500 (da Rosa et al., 2017) (Figure 1).

2.4 | Statistical analysis

To analyze the data, we used Generalized Linear Mixed Models (GLMM) with Poisson distribution and a log link function. The fixed variables were the type of prey. As we presented stimuli to

the same animals, we defined the individual, sex, and brooding as random variables. In addition, we performed Tukey's test for post-hoc analysis to find significant relationships between the variables, using the “emmeans” package. All models were subjected to data dispersion analysis, homoscedasticity, and delineate tests using model diagnostic values and plots, with the help of the package “DHARMa: residual diagnostics for hierarchical (multilevel/mixed) regression models” in R (version 4.04). For the PCA, we employed the average size of the prey species, TFAS(R) values, and the prey species themselves to investigate correlations and understand the data distribution.

3 | RESULTS

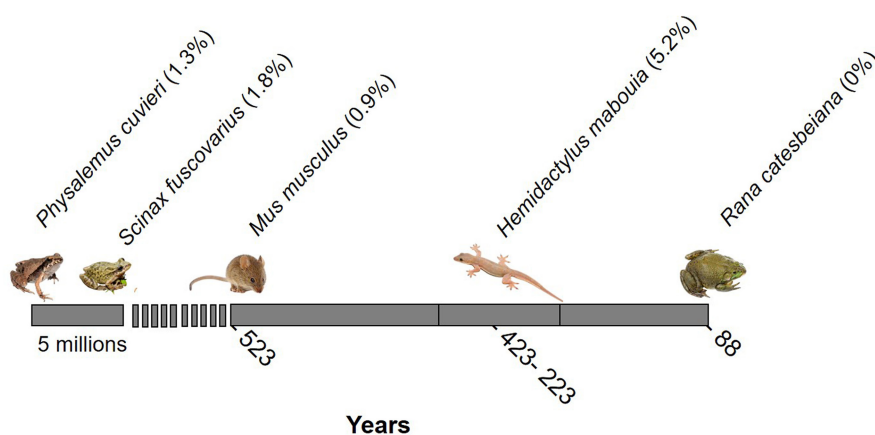
There was a difference in the TFAS(R) index depending on the prey category (native or invasive). Native prey (*S. fuscovarius* and *P. cuvieri*) elicited a significantly higher index than invasives (*M. musculus*, *H. mabouia*, and *R. catesbeiana*) ($z = 6.143$, $p < .0001$). Both prey categories differed from the control (Invasive: control- $z = 16.837$, $p < .0001$; Native: control- $z = 19.943$, $p < .0001$) (Figure 2) (Table S1).

The type of prey influenced the TFAS(R) index. The prey that elicited the highest response was *P. cuvieri*, displaying a significant difference compared to all other groups (Tables S2 and S3), except when compared to *S. fuscovarius*, which ranked as the second prey with the highest index ($z = -1.847$, $p = .0647$). The third prey was the non-native gecko, *H. mabouia*, which also showed a distinct difference from the other groups, except when compared to *S. fuscovarius* ($z = -0.169$, $p = .8658$). Later, the mice exhibited a higher response rate than the *R. catesbeiana* (Figure 3).

Furthermore, out of the 184 records of prey olfactory stimulus presentation, the caudal luring behavior of *B. jararaca* was only documented three times. Specifically, it occurred twice in response to the scent of *S. fuscovarius* and once in relation to the gecko *H. mabouia* (Figure 4).

The PCA data, involving the size (in cm) of the prey, the food interest index (TFAS), and the estimated co-occurrence time between the prey and *B. jararaca*, revealed some relationships between the

FIGURE 1 The time scale of estimated co-occurrence between *Bothrops jararaca* and its prey. Percentage values in parentheses: relative percentage of *B. jararaca*'s overall diet as described by de Moraes (2008).



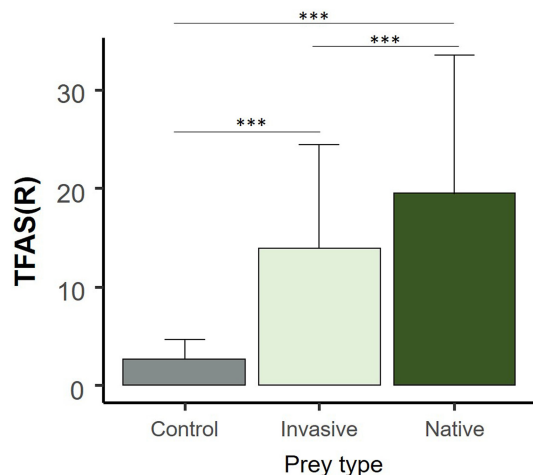


FIGURE 2 The tongue-flick/attack score (TFAS[R]) of naive *Bothrops jararaca* for invasive and native prey. * indicates that the results show a clear difference in the frequency of behaviors in relation to the type of predatory stimulus among each prey category.

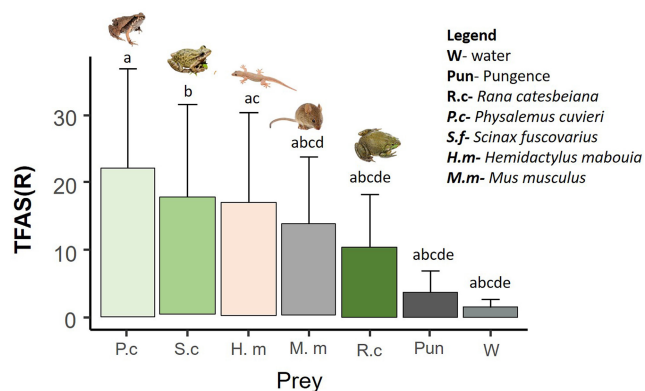


FIGURE 3 The tongue-flick/attack score (TFAS[R]) of naive *Bothrops jararaca* for different prey odors. Corresponding lowercase letters indicate a significant difference between groups ($p < .05$).

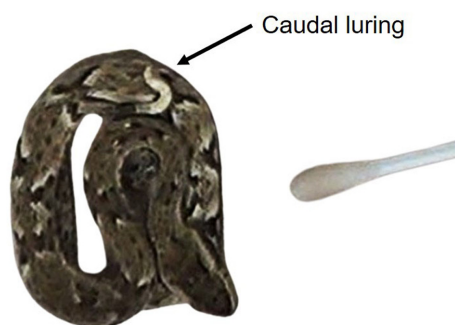


FIGURE 4 Caudal luring behavior of *Bothrops jararaca*. Caudal luring behavior of naive *B. jararaca* juvenile for swab containing *Hemidactylus mabouia* odor.

variables. Dimension 1, which explains 88.1% of the data variation, demonstrates that the food interest index and size are highly correlated (TFAS=0.950; Size=-0.970; co-occurrence time=0.895).

In contrast, Dimension 2 is primarily represented by the estimated co-occurrence time between the prey and *B. jararaca* (co-occurrence time=0.446) (Figure 5).

No significant correlation was found between TFAS(R) and the estimated years of co-occurrence between *B. jararaca* and its prey ($t=2.019$, $p=1367$). However, the average size of the prey exhibited a strong negative correlation with TFAS(R) ($t=-4.412$, $p=.02160$) (Figure 6).

4 | DISCUSSION

We found differences in food preference between native and invasive prey when it comes to naive *B. jararaca* juveniles. Furthermore, when analyzing specific prey species, we observed a preference for native amphibians over other prey. It is important to note that among the five species tested, the invasive gecko ranks third in terms of preference for *B. jararaca* offspring. A correlation was identified between food preference and prey size, but not with the co-occurrence time of the prey with *B. jararaca*.

Our results suggest that *B. jararaca* innately prefers native prey, which is a widely observed phenomenon in snakes, resulting from evolutionary processes in the predator-prey relationship (Arnold, 1977; Cooper et al., 2000; Gove & Burghardt, 1975). In the case of *B. jararaca* when they are juvenile, frogs are usually the most frequently ingested prey (Sazima, 1988, 1991, 1992). Since all native prey species evaluated in this study were frogs, the question arises as to whether the observed preference is due to the intrinsic characteristics of the prey or is influenced by the innate preference for amphibians. However, the hatchlings responded more intensely to native anurans than to bullfrogs. Thus, we suggest that the feeding preference for native amphibians is not because the prey are anurans, but rather due to the specific characteristics of each prey species.

According to the “enemy release hypothesis” (ERH), exotic species have the potential to become invasive by evading the limiting effects of their natural enemies in their original distribution areas (Keane & Crawley, 2002; Shea & Chesson, 2002). The absence of coevolved natural enemies and the tendency of native predators to prefer local species confer a competitive advantage to exotic species over native ones, facilitating invasion processes (Li et al., 2011). Thus, the coevolution between *B. jararaca* and its native anuran prey could lead to a stronger preference for native prey. As a consequence, *R. catesbeiana* might escape the effects of predation within its distribution area.

It is important to note that this invasive frog is a predator of various snakes, including *B. jararaca* (Filho et al., 2008; Wylie et al., 2003). Snakes possess highly developed abilities to identify prey and predators through chemical cues (reviewed in Gans & Crews, 1992). In general, snakes respond more strongly to scents not only of prey but also of predators (Ersan et al., 2020). However, although *R. catesbeiana* prey on snakes, such predation events may be occasional (Greene, 1997). The low response of tongue-flicks

FIGURE 5 Principal component analysis (PCA) in naïve juvenile *Bothrops jararaca*. The analysis comprises three numerical variables: Size (average prey size), TFAS (tongue-flick/attack score), and co-occurrence time (estimated years of coexistence between *B. jararaca* and its prey).

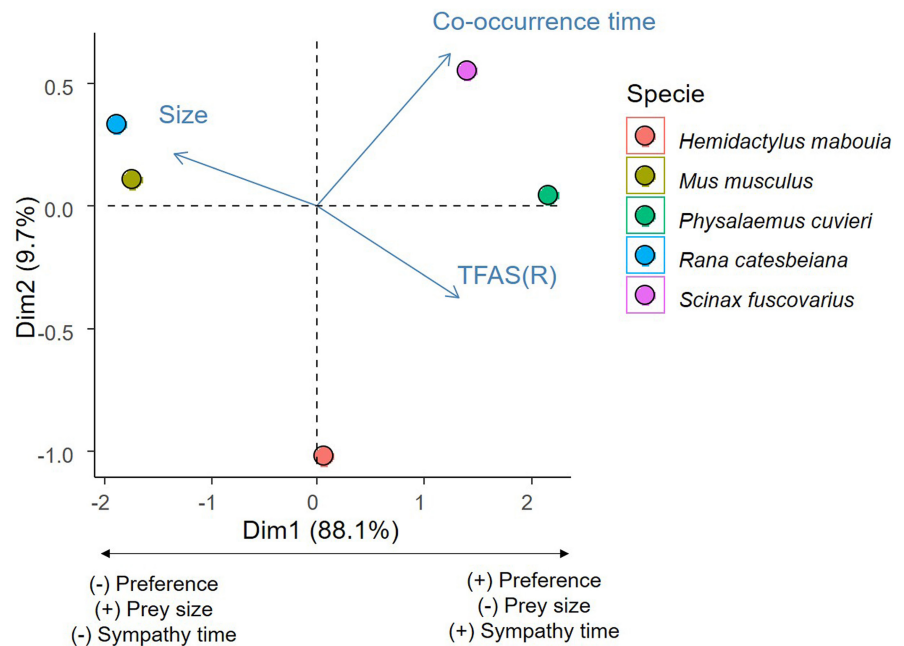
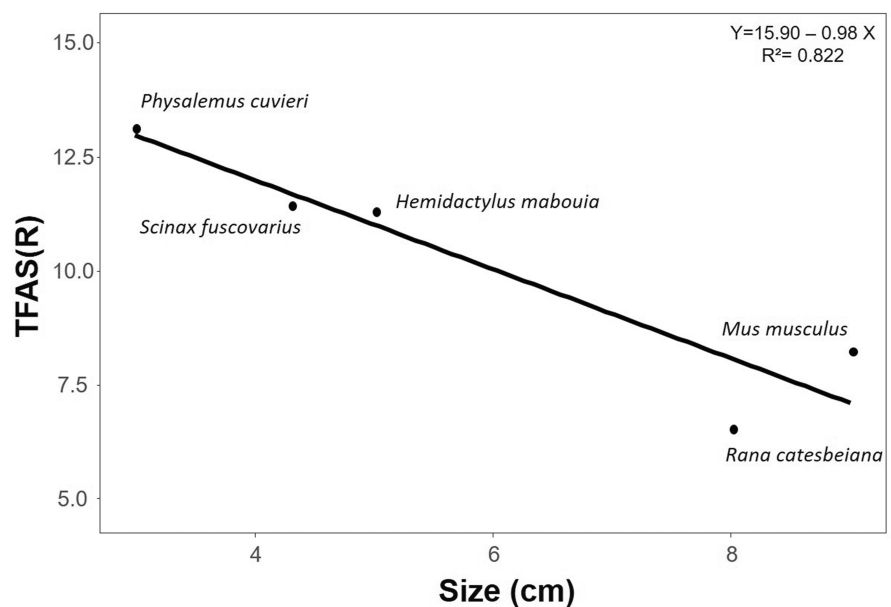


FIGURE 6 Correlation between prey size (cm) and tongue-flick/attack score (TFAS) in naïve juvenile *Bothrops jararaca*. Linear regression of the food preference index (TFAS) against prey size (cm). The species of the prey are highlighted in the data points.



emitted by *B. jararaca* may suggest that there is no recognition of *R. catesbeiana* as a predator but rather as an occasional prey.

Another prey that presented an intriguing relationship was *H. mabouia*. This species has already proven to be significant as prey for *B. jararaca*. In fact, this gecko represents approximately 5.2% of all prey items recorded by *B. jararaca* and comprises about 75% of all squamates eaten by this snake (de Moraes, 2008). This invasive species is found in natural environments and primarily in altered areas (Oliveira et al., 2016), coinciding with habitats used by *B. jararaca*. We are unaware if the dietary records of *H. mabouia* come from *B. jararaca* specimens collected in agricultural areas or near human dwellings. However, we have demonstrated that juvenile *B. jararaca* reacts innately and intensely to the odor of *H. mabouia*, without displaying significant differences compared to

the second-preferred prey, *S. fuscovarius*. Additionally, it is noteworthy that these two species were the only ones to elicit caudal luring behavior. We suggest that, although geckos may coexist with snakes employing various hunting strategies such as caudal luring, according to the "increased susceptibility hypothesis" (ISH) (Colautti et al., 2004; Sih et al., 2010), African geckos would be more vulnerable to *B. jararaca* since they have not undergone the natural selection process to develop aversive behaviors to avoid predation. *Hemidactylus mabouia* can come from an area where there are snakes that use their tails as lure, but the caudal luring used by juveniles of *B. jararaca* differs from other snakes that use this hunting strategy (cf. Sazima, 1991).

This preference for *H. mabouia* could also be attributed to a potential microevolutionary change. Similar to other squamate species,

a rapid evolutionary change may have led to *B. jararaca*'s adaptation to the presence of *H. mabouia* (Madsen & Shine, 1992; Malhotra & Thorpe, 1991). This hypothesis has also been applied to the adaptation and dietary preference for invasive prey in *Thamnophis hammondi*, which has coexisted with invasive prey for approximately 100 years (Bury & Luckenbach, 1976; Dill & Cordone, 1997; Mullin et al., 2004). In the case of geckos, it is believed that *H. mabouia* was introduced approximately 370 years ago (Agarwal et al., 2021; Dos Anjos & Da Rocha, 2008). Due to the centuries of coexistence (or sympatry) between the two species, we believe that populations of the lancehead pitviper have naturally incorporated *H. mabouia* as part of their diet.

While there is evidence supporting that *H. mabouia* was introduced in Brazil by humans around 370 years ago (Agarwal et al., 2021), the hypothesis that this gecko arrived by dispersion from Africa (Kluge, 1969) cannot be discarded. Thus, this species may have been co-occurring with *B. jararaca* for a longer period. Under this hypothesis, the dietary preference demonstrated in this study by this gecko could have been a result of a natural response process, similar to that observed in other native anurans.

While time appears to be relevant for the emergence of micro-evolutionary changes, we did not find a significant correlation between the co-occurrence time of *B. jararaca* with its prey and the food preference index. However, when we focus on the prey size, we observe a very strong correlation between prey size and food preference. The smaller the average size of the prey, the higher the food interest index.

For snakes, the size of their mouth opening establishes the upper limits for the maximum size of ingestible prey and, therefore, directly influences which prey they can or cannot consume (Arnold, 1993; Cundall & Greene, 2000). Furthermore, the size of the snake can predict the dietary preferences of certain species, with smaller snakes exhibiting a preference for smaller ectothermic prey (Barends & Naik, 2023). Our study revealed a significant correlation between prey size and feeding preference, relying solely on the scent of the prey as a cue. It suggests that naive snake hatchlings might possess an innate preference for smaller prey, when guided solely by olfactory cues. This indicates an inherently intimate relationship between predator and prey, where chemical signals can trigger *B. jararaca*'s interest in smaller natural prey. However, further studies using visual cues of the prey are required.

The introduction of bullfrogs to Brazil and elsewhere generated significant environmental impacts. Understanding the relationship between these introduced species and existing native species is essential for managing conservation efforts effectively. The results of this study confirm that *B. jararaca* is born with chemosensory preferences for prey that reflect its diet. Our data show that naive snakes tend to prefer certain natural prey over invasive ones, even though the African gecko (an introduced species) is commonly found in the stomach of *B. jararaca*. In this sense, we could support the hypothesis that *B. jararaca* coexists with *H. mabouia* earlier than has been assumed. Additionally, we observed a negative correlation between prey size and *B. jararaca*'s degree

of food interest, based solely on olfactory cues. We suggest that future research should compare adult and juvenile *B. jararaca* of varying sizes, using a broader range of natural prey. This will provide more data on the predator-prey relationship, offering better support for species conservation.

AUTHOR CONTRIBUTIONS

João Miguel Alves-Nunes helped to design the study, set up the experiments, collect data, analyze and write the manuscript. Adriano Fellone helped with the study design and data collection. Otávio A. Vuolo Marques helped coordinate the study and writing of the manuscript. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8pk0p2nwp>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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