

# Ontogenetic shifts, trophic differentiation, and morphological constraints shape dietary diversity in sympatric *Oxyrhopus* false coral snakes

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## Article

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# Abstract

Although snakes of the genus *Oxyrhopus* are generally regarded as opportunistic predators, the relative roles of interspecific dietary differentiation, ontogenetic shifts, and morphological constraints in shaping their feeding ecology remain poorly understood. We analyzed the diet of 429 preserved specimens representing six *Oxyrhopus* species from Bahia, Brazil. Dietary composition was quantified using the Index of Relative Importance (%IRI), trophic overlap was estimated with Pianka's niche overlap index, ontogenetic changes were evaluated using linear models, and morphological constraints were assessed through relationships between snake body size, head width, and prey dimensions. Species showed distinct dietary compositions and generally low trophic overlap, supporting trophic niche differentiation among sympatric congeners. Juveniles fed predominantly on lizards, whereas adults incorporated proportionally more mammals and birds. Prey size increased with snake body size rather than ontogenetic stage itself, and head width was positively associated with prey width, indicating that cranial morphology constrains maximum prey size. Together, these results show that trophic niche differentiation in *Oxyrhopus* arises from the interaction between interspecific dietary divergence, ontogenetic dietary shifts, and morphological constraints. This study provides the first comparative assessment integrating these mechanisms across multiple sympatric *Oxyrhopus* species.

## Introduction

Diet is a central component of the ecological niche and plays a fundamental role in the ecology of species by directly influencing energy acquisition, growth, survival, and reproductive success<sup>1</sup>. In snakes, the evolution of a highly kinetic skull has enabled the ingestion of whole prey and facilitated the exploitation of a wide diversity of prey types<sup>1,2</sup>. Nevertheless, prey size and type remain constrained by body size and head dimensions, which impose an upper limit on the size of prey that can be ingested (gape limitation)<sup>3–7</sup>. Consequently, understanding the factors that drive dietary variation is essential for explaining ecological patterns within and among species.

Dietary variation in snakes is shaped by multiple ecological and morphological mechanisms<sup>8–10</sup>. Throughout ontogeny, increases in body size and head dimensions enable individuals to consume progressively larger prey, leading to shifts in both prey size and dietary composition during development<sup>2,3,7,10</sup>. Likewise, variation in head dimensions may constrain the maximum size of prey that can be ingested<sup>4,11</sup>. At the interspecific level, sympatric species often differ in resource use, resulting in varying degrees of trophic niche segregation and dietary overlap<sup>12–14</sup>. Together, these mechanisms provide a conceptual framework for understanding dietary variation both within and among snake species and for identifying the factors that structure trophic niches in sympatric communities.

Species of the genus *Oxyrhopus* (Dipsadidae) provide an excellent model for evaluating how ontogenetic changes and head-size-related constraints influence dietary variation and contribute to trophic differentiation among sympatric species. This genus of false coral snakes comprises 15 species distributed throughout the Neotropical region, occupying a wide range of habitats including forests, open formations, arid environments, and oceanic islands, from southern Mexico to northern Argentina<sup>15–17</sup>. Six of these species occur in the state of Bahia, northeastern Brazil<sup>18,19</sup>. Previous studies have shown that these species differ in body size and head dimensions<sup>20</sup>, traits that are likely to influence the size and type of prey they consume.

Although species of *Oxyrhopus* have been the subject of numerous natural history studies, most available information on their diet comes from isolated prey records or local studies focused on individual species<sup>9,15,21–28</sup>. Based on these records, *Oxyrhopus* species have generally been regarded as opportunistic generalists with broad dietary spectra<sup>25,26,29,30</sup>. However, quantitative comparisons integrating multiple sympatric species remain scarce. Consequently, it remains unclear to what extent dietary variation within the genus is driven by ontogenetic shifts, head-size-related constraints, or trophic differentiation among sympatric species.

To address these knowledge gaps, we analyzed the diet of *Oxyrhopus* species occurring in the state of Bahia, Brazil, using preserved specimens deposited in scientific collections. Specifically, we tested three complementary hypotheses: (1) sympatric species differ in dietary composition and resource use; (2) diet changes throughout ontogeny, with juveniles consuming smaller prey and adults incorporating larger prey and a broader range of prey types; and (3) prey size and type are associated with snake body size and head dimensions. By integrating ontogenetic, morphological, and interspecific perspectives, this study provides a comprehensive assessment of the mechanisms underlying dietary variation and trophic niche differentiation in sympatric generalist snakes.

## Results

Of the 429 individuals examined, 255 (59.4%) contained identifiable digestive content. For *O. clathratus*, only a single juvenile female was recorded with a reptilian prey item, and for *O. formosus*, one adult female had consumed a mammal. In both cases, prey identification to a lower taxonomic level was not possible due to advanced digestion; therefore, dietary data for these species are treated as anecdotal and were excluded from quantitative analyses.

For the other species, the recorded prey items were one per snake. The final count of prey items was 12 for *O. rhombifer*, 14 for *O. guibei*, 80 for *O. petolarius*, and 147 for *O. trigeminus* in Bahia state. Species accumulation curves revealed that the number of individuals for both *O. petolarius* and

*O. trigeminus* approached an asymptote, indicating proximity to achieving representativeness in terms of food items for these two species (Fig. 1). Conversely, for *O. guibei* and *O. rhombifer*, a significantly larger number of samples would be required for a more precise determination of their dietary compositions.

## Interspecific dietary differentiation

Species of *Oxyrhopus* were found in different ecosystems (Fig. 2): *O. rhombifer* was found in one ecosystem, primarily consuming prey from families of reptiles. *O. guibei* was present in three ecosystems: Atlantic Forest (AF), Seasonal Semi-deciduous Forest (SSF), and Deciduous Seasonal Forest (DSF). It exhibited a diverse diet in AF, with significant consumption of Gymnophthalmidae. *O. petolarius* inhabited four ecosystems: AF, SSF and DSF. This species showed high dietary diversity in AF, consuming a wide range of prey including Cricetidae, and Gymnophthalmidae. *O. trigeminus* was the most widespread, found in seven ecosystems: DOF, SSF, DSF, PF, Cerrado, Ecotone, and Caatinga.

Diet composition differed markedly among species (Tables 1 and 2). In *O. rhombifer*, all prey items were reptiles, with a strong predominance of Tropiduridae (84.6%), followed by isolated records of Teiidae and Gymnophthalmidae. In *O. guibei*, reptiles accounted for 75% of all recorded prey items, whereas mammals represented 25%. Owing to the limited sample size for both species, quantitative comparisons between sexes, ontogenetic stages, and dietary overlap using Pianka's index were not possible.

Table 1

– Diet composition and intraspecific niche overlap in *Oxyrhopus* species. Food items consumed by *Oxyrhopus* species, categorized by the sex of the individuals (female (F) and male (M)) and the age group (adults (A) and juveniles (J)). The quantities consumed are also indicated. The overlap indices between different sexes and age groups within the species are provided at the end of the table.

|                              | Indices between different sexes and age groups within the species are provided at the end of the table. |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   | Total<br>general |
|------------------------------|---------------------------------------------------------------------------------------------------------|---|--------------------|---|------------------|---|----------------------|---|---------------------|---|----------------------|---|----|----|---|---|------------------|
|                              | <i>O. clathratus</i>                                                                                    |   | <i>O. formosus</i> |   | <i>O. guibei</i> |   | <i>O. petolarius</i> |   | <i>O. rhombifer</i> |   | <i>O. trigeminus</i> |   |    |    |   |   |                  |
|                              | F                                                                                                       | F | F                  | M | F                | M | F                    | M | F                   | M | F                    | M | F  | M  | F | M |                  |
| Group                        | J                                                                                                       | A | A                  | J | A                | J | A                    | J | A                   | J | A                    | J | A  | A  | J | A | J                |
| <b>Aves</b>                  |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| Passeriforme                 |                                                                                                         |   |                    |   |                  |   | 4                    |   | 1                   |   |                      |   |    | 1  |   | 1 | 7                |
| <b>Insecta</b>               |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    | 1 |   | 1                |
| <b>Mamifera</b>              |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| Rodentia                     |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| Indeterminated               |                                                                                                         | 1 |                    |   | 1                |   | 5                    | 3 | 5                   | 4 |                      |   |    | 10 |   | 7 | 36               |
| Cricetidae                   |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Akodon cursor</i>         |                                                                                                         |   | 1                  |   |                  |   | 2                    | 2 | 2                   |   |                      |   |    |    |   |   | 7                |
| <i>Calomys expulsus</i>      |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   | 4  |    | 1 |   | 5                |
| <i>Cerradomys</i> sp.        |                                                                                                         |   |                    |   |                  |   | 2                    |   |                     |   |                      |   | 2  |    |   |   | 4                |
| <i>Hyleaemys seuanezi</i>    |                                                                                                         |   |                    |   |                  |   | 1                    |   | 1                   |   |                      |   |    |    |   |   | 2                |
| <i>Necomys lasiurus</i>      |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   | 13 |    | 5 |   | 18               |
| <i>Oligorizomis</i> sp.      |                                                                                                         |   |                    |   |                  |   |                      | 1 | 4                   | 2 |                      |   | 3  | 2  |   |   | 12               |
| <i>Rhipidomys mastacalis</i> |                                                                                                         |   |                    |   |                  |   |                      |   | 1                   |   |                      |   |    |    |   |   | 1                |
| <i>Thaptomys nigrita</i>     |                                                                                                         |   |                    |   |                  |   | 1                    |   | 1                   | 1 |                      |   | 1  |    |   |   | 4                |
| <i>Juvenil</i>               |                                                                                                         |   |                    |   |                  |   | 1                    | 2 | 1                   | 3 |                      |   | 1  |    |   |   | 8                |
| Didelphidae                  |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Marmosa murina</i>        |                                                                                                         |   |                    |   |                  |   |                      |   | 1                   |   |                      |   |    |    |   |   | 1                |
| <i>Monodelphis americana</i> |                                                                                                         |   | 1                  | 1 |                  |   |                      |   |                     |   |                      |   |    |    |   |   | 2                |
| <b>Reptilia</b>              |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| Squamata                     |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| Indeterminated               | 1                                                                                                       |   |                    | 1 |                  | 1 | 1                    |   |                     |   |                      |   | 1  | 1  |   | 2 | 8                |
| Eggs                         |                                                                                                         |   | 1                  |   |                  |   |                      |   |                     |   |                      |   | 3  |    | 1 |   | 5                |
| Anguidae                     |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Ophiodes striatus</i>     |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   | 1  |    |   |   | 1                |
| Gekkonidae                   |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Hemidactylus mabouia</i>  |                                                                                                         |   |                    |   |                  |   | 1                    |   | 2                   |   |                      |   |    | 1  |   | 3 | 7                |
| Gymnophthalmidae             |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Leposoma annactans</i>    |                                                                                                         |   |                    |   | 1                |   | 3                    |   | 1                   |   |                      |   |    |    |   |   | 5                |
| <i>Leposoma</i> sp.          |                                                                                                         |   | 2                  |   | 2                |   | 6                    |   | 6                   |   |                      | 1 |    |    |   |   | 17               |
| Phyllodactylidae             |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |
| <i>Gymnodactylus</i> sp.     |                                                                                                         |   | 1                  |   | 2                |   | 1                    |   |                     |   |                      |   |    |    |   |   | 4                |
| Scincidae                    |                                                                                                         |   |                    |   |                  |   |                      |   |                     |   |                      |   |    |    |   |   |                  |

|                             | <i>O. clathratus</i> | <i>O. formosus</i> | <i>O. guibei</i> |   | <i>O. petolarius</i> |   | <i>O. rhombifer</i> |    |    | <i>O. trigeminus</i> |   |   |       | Total general |    |    |    |     |
|-----------------------------|----------------------|--------------------|------------------|---|----------------------|---|---------------------|----|----|----------------------|---|---|-------|---------------|----|----|----|-----|
|                             | F                    | F                  | F                | M | F                    | M | F                   | M  | F  | M                    | F | M | F     | M             |    |    |    |     |
| <i>Brasiliscincus</i> sp.   |                      |                    |                  |   |                      | 1 |                     |    |    |                      | 2 |   |       | 1             | 4  |    |    |     |
| <i>Copeoglossum</i> sp.     |                      |                    |                  |   |                      |   |                     |    |    |                      |   |   |       | 1             | 1  |    |    |     |
| <i>Psycosauria</i> sp.      |                      |                    |                  |   |                      | 1 |                     | 1  |    |                      | 1 | 5 | 2     | 6             | 20 |    |    |     |
| Teidae                      |                      |                    |                  |   |                      |   |                     |    |    |                      |   |   |       |               |    |    |    |     |
| <i>Ameiva ameiva</i>        |                      |                    |                  |   | 1                    |   | 1                   |    | 1  |                      | 8 | 8 | 7     | 4             | 30 |    |    |     |
| Tropiduridae                |                      |                    |                  |   |                      |   |                     |    |    |                      |   |   |       |               |    |    |    |     |
| <i>Tropidurus hispidus</i>  |                      |                    |                  |   |                      | 1 |                     | 1  |    |                      | 3 |   |       |               | 5  |    |    |     |
| <i>Tropidurus torquatus</i> |                      |                    |                  |   |                      |   |                     |    | 3  |                      | 1 |   |       | 3             | 7  |    |    |     |
| <i>Tropidurus</i> sp.       |                      |                    |                  |   |                      | 1 | 2                   |    | 2  | 5                    | 1 | 2 | 16    | 7             | 16 | 3  | 55 |     |
| Total general               | 1                    | 1                  | 3                | 5 | 1                    | 7 | 18                  | 25 | 17 | 23                   | 9 | 1 | 3     | 71            | 25 | 41 | 22 | 273 |
| Index overlap               |                      |                    |                  |   |                      |   |                     |    |    |                      |   |   |       |               |    |    |    |     |
| Sex                         |                      |                    |                  |   |                      |   | 0.758               |    |    |                      |   |   | 0.852 |               |    |    |    |     |
| Age                         |                      |                    |                  |   |                      |   | 0.409               |    |    |                      |   |   | 0.486 |               |    |    |    |     |

Table 2

— Relative importance of prey categories in *Oxyrhopus* diets. Percentage of the relative importance indices (%IRI) of the families consumed by *Oxyrhopus* species, categorized by the sex of individuals (female (F) and male (M)) and age group (adults (A) and juveniles (J)). The order category was used for Passeriformes and class for Insecta.

| Prey             | <i>O. guibei</i> |      |      |      | <i>O. petolarius</i> |      |       |      | <i>O. rhombifer</i> |      |      |      | <i>O. trigeminus</i> |      |       |      |
|------------------|------------------|------|------|------|----------------------|------|-------|------|---------------------|------|------|------|----------------------|------|-------|------|
|                  | F                |      | M    |      | F                    |      | M     |      | F                   |      | M    |      | F                    |      | M     |      |
|                  | A                | J    | A    | J    | A                    | J    | A     | J    | A                   | J    | A    | A    | J                    | A    | J     |      |
| <b>Ave</b>       |                  |      |      |      |                      |      |       |      |                     |      |      |      |                      |      |       |      |
| Passeriforme     |                  |      |      |      | 0.07                 |      | 0.005 |      |                     |      |      |      | 0.001                |      | 0.01  |      |
| <b>Insecta</b>   |                  |      |      |      |                      |      |       |      |                     |      |      |      |                      |      |       |      |
| Invertebrates    |                  |      |      |      |                      |      |       |      |                     |      |      |      |                      |      | 0.004 |      |
| <b>Mammalia</b>  |                  |      |      |      |                      |      |       |      |                     |      |      |      |                      |      |       |      |
| Crecitidae       |                  |      |      |      |                      |      |       |      |                     |      |      |      | 0.47                 | 0.07 | 0.15  |      |
| Cricetidae       | 0.53             |      |      |      | 0.66                 | 0.38 | 0.75  | 0.33 |                     |      |      |      |                      |      |       |      |
| Didelphidae      | 0.31             | 0.31 |      | 0.73 |                      |      | 0.04  |      |                     |      |      |      |                      |      |       |      |
| Rodentia indet.  |                  |      | 1.00 |      | 0.24                 | 0.06 | 0.19  | 0.13 |                     |      |      |      | 0.06                 |      | 0.06  |      |
| <b>Reptilia</b>  |                  |      |      |      |                      |      |       |      |                     |      |      |      |                      |      |       |      |
| Anguidae         |                  |      |      |      |                      |      |       |      |                     |      |      |      | 0.01                 |      |       |      |
| Gekkonidae       |                  |      |      |      | 0.01                 |      | 0.05  |      |                     |      |      |      |                      | 0.02 |       | 0.11 |
| Gymnophthalmidae |                  | 0.59 |      |      | 0.39                 |      | 0.28  |      |                     |      | 0.09 |      |                      |      |       |      |
| Phyllodactylidae | 0.17             |      |      | 0.03 | 0.02                 |      |       |      |                     |      |      |      |                      |      |       |      |
| Scincidae        |                  |      |      |      | 0.06                 |      | 0.005 |      |                     |      |      |      | 0.01                 | 0.18 | 0.04  | 0.44 |
| Teidae           |                  |      |      |      | 0.005                |      |       |      | 0.07                |      |      |      | 0.11                 | 0.38 | 0.16  | 0.15 |
| Tropiduridae     |                  |      |      |      | 0.02                 | 0.08 |       | 0.19 | 0.93                | 1.00 | 0.91 | 0.33 | 0.35                 | 0.58 | 0.28  |      |
| Squamata         |                  | 0.09 |      | 0.24 |                      |      |       |      |                     |      |      |      | 0.01                 |      |       | 0.02 |

In *O. petolarius*, digestive contents were detected in 56% of the examined individuals. The diet consisted primarily of mammals (55.4%), followed by reptiles (38.6%) and birds (6.0%). Mammals represented the most important prey category according to the percentage Index of Relative Importance (%IRI; Table 2). Dietary overlap between females and males was high (Pianka's index:  $O = 0.758$ ), indicating similar use of the main food resources despite minor differences in the frequency of individual prey categories (Table 1).

In *O. trigeminus*, digestive contents were found in 62% of the examined individuals, making it the species with the most diverse diet. Reptiles constituted the dominant prey category (67.3%), followed by mammals (30.8%) and birds (1.3%). In addition, insect remains were recorded for the first time in a juvenile female, representing the first report of insect consumption for this species. As observed in *O. petolarius*, dietary overlap between females and males was high (Pianka's index:  $O = 0.852$ ), indicating very similar patterns of resource use between the sexes (Table 1).

Interspecific comparisons based on Pianka's index revealed generally low dietary overlap among species. The only exception was the comparison between *O. trigeminus* and *O. rhombifer* ( $O_{jk} = 0.781$ ), both characterized by a high consumption of lizards, particularly species of the genus *Tropidurus*. In contrast, *O. guibei* and *O. rhombifer* exhibited virtually no dietary overlap ( $O_{jk} = 0.001$ ), whereas overlap between *O. petolarius* and *O. rhombifer* was also low ( $O_{jk} = 0.072$ ). Likewise, *O. guibei* showed low dietary overlap with both *O. trigeminus* ( $O_{jk} = 0.013$ ) and *O. petolarius* ( $O_{jk} = 0.341$ ), reflecting marked differences in prey composition among these species.

Although *O. petolarius* and *O. trigeminus* shared several broad prey categories, dietary overlap between them was low ( $O_{jk} = 0.131$ ), indicating pronounced trophic differentiation. This pattern was supported by contingency chi-square analyses, which detected significant differences in prey composition for both juveniles ( $\chi^2 = 54.726$ ;  $P < 0.001$ ) and adults ( $\chi^2 = 70.364$ ;  $P < 0.001$ ). Both species consumed lizards of the genera *Tropidurus* and *Psychosaura*, as well as unidentified rodent remains; however, the relative importance and taxonomic composition of prey differed markedly between them (Table 1).

## Ontogenetic Variation

Ontogenetic variation was detected only in *O. petolarius* and *O. trigeminus*, the two species represented by sufficient numbers of juvenile and adult individuals to allow statistical comparisons. In contrast, the limited sample sizes of *O. guibei* and *O. rhombifer* precluded quantitative analyses of ontogenetic dietary variation.

In *O. petolarius*, juveniles fed primarily on reptiles, whereas adults incorporated a greater proportion of mammals and birds into their diet (Table 2). Consequently, dietary overlap between juveniles and adults was low (Pianka's index:  $O = 0.409$ ). These differences were supported by contingency chi-square analysis ( $\chi^2 = 40.054$ ;  $P = 0.005$ ). The linear model also revealed a significant effect of snake SVL on prey length ( $F = 6.16$ ;  $P = 0.016$ ; Fig. 3a), whereas the effect of ontogenetic stage was only marginally significant ( $P = 0.055$ ).

A similar pattern was observed in *O. trigeminus*. Juveniles consumed predominantly reptiles, with mammals accounting for less than 5% of prey items, whereas adults incorporated a greater proportion of mammals and birds while reptiles remained the dominant prey category (Table 2). Dietary overlap between juveniles and adults was low (Pianka's index:  $O = 0.486$ ), and these differences were supported by contingency chi-square analysis ( $\chi^2 = 47.578$ ;  $P < 0.001$ ). Likewise, the linear model detected a significant positive effect of SVL on prey length ( $F = 13.79$ ;  $P < 0.001$ ; Fig. 3b), whereas the effect of ontogenetic stage was not significant ( $P = 0.483$ ). Thus, although juveniles and adults differed in prey composition, prey size was primarily explained by body size rather than ontogenetic stage itself.

## Morphological constraints

To evaluate morphological constraints on prey size, we examined whether body size and head dimensions limited the maximum size of prey consumed. Specifically, we analyzed the relationship between snake snout–vent length (SVL) and prey length (Fig. 3), as well as between head width and prey width (Fig. 4).

In *O. petolarius* and *O. trigeminus*, the linear models presented above showed that prey length increased significantly with snake SVL (Fig. 3), indicating that body size was an important predictor of prey size. In both species, the effect of ontogenetic stage became weak or non-significant after accounting for body size.

In *O. guibei*, where ontogenetic analyses were not possible because of the limited number of adults, simple linear regression revealed a strong positive relationship between snake SVL and prey length ( $R^2 = 0.730$ ;  $P < 0.001$ ; Fig. 3c), indicating a close association between body growth and prey size. Likewise, head width was positively related to prey width ( $y = 1.3482x - 4.8982$ ;  $R^2 = 0.461$ ;  $P = 0.022$ ; Fig. 4a), suggesting that cranial morphology constrains the dimensions of prey consumed.

Similarly, in *O. rhombifer*, prey length increased significantly with predator body size ( $R^2 = 0.375$ ;  $P = 0.045$ ; Fig. 3d). Although a positive relationship was also observed between head width and prey width, this relationship was not statistically significant ( $y = 1.5511x - 1.5719$ ;  $R^2 = 0.148$ ;  $P = 0.306$ ; Fig. 4b).

In *O. petolarius*, head width was positively associated with prey width ( $y = 0.1857x - 0.5666$ ;  $R^2 = 0.452$ ;  $P < 0.001$ ; Fig. 4c). A similar relationship was detected in *O. trigeminus* ( $y = 1.4852x - 0.9571$ ;  $R^2 = 0.364$ ;  $P < 0.001$ ; Fig. 4d), indicating that cranial dimensions represent an important constraint on the maximum size of prey consumed.

## Discussion

This study provides the first comparative assessment of the feeding ecology of *Oxyrhopus* species occurring in Bahia. Despite belonging to the same genus and occurring sympatrically, the species differed markedly in prey composition and trophic overlap. Our results also revealed ontogenetic dietary shifts and demonstrated that prey size is associated primarily with snake body size and head dimensions rather than ontogenetic stage itself. Together, these findings indicate that trophic niche differentiation in *Oxyrhopus* results from the combined effects of prey availability, morphological constraints, and ontogenetic changes.

The coexistence of closely related species represents a central question in ecology because high potential niche overlap may increase competition for resources<sup>12,13</sup>. Under this framework, niche differentiation along spatial, temporal, or trophic axes is considered one of the primary mechanisms facilitating coexistence. Our results show that sympatric *Oxyrhopus* species in Bahia exhibit generally low dietary overlap, supporting trophic segregation as an important mechanism of niche partitioning within the genus.

The only notable exception was the overlap between *O. rhombifer* and *O. trigeminus*, particularly among juveniles, which fed predominantly on reptiles. Dietary overlap during early life stages may reflect shared constraints imposed by prey size, prey handling ability, or prey availability. In contrast, the dietary divergence observed among adults—especially the absence of mammalian prey in *O. rhombifer*—may reduce competitive interactions later in life. Although this pattern suggests that ontogenetic dietary shifts may contribute to species coexistence, the limited sample size available for *O. rhombifer* warrants cautious interpretation.

Although *O. trigeminus* overlapped with the greatest number of congeners, Pianka's overlap values remained low for most species except *O. rhombifer*. This pattern is consistent with the broad trophic niche of *O. trigeminus*. Nevertheless, geographical overlap does not necessarily imply direct competition because differences in prey size, microhabitat use, foraging behavior, or temporal activity patterns may substantially reduce competitive interactions. Consequently, the dietary overlap observed for *O. trigeminus* likely reflects ecological flexibility rather than competitive dominance. Overall, these results indicate that although *Oxyrhopus* species share a broad potential prey spectrum, the effective use of food resources differs among species and across regions.

Previous studies consistently describe *Oxyrhopus* species as opportunistic generalists that feed primarily on lizards and small mammals, although birds, snakes, and occasionally amphibians have also been reported<sup>5,6,9,14,23,24,29,31–33</sup>. Our results are consistent with this general pattern while substantially expanding the known diet of the genus in Bahia through numerous new prey records across all five species.

For *O. guibei*, previous records included four rodent species, seven lizard species, and one bird species<sup>14,31</sup>. Here, we add new dietary records including the lizard *Leposoma* sp. and the mammals *Akodon cursor* and *Monodelphis americana*. Likewise, the known diet of *O. rhombifer* previously included five lizard species, one snake, and two rodents<sup>14,34,35</sup>. Although our data suggest that *O. rhombifer* feeds predominantly on lizards—and that this apparent dietary specialization may contribute to its reduced trophic overlap with congeners—the limited sample size prevents robust conclusions regarding interspecific differentiation and highlights the need for additional data for both species.

The larger sample size available for *O. petolarius* substantially expands previous knowledge of its diet, which already included a variety of lizards, mammals, and birds<sup>23,25,29,32,36</sup>. Our study adds 13 previously unreported prey items, primarily reptiles and mammals, considerably broadening its known trophic spectrum. The absence of amphibians and bats in our samples may reflect regional differences in prey availability or local foraging behavior.

Similarly, *O. trigeminus* exhibited a highly diverse diet, including lizards, small mammals, birds, and snakes<sup>14,15,24,33</sup>. We report additional prey records including *Ophioides striatus*, *Psychosaura* sp., and the mammals *Calomys expulsus*, *Cerradomys* sp., and *Thaptomys nigrita*, further emphasizing the ecological versatility of this species. Although marsupials were absent from our samples, their occasional consumption reported elsewhere suggests that they likely represent a relatively minor or geographically variable dietary component.

Dietary information remains scarce for *O. formosus* and *O. clathratus*. Previous studies reported *Arthrosaura* sp. as prey of *O. formosus*<sup>29</sup>, whereas *O. clathratus* has been documented feeding on *Colobodactylus dalcyanus* and exhibiting neonatal cannibalism<sup>22,37</sup>. Our study adds the first rodent record for *O. formosus* and an additional reptile record for *O. clathratus*, highlighting both the rarity of these species and the need for further studies on their trophic ecology.

Geographic variation also appears to influence diet composition, as previous studies reported a higher proportion of lizards in Caatinga populations than in Atlantic Forest populations<sup>24,38</sup>. Such differences are likely driven by local prey availability rather than fundamentally different feeding strategies and may be further influenced by seasonal fluctuations in prey abundance.

Overall, these findings show that the known dietary breadth of *Oxyrhopus* species increases substantially when records from different geographic regions are combined, demonstrating considerable trophic plasticity. Consequently, appears to arise primarily from opportunistic feeding behavior combined with spatial variation in prey availability, rather than from strict dietary specialization.

Although information on the diet of *Oxyrhopus* remains fragmentary, our results reveal consistent intraspecific patterns that support both the ontogenetic shift and morphological constraint hypotheses proposed in this study. Across the species analyzed, juveniles fed primarily small reptiles, whereas adults progressively incorporated mammals and, to a lesser extent, birds into their diets. This pattern agrees with that reported for many Neotropical snakes and is consistent with early-life limitations imposed by body size and gape dimensions<sup>3,39</sup>.

The ontogenetic dietary shift observed here follows the classical predictions for snakes, whereby increases in body size expand the spectrum of potential prey by allowing the capture, handling, and ingestion of progressively larger prey<sup>3</sup>. Similar patterns have been documented in other dipssadids, such as species of *Philodryas*, whose juveniles feed primarily on small reptiles before incorporating mammals as adults<sup>39,40</sup>. Although capturing larger prey entails greater energetic costs and potentially higher handling risks, it also provides greater energetic returns per feeding event, making this transition advantageous as snakes increase in size<sup>3,5,11</sup>.

Our analyses indicate that ontogenetic dietary shifts are largely explained by morphological constraints associated with increases in body size and head dimensions. These findings support the hypothesis that increases in cranial dimensions expand the mechanical limits imposed by gape, thereby allowing the consumption of progressively larger prey<sup>4,11</sup>. Together, these results indicate that ontogenetic dietary shifts are driven not only by changes in prey preference but also by biomechanical constraints that become progressively relaxed as snakes grow.

Although previous studies suggested limited ontogenetic dietary differences in *O. trigeminus*<sup>15</sup>, our results demonstrate clear shifts in diet composition between juveniles and adults in both *O. trigeminus* and *O. petolarius*. In *O. guibei*, although the limited sample size precluded formal statistical analyses, the observed trends were consistent with the same pattern and reinforce previous observations for the species<sup>21</sup>. Collectively, these findings highlight the importance of large sample sizes for detecting ontogenetic dietary shifts in generalist snake species.

Despite the sexual size dimorphism previously described for these species<sup>20</sup>, we found no substantial differences in diet composition between males and females. The high Pianka overlap values indicate that both sexes exploit similar food resources, a pattern previously reported for *O. trigeminus*<sup>24</sup> and species of *Philodryas*<sup>40</sup>. This suggests that sexual differences in body size are insufficient to generate marked trophic segregation, likely because both sexes remain within a functional size range capable of exploiting the same prey resources.

Finally, our results show that *O. petolarius* and *O. trigeminus* are capable of consuming relatively large prey in relation to their body size. This ability is probably facilitated by a combination of cranial adaptations and functional traits, together with their opisthoglyphous dentition, which may aid in subduing potentially dangerous prey<sup>41,42</sup>. We also recorded gravid females consuming relatively large prey, suggesting that feeding may continue during pregnancy rather than ceasing entirely, as has been proposed for some snake species<sup>43</sup>.

Overall, our findings indicate that dietary structure in *Oxyrhopus* emerges from the interaction between interspecific trophic differentiation, ontogenetic dietary shifts, and morphological constraints imposed by body size and cranial dimensions. These patterns highlight the remarkable ecological plasticity of the genus and suggest that resource partitioning contributes substantially to the coexistence of sympatric species. Although this study focused on *Oxyrhopus* species from Bahia and did not explicitly evaluate environmental or geographic effects on diet, it provides a robust comparative framework for future studies integrating spatial, environmental, and evolutionary drivers of trophic ecology. Beyond describing diet composition, this study represents the first comparative assessment integrating interspecific trophic differentiation, ontogenetic dietary shifts, trophic overlap, and morphological constraints across multiple sympatric *Oxyrhopus* species within a single geographic region.

## Methods

We examined 429 preserved specimens deposited in the Zoological Museum of the State University of Santa Cruz (MZUESC, Bahia, Brazil), including 226 *Oxyrhopus trigeminus*, 142 *O. petolarius*, 35 *O. guibei*, 17 *O. rhombifer*, seven *O. formosus*, and two *O. clathratus*. Snakes were classified by sex and ontogenetic stage (juvenile or adult), determined through gonadal examination following the criteria of De la Quintana and Solé (2025)<sup>20</sup>. To determine dietary composition, a midventral incision was made in each specimen and all prey items present in the digestive tract, including the posterior intestine, were carefully removed. Prey items were identified to the lowest possible taxonomic level<sup>15,44</sup>. Although diet studies based on museum specimens may underestimate the frequency of soft-bodied prey because of differential digestion rates, they provide a robust source of information for assessing dietary composition, prey size, and trophic niche differentiation among species. Sampling completeness was evaluated for each species using species accumulation curves based on the Chao estimator<sup>45</sup>, with iNEXT program<sup>46</sup>. These analyses were used to determine whether the number of examined specimens adequately represented the dietary diversity of each species<sup>47</sup>.

## Diet characterization

We used the volume of the prey since it provides a reasonable estimate of the space occupied within snakes <sup>4</sup>. The volume estimation was calculated using the formula (1) for an elongated spheroid:

$$(1) V = \frac{2}{3} \pi \cdot \frac{L}{2} \cdot \left(\frac{W}{2}\right)^2$$

Where W denotes the width and L signifies the length of the prey <sup>15,24</sup>. Only the prey that were sufficiently intact to allow for accurate volume measurements were used. To assess the relative importance of each prey category, we calculated the Index of Relative Importance (IRI) with formula (2):

$$(2) IRI = (\%N + \%V) \cdot \%FO$$

Where %N represents the percentage of the number of individuals of each prey category relative to the total number of prey items consumed by each species, %V is the percentage contribution of prey volume to the total prey volume, and %FO is the percentage frequency of occurrence of each prey category <sup>47,48</sup>. Index values were converted to percentages (%IRI) following Cortés (1997) and Lemos (2021) <sup>47,49</sup>. The resulting values range from 0 to 100, with higher %IRI values indicating prey categories of greater dietary importance. For analytical and comparative purposes, %IRI values were subsequently rescaled to range from 0 to 1 (i.e., proportional values), where 1 corresponds to 100% dietary importance. By integrating prey number, volume, and frequency of occurrence, the IRI reduces biases associated with the use of a single dietary metric <sup>48,50</sup>. Proportional %IRI values were used to quantify the relative importance of prey categories for each species and subsequently to estimate dietary overlap among sexes, ontogenetic stages, and species.

## Interspecific trophic differentiation

Dietary overlap was quantified using Pianka's niche overlap index ( $O_{jk}$ ), calculated with formula (3):

$$(3) O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

Here,  $P_{ij}$  and  $P_{ik}$  represent the proportional importance of prey categories (%IRI) consumed by (a) females and males, (b) juveniles and adults, and (c) pairs of *Oxyrhopus* species. The index ranges from 0 (no dietary overlap) to 1 (complete overlap), with values > 0.6 considered to indicate biologically meaningful overlap <sup>24,48,49</sup>. Contingency chi-square tests were also performed to assess differences in dietary composition among sexes, ontogenetic stages, and species.

## Ontogenetic variation

Ontogenetic changes in prey size were assessed using linear models for species with sufficient representation of both juveniles and adults. Prey length was used as the response variable, whereas ontogenetic stage (juvenile or adult) and snout–vent length (SVL) were included as explanatory variables. Differences in dietary composition between juveniles and adults were additionally evaluated using contingency chi-square tests.

## Morphological constraints

To evaluate morphological constraints on prey size, we examined the relationship between predator size and prey dimensions using complementary approaches. For species with sufficient representation of juveniles and adults, evidence of body-size constraints was obtained from the ontogenetic linear models described above. For species where sample sizes did not permit ontogenetic analyses, the relationship between snake SVL and prey length was assessed using simple linear regressions. Additionally, linear regressions were performed between head width (HW; measured at the level of the quadrate bones) and prey width (PW) to evaluate whether head dimensions constrained the maximum size of prey consumed. Head width and prey width were measured with digital calipers (0.01 mm precision) <sup>20,51</sup>. Together, these analyses allowed us to assess whether increases in body size and head dimensions were associated with the consumption of larger prey <sup>44</sup>.

## Statistical analyses

Prior to all analyses, assumptions of normality and homogeneity of variance were evaluated using Shapiro–Wilk and Levene tests, respectively. Statistical significance was set at  $\alpha = 0.05$ . All analyses were conducted in R version 4.3.1 (R Core Team, 2024).

## Declarations

## Contributions

Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Writing—original draft: PD; Writing—review & editing: MS.

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## Data Availability

All data supporting this study have been deposited in Zenodo and can be accessed via the DOI: 10.5281/zenodo.18422198

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## Figures

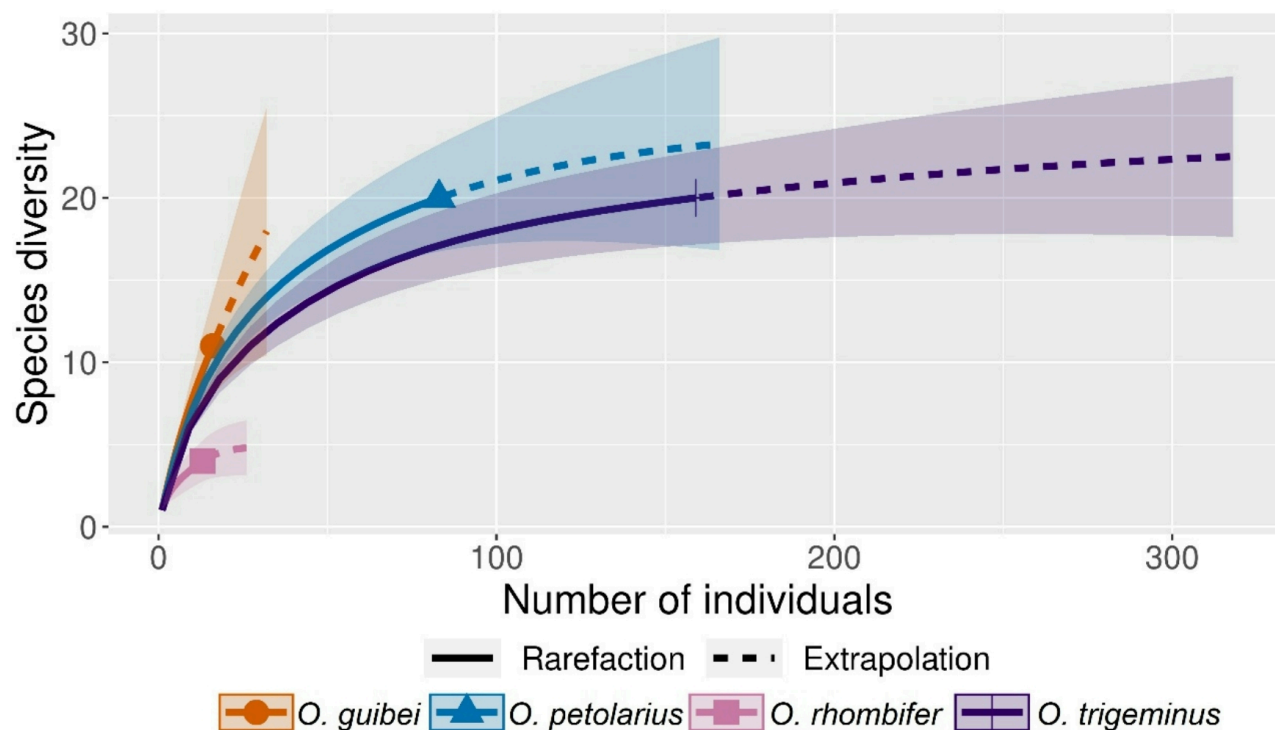


Figure 1

Sampling completeness of the diet of *Oxyrhopus* species. Diet sampling adequacy, based on richness estimators for each *Oxyrhopus* species analyzed, both *O. petolarius* and *O. trigeminus* are close to reaching the plateau, indicating that we adequately sampled the diet of these species. On the other hand, *O. guibei* and *O. rhombifer* are far from reaching this plateau, and a greater number of samples are needed to determine the diet of these species.

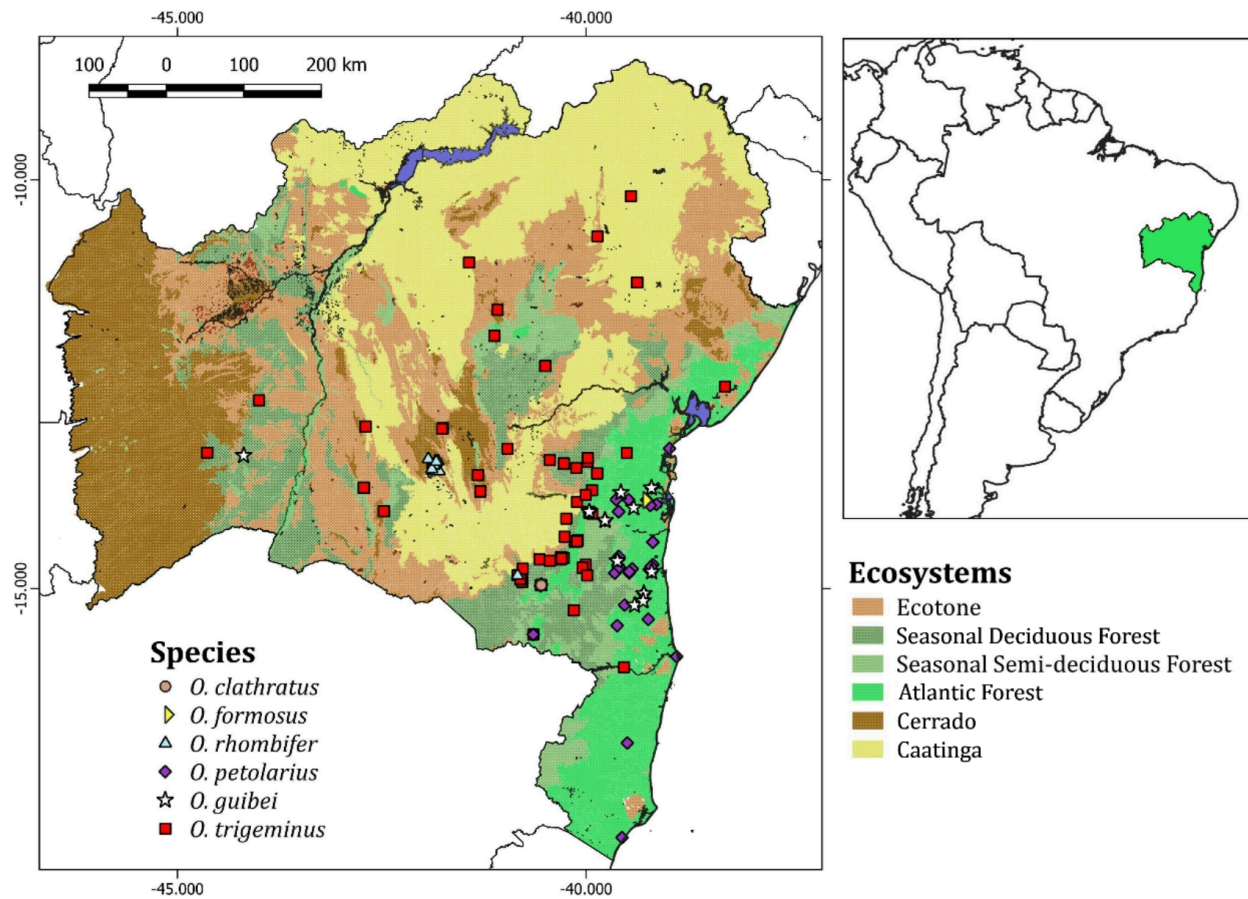


**Figure 2**

Geographic distribution of the examined *Oxyrhopus* specimens across Bahia, Brazil. Symbols indicate the collection localities of the six *Oxyrhopus* species included in this study. Background colors represent the major ecosystems of Bahia according to the official ecosystem classification of the State of Bahia (SEI-BA).

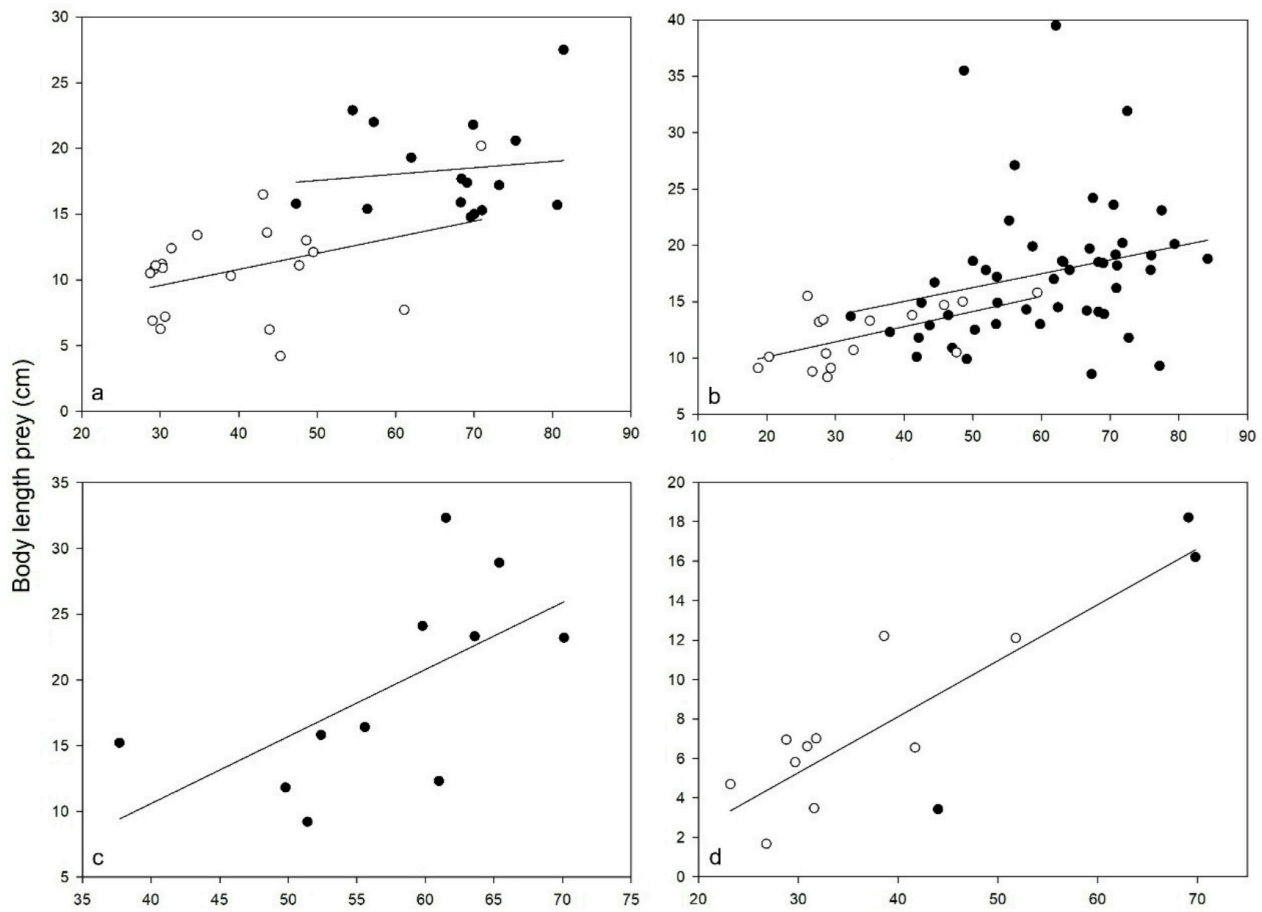


**Figure 3**

Relationships between snake body size and prey size. Relationship between snake snout–vent length (SVL) and prey body length. Black circles represent adults and white circles juveniles. (A) *Oxyrhopus petolarius*. (B) *O. trigeminus*. (C) *O. guibei*. (D) *O. rhombifer*. Regression lines are shown for each dataset. For *O. petolarius* and *O. trigeminus*, the lines represent the fitted relationships from the ontogenetic linear models. For *O. guibei* and *O. rhombifer*, simple linear regressions were fitted because of the limited number of juvenile specimens.

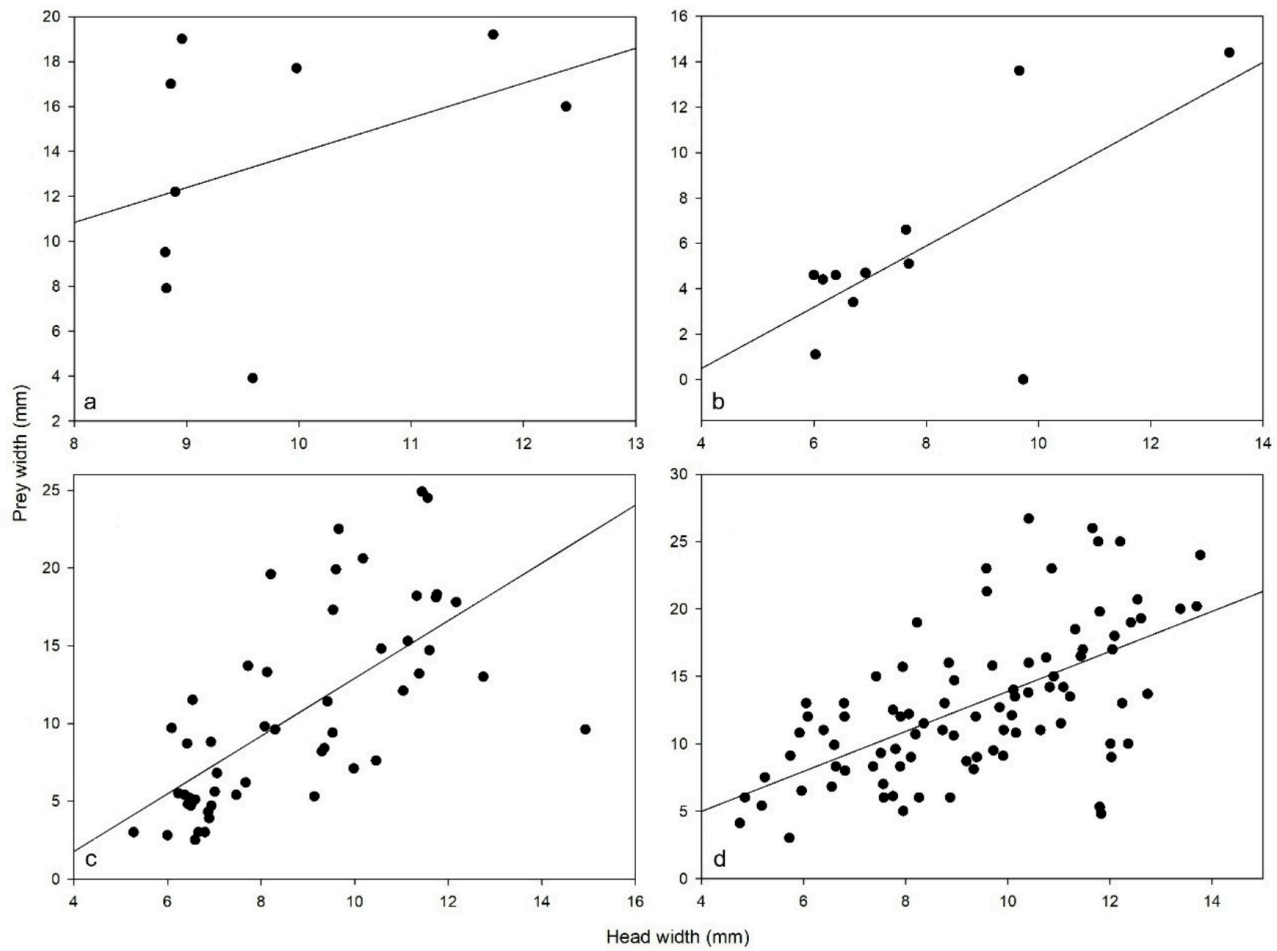


**Figure 4**

Relationship between snake head width and prey width. Relationships between head width and prey width in adult individuals of (A) *O. guibei*, (B) *O. rhombifer*, (C) *O. petolaris*, and (D) *O. trigeminus*. Solid lines represent fitted linear regressions.