Hunting the hunter: evidence of intraguild predation among bark-dwelling pseudoscorpions in the Brazilian savanna

Caçando o caçador: evidências de predação intraguilda entre pseudoescorpiões arborícolas no cerrado brasileiro

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Abstract: Intraguild predation, in which animals within the same guild prey on each other, is quite common among arachnids, especially dwelling on the ground. While pseudoscorpions can be found on the ground, tree trunks, and canopies, there is limited evidence of predation among pseudoscorpion species in their natural habitats. This study reports predatory interactions among four species of bark-dwelling pseudoscorpions in the Brazilian *Cerrado*. We observed two species of *Victorwithius* (Withiidae) (*V. similis* and *V. rufus*) opportunistically attacking and feeding on nymphs of *Paratemnoides nidificator* (Atemnidae). Additionally, *Parachernes melanopygus* (Chernetidae) acted as a social parasite, feeding on juveniles within colonies. These observations were made in six different regions of the Brazilian *Cerrado*. In all cases, *P. nidificator* was placed as the intraguild prey, while the other species acted as intraguild predators. In this system, *Paratemnoides* colonies may represent a predictable food resource for other pseudoscorpions, especially during the dry season when prey is scarce.

Keywords: Arachnida. *Cerrado* biome. Neotropical savanna. Pseudoscorpiones. Species interactions.

Resumo: Predação intraguilda é um fenômeno relativamente comum entre aracnídeos, especialmente aqueles da fauna edáfica. Pseudoescorpiões ocorrem no solo, assim como em troncos de árvores e copas, mas há poucas evidências de predação entre espécies de pseudoescorpiões no ambiente natural. Aqui, relatamos interações de predação entre quatro espécies de pseudoescorpiões arborícolas no Cerrado brasileiro. Encontramos duas espécies de *Victorwithius* (Withiidae) (*V. similis* e *V. rufus*) que atacam e se alimentam oportunisticamente de ninfas de *Paratemnoides nidificator* (Atemnidae), enquanto registramos indivíduos de *Parachernes melanopygus* (Chernetidae) agindo como parasitas sociais e se alimentando de juvenis nas colônias. Os registros foram feitos em seis regiões diferentes do Cerrado brasileiro e, em todos os casos, *P. nidificator* atuou como uma presa IG e as outras espécies como predadores IG. Neste sistema, as colônias de *Paratemnoides* podem representar um recurso alimentar mais previsível para outros pseudoescorpiões, principalmente na estação seca, quando as presas são escassas.

Palavras-chave: Arachnida. Bioma Cerrado. Savana neotropical. Pseudoescorpiões. Interações entre espécies.

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INTRODUCTION

Intraguild predation is a phenomenon in which two or more species that share similar resources also engage in predatory interactions. It is recognized for its complexity in disrupting traditional trophic hierarchies and influencing the dynamics of food webs and ecological communities (Polis et al., 1989; Holt & Polis, 1997; Arim & Marquet, 2004; Wang et al., 2019; Parimuchova et al., 2021). This intricate form of interaction is particularly evident among arachnids, which are known for their diverse predatory strategies and behavioral adaptations (Rypstra & Samu, 2005; Punzo, 2007; Houser et al., 2014; Petráková et al., 2016; Wise et al., 2023).

Arachnids represent one of the most diverse groups of terrestrial arthropods, characterized by a wide array of life strategies and feeding habits (Schausberger, 2022; Agnarsson, 2023). In this group, there are active predators like hunting spiders and scorpions, as well as more specialized species like pseudoscorpions and whip scorpions that wait for prey. The intraguild predation among these arachnids occurs in different ecological environments, from tropical forests to arid deserts, involving direct competitors and opportunistic predators (Lira et al., 2017; Hambäck et al., 2021; Silva-Júnior et al., 2021; Wise et al., 2023). To understand the dynamics of intraguild predation among arachnids, it is important to analyze factors such as competition for resources, prey selection, and the behavioral adaptations driving species interactions (Hambäck et al., 2021; Cubas-Rodríguez et al., 2024). Additionally, the influence of ecological factors on the occurrence of intraguild predation, as well as its impacts on the structure of arachnid communities and the evolution of predation strategies, represent key research issues in understanding ecological interactions (Hambäck et al., 2021; Wise et al., 2023).

Pseudoscorpions are generalist predators that live in a wide variety of habitats and feed on small insects and arachnids (Weygoldt, 1969; Harms & Dunlop, 2017; Bedoya-Roqueme & Tizo-Pedroso, 2021). Despite being one of the most diverse orders of arachnids, with over 4,200 species worldwide (World Pseudoscorpiones Catalog, 2024), the behavioral ecology of pseudoscorpions is still little known, especially in the context of Brazilian ecosystems. In Brazil, there are over 184 species of pseudoscorpions. These animals are found in all Brazilian biomes, living in environments ranging from leaf litter and canopy layers to tree trunks. Among these species, *Paratemnoides nidificator* (Balzan, 1888) is notable as one of the most widespread pseudoscorpions in Brazil. They form large colonies under tree bark and cooperate in prey capture of large arthropods (Moura et al., 2018, 2021; Ribeiro et al., 2018; Tizo-Pedroso & Del-Claro, 2018).

In the Brazilian *Cerrado* biome, several pseudoscorpion species share the same habitat, the bark of living trees, and rely on similar prey (Tizo-Pedroso & Del-Claro, 2007, 2014; Moura et al., 2018; Bedoya-Roqueme et al., 2023; Gonçalves et al., 2024; Tizo-Pedroso et al., 2024), which increases the likelihood of intraguild predation among them. Given these overlapping ecological niches, our study aims to investigate intraguild predation within this group. Specifically, we document the first observed case of intraguild predation involving pseudoscorpions in the *Cerrado*, with individuals of the genus *Victorwithius* (Feio, 1945), preying on juveniles of the social pseudoscorpion *Paratemnoides nidificator*. This study explores the ecological implications of this interaction, analyzing its potential impact on the dynamics of pseudoscorpion communities in this unique neotropical savanna.

MATERIAL AND METHODS

The data includes information from various field data collection events. Four data sets were recorded during previous years: in 2012, 2015, 2016, and 2018. These studies focused on the behavior and ecology of bark-dwelling pseudoscorpions and were conducted in different locations in the southeastern (Ribeirão Preto,

São Paulo State) and central-western regions of Brazil (Abadia de Goiás, Anápolis, Caldas Novas, Morrinhos, and Piracanjuba, Goiás State). More recently, field observations of pseudoscorpion behavior in 2023 have also been included. The region is covered by the *Cerrado* biome, a tropical savannah formation, and the observations occurred within a mesophilic forest type phytophysiognomy (Figure 1).

During our observations, we saw pseudoscorpion species interacting with colonies of *Paratemnoides nidificator*. Pseudoscorpion behaviors were recorded in situ by one or two researchers simultaneously ad libitum (Altmann, 1974). Each observation lasted 20 minutes per tree. The total sampling effort for all plots was approximately 200 hours. After each observation, the pseudoscorpions were collected for identification in the laboratory, and the trees where they were found were identified. This allowed us to describe the interactions between pseudoscorpion species.

RESULTS

The observations were carried out at six different locations across three Brazilian states. Pseudoscorpions were found on four tree species. It's worth noting that the structure of the trunks varied significantly among the tree species. *Cenostigma pluviosum* (DC.) had a more complex trunk

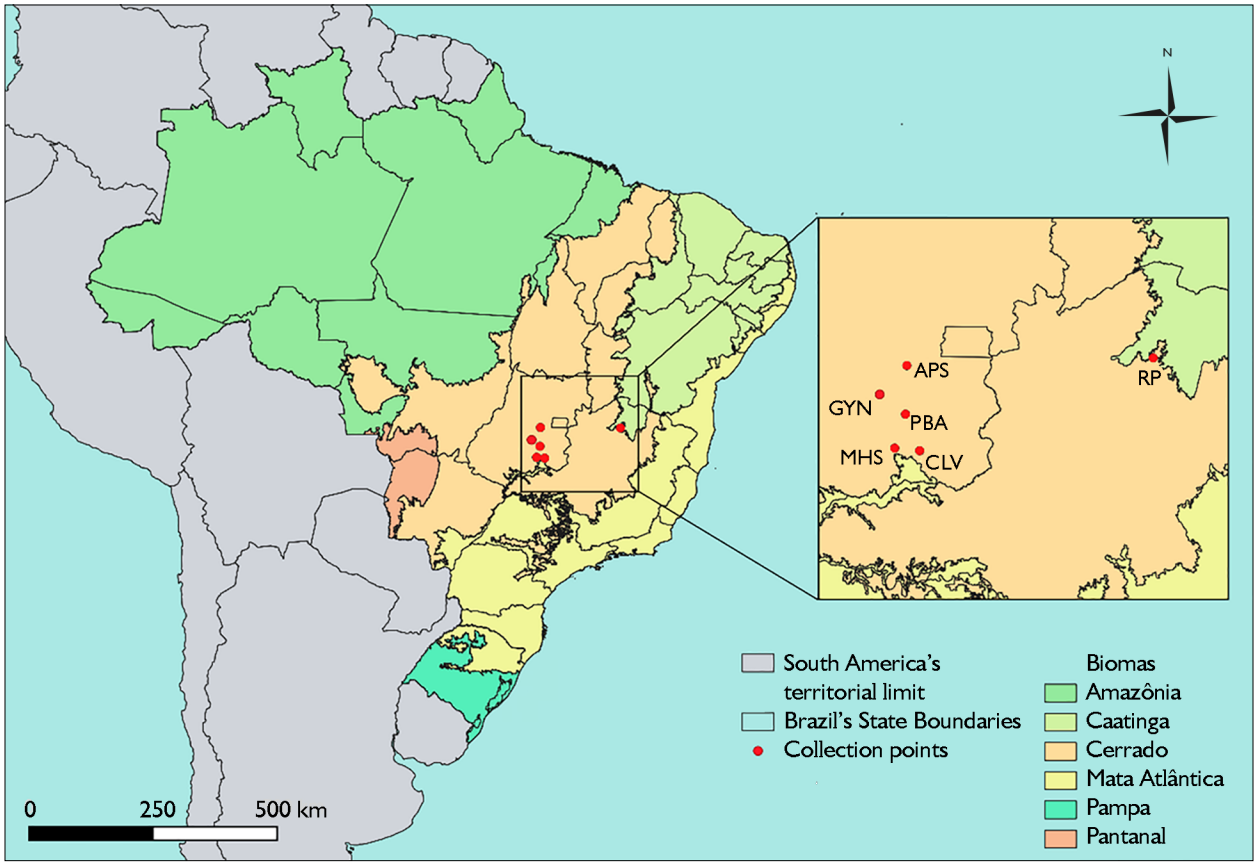

Figure 1. Map of Brazilian states and biomes. The samples were collected in the states of São Paulo, Minas Gerais and Goiás. The red dots highlight the mesophytic forest vegetation collection sites in the municipalities of Ribeirão Preto (RP) (21° 9' 54.91" S, 47° 51' 18.08" W), Anápolis (APS) (16° 18' 31.41" S, 48° 57' 19.05" W), Abadia de Goiás (GYN) (16° 45' 31.88" S, 49° 26' 11.21" W), Piracanjuba (PBA) (17° 18' 21.84" S, 49° 2' 5.19" W), Morrinhos (MHS) (17° 43' 42.14" S, 9° 7' 57.59" W) and Caldas Novas (CLV) (17° 46' 9.12" S, 48° 39' 36.99" W). Map: edited by J. S. Reis.

structure with long bark fragments. *Apuleia leiocarpa* (Vogel) J.F. Macbr and *Dipteryx alata* Vogel had intermediate structures with scale-like bark fragments well distributed along the trunk, while *Vochysia haenkeana* Mart. had a simpler, smoother trunk appearance, with scale-like bark formation near the base (Figure 2).

During the field study, we identified seven pseudoscorpion species across all six locations. In the family Atemnidae, we found colonies of *Paratemnoides nidificator*. In the family Chernetidae, we observed *Americhernes bethaniae* (Mahnert, 1979), *Pachychernes subrobustus* (Balzan, 1892), *Pachychernes baileyi* (Feio, 1945), and *Parachernes melanopygus* (Beier, 1959). Additionally, in the family Withiidae, we found *Victorwithius similis* (Beier, 1959) and *Victorwithius rufus* (Balzan, 1887). We recorded a total of 18 interaction events between pseudoscorpion species.

These observations involved *P. nidificator* colonies and at least one of three other pseudoscorpion species: *P. melanopygus*, *V. similis*, or *V. rufus*. In all instances, one of these three pseudoscorpion species was seen attacking and feeding on *P. nidificator* nymphs. *Parachernes melanopygus*, known as a social parasite, lives in *P. nidificator* colonies, using their silk chambers and preying on the nymphs, particularly during the pre-ecdysis torpor. On the other hand, *Victorwithius* species, which are solitary, do not behave in the same way. They are not found within *P. nidificator* colonies. When *Victorwithius* and *P. nidificator* coexist on the same tree, *Victorwithius* usually shelters in pieces of bark near the *Paratemnoides* colonies.

At times, adult *Victorwithius* were seen approaching *Paratemnoides* colonies. These individuals would take on a lurking posture, moving slowly with their pedipalps facing forward. Upon reaching the edge of the bark piece housing the *Paratemnoides* colony, the *Victorwithius* adult would remain motionless, with its pedipalps extended forward for several minutes. Even though *Paratemnoides* adults might approach or touch *Victorwithius*, they showed no reactions, exploratory behaviors, or agonistic responses.

Figure 2. Examples of the structure of the trunks of the trees sampled in this study: A) *Cenostigma pluviosum*; B) *Apuleia leiocarpa*; C) *Dipteryx alata*; D) and *Vochysia haenkeana*. Photos: by J. S. Reis (2024).

When *Paratemnoides* touched *Victorwithius*, the latter remained still with its pedipalps extended. It only started capturing the *Paratemnoides* nymph when approached, swiftly grabbing and dragging it away from the colony. After killing the nymph, *Victorwithius* assumed a defensive posture and began feeding. Sometimes, *Victorwithius* attacked multiple *Paratemnoides* nymphs, feeding on one and leaving the others even after killing them.

Despite *Paratemnoides* adults defending their colonies against predators, such as being aggressive towards conspecifics from other colonies, we did not observe *Paratemnoides* adults attacking or repelling *Victorwithius*. Later, in the laboratory, we confirmed that two species of *Victorwithius*, *V. rufus* and *V. similis*, preyed on *P. nidificator* nymphs (Figure 3). After confirming *Victorwithius* predation in the field, we photographed and collected the pseudoscorpions (Figure 4). We also collected *Paratemnoides* colonies to analyze their structure and composition in the laboratory, aiming to determine whether the colonies had sufficient numbers of adults for defense and whether *Victorwithius* targeted small or large colonies. The detailed information about *P. nidificator* colonies, the species involved in predation interactions, host trees, localities, and year of observation can be found in Table 1.

Figure 3. Pseudoscorpion species in the intraguild predation system in the Brazilian *Cerrado*: A) a female of *Paratemnoides nidificator*; B) a female of *Parachernes melanopygus*; C) a male of *Victorwithius rufus*; D) a male of *Victorwithius similis*. Scale bars = 1 mm.

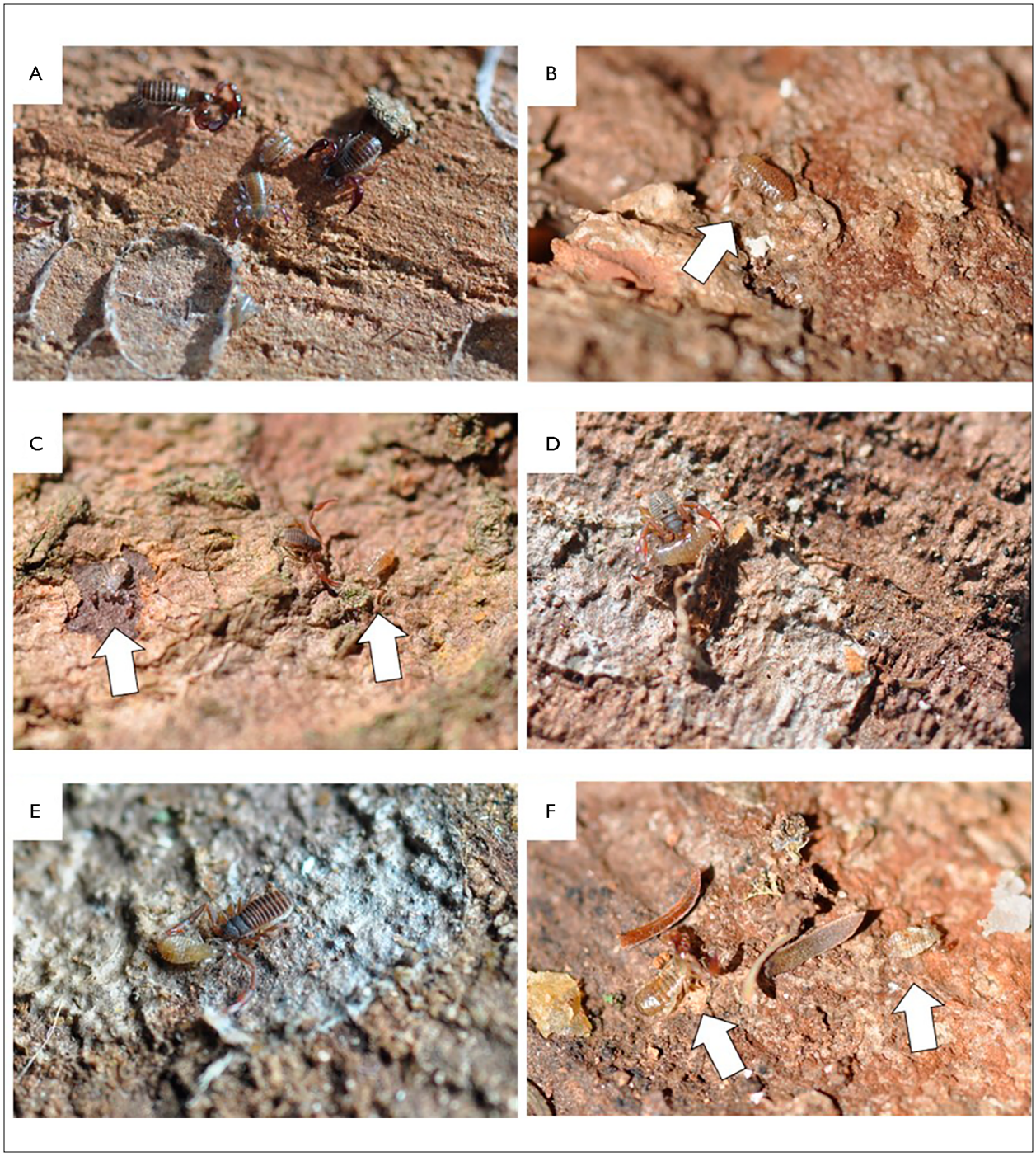

Figure 4. Relationships among pseudoscorpions in the Brazilian savannah: A) a small colony of *Paratemnoides nidificator*, with its silk chambers, and constituted in the image with two adults and two nymphs; B) a deutonymph of *Paratemnoides* moving away from the silk chambers; C) an adult of *Victorwithius rufus* after killing a tritonymph and deutonymph of *P. nidificator*; D) an adult of *V. rufus* feeding on a deutonymph of *P. nidificator*; E) an adult of *V. similis* feeding on a *P. nidificator* deutonymph; F) an exoskeleton of a deutonymph of *P. nidificator* discarded after an adult of *V. similis* had completed feeding.

Table 1. Composition of *Paratemnoides nidificator* colonies and cases of predation by other pseudoscorpions species.

Colony composition	Predator	Tree species	Year	Season	Location
7 adults, 18 nymphs	*Parachernes melanopygus*, 3 adults	*Cenostigma pluviosum*	2016	Dry	Morrinhos, Goiás
3 adults, 8 nymphs	*Parachernes melanopygus*, 2 adults; 3 nymphs	*Cenostigma pluviosum*	2018	Dry	Anápolis, Goiás
5 adults, 7 nymphs	*Parachernes melanopygus*, 2 adults; 2 nymphs	*Cenostigma pluviosum*	2018	Dry	Caldas Novas, Goiás
4 adults, 3 nymphs	*Victorwithius similis*, 1 male	*Cenostigma pluviosum*	2015	Wet	Caldas Novas, Goiás
12 adults, 15 nymphs	*Victorwithius similis*, 1 nymph	*Cenostigma pluviosum*	2012	Dry	Ribeirão Preto, Minas Gerais
13 adults, 28 nymphs	*Victorwithius similis*, 1 female; *Victorwithius rufus*, 1 nymph	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
5 adults, 23 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
8 adults, 34 nymphs	*Victorwithius similis*, 1 female	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
17 adults, 52 nymphs	*Victorwithius similis,* 1 nymph	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
16 adults, 47 nymphs	*Victorwithius similis,* 2 males	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
2 adults, 15 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
1 adult, 4 nymphs	*Victorwithius similis,* 2 males	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
12 adults, 27 nymphs	*Victorwithius rufus,* 1 male	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
11 adults, 28 nymphs	*Victorwithius rufus,* 1 female	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
3 adults, 25 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
3 adults, 4 nymphs	*Victorwithius rufus,* 1 nymph	*Vochysia haenkeana*	2024	Wet	Abadia de Goiás, Goiás
7 adults, 23 nymphs	*Victorwithius rufus,* 1 nymph, 1 male	*Dipteryx alata*	2024	Wet	Abadia de Goiás, Goiás
1 adult, 22 nymphs	*Victorwithius similis,* 1 male	*Vochysia haenkeana*	2024	Wet	Abadia de Goiás, Goiás

DISCUSSION

Intraguild predation is quite common among arachnids, especially in ground spiders and scorpions. However, evidence of such predation among pseudoscorpions in natural environments is limited. Pseudoscorpions are cryptic animals found in various biomes worldwide, often living in leaf litter, tree bark, or the canopy. Their small size makes it difficult to observe their behavior in the field (Del-Claro & Tizo-Pedroso, 2009; Bedoya-Roqueme & Tizo-Pedroso, 2021; Bedoya-Roqueme et al., 2023). Hence, intraguild predation may be more common among pseudoscorpions than is currently known, especially given their high diversity and tendency to co-occur and compete for similar prey.

Paratemnoides nidificator is a social pseudoscorpion species found throughout South America. Colonies of this species can be quite large, sometimes numbering in the hundreds (Tizo-Pedroso & Del-Claro, 2005, 2007). These pseudoscorpions capture cooperatively various arthropods living in trees, such as ants, beetles, bugs, and spiders. Their prey can range in size from a few millimeters to 4 or 5 cm (Moura et al., 2018, 2021; Ribeiro

et al., 2018; Tizo-Pedroso & Del-Claro, 2018). Solitary pseudoscorpions, on the other hand, depend mainly on small prey (< 2 mm). So, considering that *Paratemnoides* colonies demand a high amount of food, mainly because of the numerous nymphs, in this system there must be marked competition for small prey, especially during the dry season, when food is scarcer.

Alternatively, the high abundance and year-round presence of *P. nidificator* colonies suggests that they may serve as a consistent and predictable food source (Figure 5) (Tizo-Pedroso & Del-Claro, 2007; Garcia et al., 2016; Moura et al., 2018; Ribeiro et al., 2018; Bedoya-Roqueme & Tizo-Pedroso, 2023). Therefore, *Victorwithius* species may take advantage of these colonies opportunistically due to their predictable availability. This predictability of resources is especially beneficial during the dry season, when the population of other arthropods tends to be low, potentially improving the survival prospects for *Victorwithius*.

In this system, there are seven pseudoscorpion species present. We found no evidence of predation by the *Americhernes* and *Pachychernes* species. However, we observed multiple instances where adult *Americhernes bethaniae* individuals were captured and killed by *P. nidificator* when they approached their colonies. Although *Paratemnoides* did not prey on *Americhernes*, they still ended up being killed and expelled from the colony. Interestingly, we did not see adult *Paratemnoides*

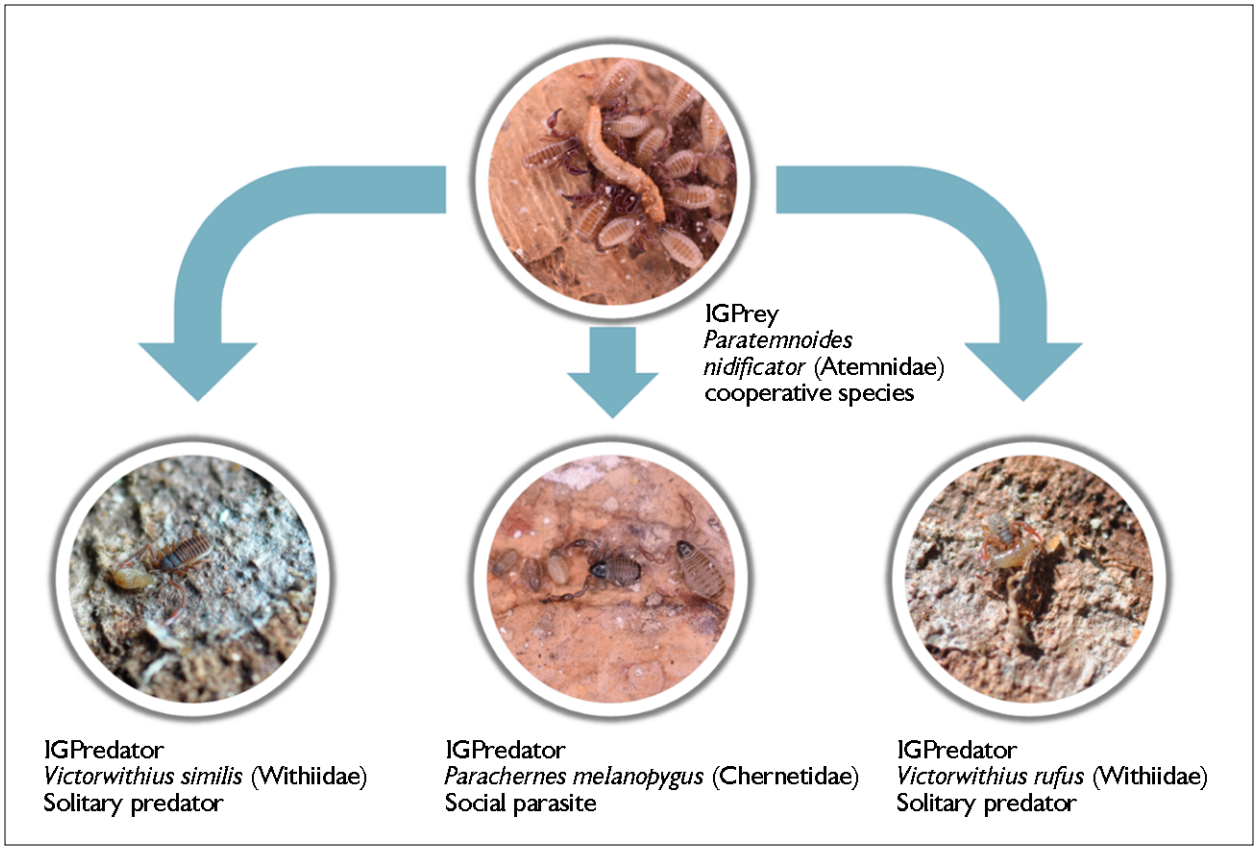

Figure 5. Schematic description of the relationship of intraguild predation among pseudoscorpions in the Brazilian savannah. In this system, *Paratemnoides nidificator* acts as an Intraguild Prey (IG Prey), serving as food for three other species of pseudoscorpions, which act as Intraguild Predators in the system, *Victorwithius similis* and *V. rufus*, both generalist solitary predators and probably opportunistic consumers of *Paratemnoides nidificator*, while *Parachernes melanopygus* adopts a life strategy as a social parasite, being a specialized predator.

repelling *Victorwithius*. *Victorwithius* species were found in smaller colonies with fewer adults, which may make them less likely to be detected. On the other hand, the *Parachernes melanopygus*, a known social parasite, can disguise itself chemically and invade colonies without being noticed (Tizo-Pedroso & Del-Claro, 2014). The lack of aggression between *Paratemnoides* and *Victorwithius* seems notable and warrants further investigation.

The fact that intraguild predation among pseudoscorpions has been observed in areas hundreds of kilometers apart suggests that this behavior isn't isolated and may occur across different pseudoscorpion populations. Understanding these intraguild relationships is fundamental for advancing our knowledge of the life history, behavior and ecology of pseudoscorpions, especially in regions like the Brazilian savanna.

CONCLUSION

In the Brazilian *Cerrado*, intraguild predation among pseudoscorpions involves social species as prey and two solitary species as predators. It seems that competition for the same food resource is not the main driver of this behavior. The abundance and predictability of *Paratemnoides* colonies as a food source for other predators may lead to opportunistic interactions between pseudoscorpion species. This behavior appears to be relatively common among pseudoscorpion populations due to the wide geographic distribution of these species.

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AUTHOR'S CONTRIBUTION

J. S. Reis contributed to conceptualization, methodolody, field data collection, data curation, and writing (original draft, proofreading and editing); M. H. A. Deus contributed to conceptualization, field data collection, and writing (original draft); A. F. S. Tizo contributed to formal analysis, validation, and writing (proofreading and editing); E. Tizo-Pedroso contributed to formal analysis, project management, conceptualization, methodolody, data curation, validation, and writing (original draft, proofreading and editing).