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ESTRUTURA DE HABITAT E TAMANHO DA PRESA MODULAM A ECOLOGIA DA PREDAÇÃO DE UM PSEUDOESCORPIÃO SOCIAL NEOTROPICAL

Renan Fernandes Moura

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Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais.

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ÍNDICE

RESUMO

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Estratégias de predação são influenciadas pelas características da presa, como seu valor nutricional ou estrutura de habitat. Fatores intrínsecos como hábito de vida, plasticidade comportamental e adaptações moduladas pelo estágio de desenvolvimento também interferem na ecologia da predação. Hábitos sociais e interações comportamentais entre indivíduos coloniais favorecem o surgimento de dinâmicas de predação e alimentação complexos. Aqui, avaliamos os hábitos alimentares do pseudoescorpião social *Paratemnoides nidificator* (Atemnidae) em duas áreas de Cerrado. Esses pseudoescorpiões vivem sob as cascas de árvores que variam em tamanho, profundidade e forma. Potencialmente, a estrutura do habitat é capaz de interferir no comportamento alimentar e no acesso às presas desses animais. Portanto, nós testamos as hipóteses de que: (i) colônias maiores são capazes de capturar presas maiores e de tamanhos mais variados; (ii) a estrutura do habitat limita o tamanho da presa capturada; (iii) a escolha das presas é mediada pelo estágio de desenvolvimento do pseudoescorpião, onde os adultos apresentam preferência por presas maiores. Avaliamos os itens alimentares, a composição das colônias e a estrutura do habitat dos pseudoescorpiões nas duas áreas. Em condições laboratoriais, determinamos se *P. nidificator* apresenta preferência por presas de acordo com o estágio de desenvolvimento oferecendo presas de diferentes tamanhos. O comprimento e abundância das presas variaram de acordo com os locais de estudo, e as colônias de pseudoescorpiões foram mais numerosas no ambiente mais urbanizado. Além disso, colônias maiores capturaram uma maior variedade de tamanho de presas. As colônias são capazes de capturar grandes presas utilizando a abertura das cascas de árvores como uma armadilha; todavia, observamos este efeito apenas em colônias que viviam sob cascas de tamanho intermediário. Provavelmente, a abertura das cascas funciona como um tipo de fenótipo estendido, fornecendo condições ou limitações quanto ao acesso às presas, gerando um beneficio diferencial entre as colônias. Em laboratório, ninfas não demonstraram preferência pelo tamanho das presas, enquanto que os adultos se alimentaram, principalmente, das formigas maiores. Presas pequenas podem representar um complemento energético paras as ninfas, reduzindo a competição intraespecífica e a exposição às grandes e perigosas presas.

Palavras-chave: captura de presa, comportamento social, escolha do predador, fenótipo estendido, forrageio, heterogeneidade de habitat, *Paratemnoides nidificator*

INTRODUÇÃO GERAL

Ao longo da evolução, os predadores adiquiriram diversas adaptações que os permitiram localizar e capturar suas presas (PIANKA, 2011). Os dois tipos mais comuns de predadores incluem os organismos que buscam ativamente por suas presas e os “senta-e-espera”, indivíduos que se posicionam de modo a emboscar suas presas (ALCOCK, 2009; GREENE, 1983; HUEY; PIANKA, 1981). É importante destacar que as estratégias de captura são relacionadas, em parte, aos tipos de presas (MILLON et al., 2009; O’BRIEN; BROWMAN; EVANS, 1990). Dessa forma, organismos que capturam presas grandes, tendem a demonstrar um comportamento de caça mais furtivo e cauteloso, enquanto que os predadores especializados na captura de presas pequenas costumam persegui-las de modo mais ativo (BARNARD, 2004; GRIFFITHS, 1980; O’BRIEN; BROWMAN; EVANS, 1990).

Outro fator importante da relação predador/presa é a estrutura de habitat, que segundo McCoy e Bell (1991), é definida como o conjunto das estruturas físicas no espaço que sustentam as comunidades vegetais e animais. Por exemplo, em habitats mais estruturados, presas podem encontrar abrigos mais facilmente (KLECKA; BOUKAL, 2014; PIRTLE; ECKERT; STONER, 2012); de outro modo, predadores – especialmente os do tipo “senta-e-espera” – também podem beneficiar-se de ambientes mais estruturados, porém, em níveis extremos, apresentam dificuldades para capturar as presas (FOLSOM; COLLINS, 1984; MANATUNGE; ASAEDA; PRIYADARSHANA, 2000). Além da estrutura do habitat e da estratégia de forrageio, o predador, ao iniciar o comportamento predatório, precisa decidir em qual local atuar, e ao capturar uma presa, deve decidir se vai alimentar-se dela ou não (DUGATKIN, 2014; HOUSTON; MCNAMARA, 1999; STEPHENS; KREBS, 1986). Essas preferências são moldadas evolutivamente e, de acordo com a teoria do forrageio ótimo, predadores tenderão a alimentar-se de presas de maior valor energético (KAMIL; KREBS; PULLIAM., 1987; STEPHENS; KREBS, 1986; STEPHENS, 2008).

O tamanho da presa é um fator fundamental para a sobrevivência do predador, pois define o potencial energético a ser obtido pelo mesmo (BRECHBÜHL; CASAS; BACHER, 2011; HARPER; BLAKE, 1988; KRIVAN, 1996). Todavia, presas excessivamente grandes podem causar danos físicos ao predador, representando grande risco ou custo adaptativo (DIETL, 2003; FORBES, 1989; RUTTEN et al., 2006). Por outro lado, presas demasiadamente pequenas são fáceis de serem capturadas e manipuladas, mas podem ser insuficientes para o predador, em termos energéticos (CHEN; JIANG, 2006; FOSSETTE et al., 2011). Em espécies sociais, o valor energético das presas é um fator ainda mais importante, pois deve ser suficiente para manter toda estrutura da colônia (WARD; WEBSTER, 2016). Pesquisadores demonstraram que grandes colônias de aranhas do gênero *Anelosimus* capturam um menor número per capita de presas, entretanto, são capazes, coletivamente, de capturar presas maiores, o que compensa o déficit númerico de alimento (YIP; POWERS; AVILÉS, 2008).

O valor energético de uma presa não é absoluto, ele varia de acordo com a capacidade de assimilação e as necessidades fisiológicas de cada espécie de predador; essas necessidades podem variar de modo intraespecífico (CHASE et al., 2002; GONZAGA; VASCONCELLOS-NETO, 2002; KREBS; DAVIES, 1993). Mudanças na dieta mediadas pela idade ou estágio de desenvolvimento podem ocorrer devido a alterações na morfologia, necessidades fisiológicas ou no acúmulo de experiência (HAMILTON; BARCLAY, 1998). Esse fenômeno beneficia, principalmente, espécies sociais (BYK; DEL-CLARO, 2011; O'BRIEN; BROWMAN; EVANS, 1990). Em muitas espécies de insetos e lagartos, as mudanças na dieta mediadas pela idade mitigam os efeitos da competição intraespecífica (POUGH et al., 2016). Apesar de bem estudadas em grupos como aves (ALONSO et al., 2015; DURST et al., 2008; KITOWSKI, 2003; STEENWEG; RONCONI; LEONARD, 2011; YOERG, 1994), mamíferos (ANTHONY; KUNZ, 1977; FIELD et al., 2007; HAMILTON; BARCLAY, 1998; PAGE; MCKENZIE; GOLDSWORTHY, 2005; ROLSETH; KOEHLER; BARCLAY, 1994), peixes (BELLEGGIA et al., 2014; LUCIFORA et al., 2009; PERSSON; HANSSON, 1999; WU; CULVER, 1992) e insetos (BOGGS, 2009; CISNEROS; ROSENHEIM, 1998; HOCHULI, 2001; SANDLIN; WILLIG, 1993), os efeitos do tamanho da presa e da mudança na dieta mediada pela idade, foram muito menos explorados em aracnídeos, particularmente em espécies sociais como o pseudoescorpião *Paratemnoides nidificator*, onde esses efeitos podem ser mais evidentes (TIZO-PEDROSO; DEL-CLARO, 2011).

Paratemnoides nidificator é uma pequena espécie social de pseudoescorpião (4–8 mm) que vive sob as cascas de algumas espécies de árvores presentes no Cerrado e em outros ambientes neotropicais (ADIS, 2002). Suas colônias são constituidas de até 300 indivíduos e exibem elevada tolerância intraespecífica e outras características sociais incomuns para a maioria das espécies de pseudoescorpiões, como cuidado parental extendido, matrifagia e caça cooperativa (TIZO-PEDROSO; DEL-CLARO, 2005; 2007). Além dessas características, eles exibem divisão de trabalho. Ninfas alocam mais tempo construindo câmaras de seda do que os adultos, que passam mais tempo forrageando e exercendo tarefas relacionadas à proteção da colônia (TIZO-PEDROSO; DEL-CLARO, 2011).

A organização social de *P. nidificator* os permite capturar uma ampla variedade de itens alimentares, como formigas, besouros e aranhas de diferentes tamanhos (TIZO-PEDROSO; DEL-CLARO, 2007). Eles são predadores do tipo "senta-e-espera" e, frequentemente capturam suas presas agarrando suas antenas ou pernas, arranstando-as para debaixo da casca de árvore onde vivem. Presas grandes, como formigas do gênero *Camponotus,* costumam ficar presas sob a casca, facilitando a alimentação desses pseudoescorpiões. Esses animais alimentam-se coletivamente, mas parece haver um padrão hierárquico comportamental. Enquanto as ninfas alimentam-se, parte dos adultos efetua a imobilização da presa, e os demais, posicionam-se ao redor do indivíduo capturado, protegendo as ninfas (TIZO-PEDROSO; DEL-CLARO, dados não publicados). Apesar dos adultos realizarem a maior parte dos comportamentos relacionados à proteção da colônia e captura de presas, eventualmente, as ninfas também participam da captura, por vezes, em grande número (TIZO-PEDROSO; DEL-CLARO, 2007; 2011). Mesmo assim, pouco sabemos a respeito de como eles forrageiam e alimentam-se de presas de diferentes tamanhos e também não sabemos se seus comportamentos de forrageio modificam-se de acordo com seu desenvolvimento.

Assim, suspeitamos que os hábitos sociais e a dependência da caça coletiva em *P. nidificator* direcionaram sua preferência por tipos específicos de presas e tamanhos, de acordo com o estágio de desenvolvimento e das necessidades nutricionais de seus indivíduos (e.g. KREBS; DAVIES, 1993). Conjecturamos que os hábitos de *P. nidificator* tenham gerado comportamentos e preferências alimentares variáveis entre os membros de suas colônias; seus padrões de alimentação devem ser influenciados pela disponibilidade de presas e pela estrutura de habitat. Esses pseudoescorpiões vivem embaixo de cascas de árvore que variam em tamanho, forma e profundidade. A estrutura das cascas pode interferir no comportamento predadório (de emboscada) e no acesso às presas.

Portanto, nosso principal objetivo foi avaliar como a disponibilidade de presas, a estrutura do habitat e as preferências alimentares entre indivíduos adultos e jovens modulam a estratégia de predação de *P. nidificator*. Para atingir este objetivo, estudamos 37 colônias desses pseudoescorpiões em duas áreas de Cerrado e amostramos seus itens alimentares. Considerando a elevada demanda energética atribuída às espécies sociais e suas preferências por presas maiores (AVILÉS et al., 2007; POWERS; AVILÉS, 2007; PURCELL, 2011), testamos as hipóteses de que (i) colônias grandes de *P. nidificator* são capazes de capturar presas maiores e de tamanhos mais variados. Com relação ao comportamento "senta-e-espera" e à estratégia de forrageio desses animais, testamos a hipótese de que (ii) o tamanho da abertura das cascas de árvore influencia o tamanho das presas que eles podem capturar; aberturas maiores permitem a captura de presas maiores e mais variadas, o que é esperado para predadores sociais do tipo senta-e-espera (BARNARD, 2004; GRIFFITHS, 1980; O'BRIEN; BROWMAN; EVANS, 1990; PURCELL, 2011; YIP; POWERS; AVILÉS, 2008). Finalmente, baseando-nos na teoria do forrageio ótimo (KAMIL; KREBS; PULLIAM, 1987; STEPHENS; KREBS, 1986; STEPHENS, 2008), testamos a hipótese de que (iii) adultos de *P. nidificator* apresentam menor interesse em presas pequenas quando comparados às ninfas, pois as presas menores oferecem pouca energia aos mesmos, entretanto, proporcionalmente, são mais nutritivos às ninfas.

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Observação

Este manuscrito foi redigido em língua inglesa e formatado de acordo com as normas do periódico científico *Behavioral Ecology* (publicado pela *International Society for Behavioral Ecology*), ao qual está submetido. O texto e a formatação foram revisados profissionalmente pela empresa *Proof-Reading-Service.com*.

Embora redigida na forma de publicação, esta dissertação possui mais conteúdo em relação ao manuscrito submetido.

Title: Habitat structure and prey size modulate the predation ecology of a social pseudoscorpion from a tropical savanna

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Abstract

Predation strategies are driven by prey characteristics, such as nutritional value, or by habitat structure. Intrinsic factors such as living habits, behavioral plasticity and age-dependent nutritional requirements also shape predator ecology. Social living and behavioral interactions among nestmates favor more complex prey capture behaviors and group feeding dynamics. Here, we evaluated the feeding habits of the social pseudoscorpion *Paratemnoides nidificator* in two areas of Brazilian Cerrado savanna. These pseudoscorpions live under the bark of tree trunks that varies in size, depth and shape. Potentially, habitat structure could interfere with pseudoscorpion ambushing behavior and prey accessibility. We therefore assessed the hypotheses that: (i) larger colonies can capture larger and more variable prey sizes; (ii) habitat structure limits the size of captured prey; (iii) there is an age-dependent prey choice in which adult pseudoscorpions prefer larger prey. We evaluated prey items, colony composition and habitat structure of pseudoscorpions at two sites. Under laboratory conditions, we determined whether *P. nidificator* presents age-dependent feeding preferences by offering prey items of different sizes. Prey length and abundance varied between study sites and pseudoscorpion colonies were more numerous within a more urban. Additionally, larger colonies captured a wider variety of prey sizes. Colonies are able to capture large prey by using openings in tree bark as a trap; however, we observed this effect only in colonies situated under bark of intermediate width. Tree bark may play a role as a phenotype extension, providing conditions for or limitations to prey access and generating a heterogeneous benefit for colonies. In the laboratory, nymphs showed no preference for prey size, while adults mainly fed on larger ants. Small prey might represent an energetic complement for nymphs, reducing intraspecific competition and their exposure to larger, dangerous prey.

Key words: extended phenotype, foraging, habitat heterogeneity, predator choice, prey capture, social behavior

INTRODUCTION

Throughout evolution, predators have developed countless strategies to capture and subdue prey (Pianka 2011). These strategies are commonly divided in two major groups: the “cruise” or “widely ranging” and the “ambush” or “sit-and-wait” (Huey and Pianka 1981, Greene 1983). Not every predator fits into these two categories (Brownsmith 1977, Janssen 1982, Pienkowski 1983, Moreno 1984, Ehlinger and Wilson 1988), but, in a broad sense, the cruise predator behaves by actively pursuing its prey, while the sit-and-wait predator remains in one location until its prey passes nearby (Alcock 2009). It is important to highlight that predation strategies are evolutionary traits that depend largely on the available prey’s characteristics, behavior and ecology (O’Brien et al. 1990, Millon et al. 2009). For instance, predators specialized in catching small prey often perform a slow and furtive approach, while predators specialized in catching larger prey often present a sit-and-wait behavior (Griffiths 1980, O’Brien et al. 1990, Barnard 2004). However, foraging behavior is not static and may change under the influence of factors such as food availability, seasonal shifts and morphological changes due to predator growth and development (Morse and Fritz 1982, Morse 1983, Carpenter 1987, Gustafsson 1988, Török and Ludvig 1988, Stephens et al. 2007).

Habitat structure may also play a role in predator behavior, choices and performance. Prey can benefit from a more complex habitat that provides more compartments and shelters (Pirtle et al. 2012, Klecka and Boukal 2014). Alternatively, predators (particularly ambush species) can benefit from increased habitat structure, however, highly structured habitat can also increase the difficulty of prey detection and capture (Folsom and Collins 1984, Manatunge et al. 2000). Regardless of the predator’s main strategy, once foraging, it must decide whether and where to search for prey, and if they capture it, whether it is worth eating (Stephens and Krebs 1986, Houston and McNamara 1999, Dugatkin 2014). These preferences are molded mainly by natural selection and, according to optimal foraging theory, foragers should prefer more nutritious (energetically) prey, rather than those of low value, considering their relative abundances (Stephens and Krebs 1986, Kamil et al. 1987, Stephens 2008).

Prey size is an important factor as it defines how much energy a predator obtains from consumption (Harper and Blake 1988, Krivan 1996, Brechbühl et al. 2011). However, larger prey can cause injury to the predator (Forbes 1989, Dietl 2003, Rutten et al. 2006) and the time spent weakening and handling the prey may also be excessive (Rovero et al. 2000). Conversely, small prey can be easier to kill and handle, but the amount of energy they provide may be insufficient (Chen and Jiang 2006, Fossette et al. 2011). The overall benefits of small prey may therefore not surpass the costs; for social species, these costs include the size of the group and the requirement to share the food (Ward and Webster 2016). Yip et al. (2008) found that large colonies of the social spider *Anelosimus eximius*, catch a smaller number of *per capita* prey than small colonies due to their lower area/volume ratio. However, this issue is combated by the larger prey that large colonies are able to capture, increasing the amount of energy obtained. These findings support the recent prey size hypothesis (Avilés et al. 2007, Powers and Avilés 2007, Purcell 2011), which proposes that a given abundance of large insects is required in order to energetically support large colonies of spiders.

The amount of energy provided by prey involves not only its size, but also the assimilation ability and preference of its predators, which can also vary intraspecifically (Krebs and Davies 1993, Chase et al. 2002, Gonzaga and Vasconcellos-Neto 2002). Factors such as age are related to shifts in species' diets, which are determined by the relative costs and benefits that vary with differences in morphology, physiological needs, experience and competitive ability (Hamilton and Barclay 1998). Furthermore, age-shifts in diet can also benefit species and populations that share the same space. For example, insects and lizards that change diets benefit from avoiding competition with their own kind (Pough et al. 2016).

Therefore, prey size and age-shifts in diet may play an important role in the maintenance of social species (O'Brien et al. 1990, Byk and Del-Claro 2011). Despite being well studied in diverse groups such as birds (Yoerg 1994, Kitowski 2003, Durst et al. 2008, Steenweg et al. 2011, Alonso et al. 2015), mammals (Anthony and Kunz 1977, Rolseth et al. 1994, Hamilton and Barclay 1998, Page et al. 2005, Field et al. 2007), fishes (Wu and Culver 1992, Persson and Hansson 1999, Lucifora et al. 2009, Belleggia et al. 2014) and insects (Sandlin and Willig 1993, Cisneros and Rosenheim 1998, Hochuli 2001, Boggs 2009), age-shift diets and prey size effects were less explored in arachnids, especially in social species such as the *Paratemnoides nidificator* (Balzan, 1888) pseudoscorpion, in which these effects should be more evident (Tizo-Pedroso and Del-Claro 2011).

Paratemnoides nidificator is a small pseudoscorpion (4–8 mm, Figure 1) that lives under rough bark of trees in the Brazilian Cerrado savanna. Their colonies can contain up to 300 individuals, and they exhibit high intraspecific tolerance and social features that are uncommon among other pseudoscorpion species, such as extended parental care, matriphagy and cooperative hunting (Tizo-Pedroso and Del-Claro 2005, 2007). They also present division of labor: nymphs spend more time building silk chambers than adults, which instead tend to forage and perform tasks related to the protection of the colony (Tizo-Pedroso and Del-Claro 2011). The social organization of *P. nidificator* enables it to capture a wide range of prey items, including ants, beetles and spiders of different sizes (Tizo-Pedroso and Del-Claro 2007). They are sit-and-wait predators, often capturing prey by catching their legs or antennae and pulling them under the bark of the tree in which they live (Del-Claro and Tizo-Pedroso 2009). Large prey frequently gets trapped under the tree bark, allowing *P. nidificator* to feed on it. The pseudoscorpions feed collectively, but in a hierarchical pattern, starting with nymphs. While most of the adults immobilize the prey, others stand by, protecting the feeding nymphs (Tizo-Pedroso and Del-Claro unpublished). Even though adults perform most of the protective behavior and prey capture, nymphs also participate in hunts, sometimes in large numbers (Tizo-Pedroso and Del-Claro 2005, 2011). Nevertheless, we currently only have a poor understanding of how they forage and feed on different prey items, and we do not know if their feeding behavior changes with age.

Given this, we supposed that the cooperative habits and dependence on collective hunting in *P. nidificator* may drive a preference for a particular prey size or type, according to the individual's age (or developmental stage) and nutritional requirements. We hypothesize that this generates variable behavior and feeding choices among colony members. Their feeding patterns should be influenced by prey availability (predator choices and preferences may respond to variations in prey type and abundance) and by habitat structure. These social pseudoscorpions live in the bark of tree trunks that varies in size, depth and shape. The habitat structure could therefore interfere with pseudoscorpion ambushing behavior and prey accessibility. Thus, our main objective was to evaluate how prey availability, habitat structure and age-based feeding preferences mold the predation strategy of *P. nidificator*. In order to achieve this objective, we studied multiple pseudoscorpion colonies in two distinct natural areas and sampled their prey items. Given the higher energetic demands of social species (Avilés et al. 2007, Powers and Avilés 2007, Purcell 2011) and their known preference for large prey (Tizo-Pedroso and Del-Claro 2007, 2011), we hypothesize that (i) larger colonies of *P. nidificator* are able to capture larger and more variable prey sizes. Given the sit-and-wait behavior and foraging strategy of *P. nidificator*, we hypothesize that (ii) the height of openings in the tree bark influences the size of prey they can capture; large openings might allow the capture of larger and more variable prey (Figure 1), which is expected from social sit-and-wait predators (Griffiths 1980, O'Brien et al.

1990, Barnard 2004, Yip et al. 2008, Purcell 2011). Finally, based on optimal foraging theory (Stephens and Krebs 1986, Kamil et al. 1987, Stephens 2008), we hypothesize that, in a controlled test, (iii) adults of *P. nidificator* have less interest in small prey items when compared to nymphs (Figure 2), as smaller prey offer less energy to them, however, proportionally, small prey are more nutritious to nymphs.

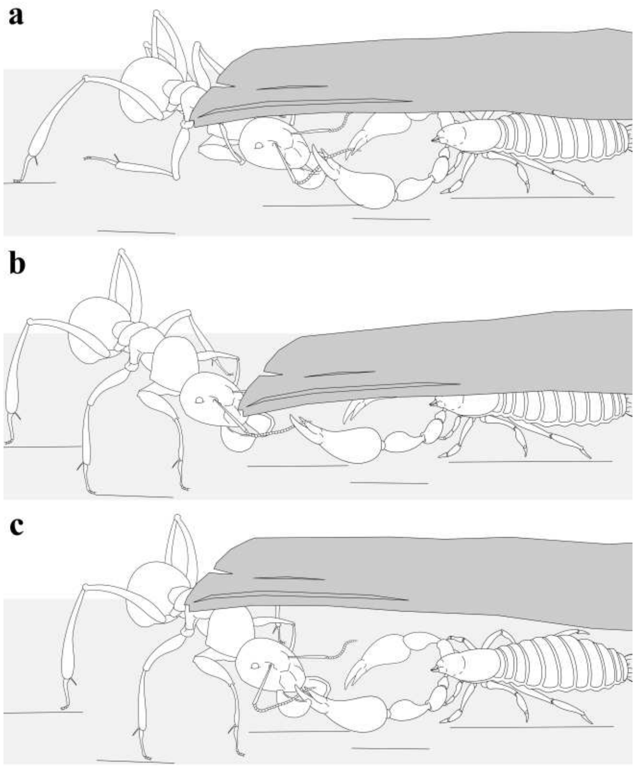

Figure 1. Hypothetical use of bark openings in three capture processes of large prey by *Paratemnoides nidificator*. Illustrated ants have the same size. (a) *P. nidificator* can use a bark opening to trap prey. (b) In narrow openings, *P. nidificator* can still capture the prey, but is unable to trap it under the bark. (c) Excessively wide openings cannot be used as a trap by *P. nidificator* and in addition, some arthropods are able to fight back and cause them harm. Illustration by Jefferson Nascimento

Figure 2. Adult (right) and nymph (left) specimens of the *Paratemnoides nidificator* pseudoscorpion.

METHODS

Field study

We undertook fieldwork in two study sites, the Sabiá Municipal Park (18°55'S, 48°17'W) and the Caça e Pesca Itororó de Uberlândia Reserve (18°59'S, 48°18'W), both at Uberlândia city, Minas Gerais state, Brazil. Sabiá Municipal Park covers an area of 18,500,000 m² including 350,000 m² of woods and a hydrographic set of water sources, and is surrounded by urban development. Caça e Pesca Reserve is a private establishment within a conservation unity, consisting of 7,066,400 m² of Cerrado vegetation, sustained by the Uberabinha River (for area characterization see Vilela et al. 2014, Velasque and Del-Claro 2016). Both areas contain trees (*Caesalpinia peltophoroides* Benth. [Fabaceae]) in which colonies of *P. nidificator* are commonly found (Tizo-Pedroso and Del-Claro 2007).

Predation strategy and colony characterization

From August 2015 to May 2016 we located and marked 30 colonies in each area; one colony per tree was used to maintain data independence. After capturing and killing prey, pseudoscorpions feed on the internal tissues by injecting a digestive into the pleura and sucking the dissolved tissues. The prey's exoskeletons are discarded from the colonies almost intact, which allow for their collection and identification by fixing collectors immediately below the colony on the tree trunks (Tizo-Pedroso and Del-Claro 2007). We installed collectors (about 17 centimeters of width) on 30 trees in each area (one collector per tree) with previously identified *P. nidificator* colonies. Each collector (designated as a treatment group) was placed under one colony, so we could survey the discarded prey exoskeletons of *P. nidificator* (Figure 3). On each tree, we also installed a collector on the opposite side to the treatment and at a similar height, but in a spot that did not contain a colony, to act as a negative control. We made the collectors with plastic bottles and attached them to the trees using pins and silicon glue to avoid the prey slipping between the collectors' edges. We measured the openings of the colonies – the maximum and minimum space between the bark and the trunk where *P. nidificator* lives – with a digital caliper, and weekly, we collected all prey found in the treatment and control collectors using a wet, small brush. All the biological material was conserved in 70% alcohol, organized by colony. At the end of the study, we identified the taxonomic orders of the collected arthropods, and counted and measured the individuals that were found in one piece (length and width) using a digital caliper. Once the prey-sampling period was complete, we collected the studied colonies and counted the number of individuals, both adults and nymphs, within each colony.

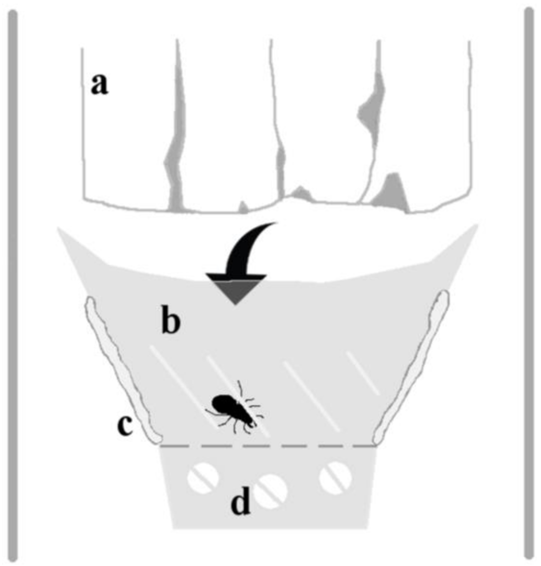

Figure 3. Prey collector of *Paratemnoides nidificator* installed in a tree trunk. Prey captured under the rough bark (a) is discarded and falls into the collector (the arrow represents the direction of discarded prey). The grey area represents the collector (b), holding a prey item. On its sides, there is silicon glue to prevent spaces between the trunk and the collector (c). The three divided circles are pins that were used to fix the collector (d). Traces represent the bottom of the collector.

Prey size preference

We raised 15 colonies of *P. nidificator* in the Laboratory of Behavioral Ecology and Interactions of the Federal University of Uberlândia. They were housed in Petri dishes (15 cm in diameter) with a fixed piece of bark, so we could see the colony through the glass (Figure 4, e.g. Tizo-Pedroso and Del-Claro 2014). We treated each colony with food deprivation for one week, then, we established two treatments. First, we offered workers of *Tapinoma sessile* ants of 2 mm length to each colony and observed the behavior for one hour. This ant is commonly found under rough bark of *C. peltophoroides* trees where *P. nidificator* also lives, so these organisms have natural contact. The number of ants offered was in relation to the size of each colony. We ensured that each pseudoscorpion had at least one ant to feed on and we observed one colony at a time, noting every individual (adult or nymph) that fed on the captured ants. We considered the feeding process to be valid when the individual fed for at least two minutes.

Figure 4. Example of a *P. nidificator* colony raised in a Petri dish (15 centimeters of diameter). Colored spots at the pseudoscorpions are markings unrelated to this study.

For the second treatment, we used *Camponotus mus* ants. As in *T. sessile*, this species is also commonly found on the trunk of *C. peltophoroides* trees and is consumed by *P. nidificator*. We offered one *C. mus* (0.6–1.0 cm) to each colony and observed its capture and the number of adults and nymphs that fed on it. Previous observations showed that we needed to observe each colony for more time (two hours) for two reasons: first, the time *P. nidificator* took to subdue the prey until its death was greater due to the size of the ant; second, as we offered one ant to the colony, some individuals took more time to find the prey. As in the first treatment, we noted every individual that fed for at least two minutes on the ant.

Statistical analysis

We used a Student's t-test to analyze possible differences in prey length from each studied site. In order to achieve normality for this test, we transformed the data using a logarithmic transformation and we checked normality both visually, using boxplots and histograms, and by a Lilliefors probability test ($P = 0.15$; $n = 310$). Prey width did not conform to a normal distribution, so we used a non-parametric Mann-Whitney test to verify whether this factor differed between the studied sites. We used linear and nonlinear regressions associating the mean size (for both length and width) and the Δ width (maximum width - minimum width) of prey collected from each colony with the variation found in the bark openings of each tree, the Δ opening (maximum opening - minimum opening in bark). We also used linear regressions to examine the association between the number of individuals of *P. nidificator* from each colony and the mean size (length and width) and the Δ width of the sampled prey. In the laboratory study, we used chi-square tests to verify any differences in preference for small or large prey by adults and nymphs of *P. nidificator*, in which the final numbers of adults and nymphs feeding on prey were used to create the 2 x 2 contingency table.

RESULTS

Predation strategy and colony characterization

We found 310 prey items in the collectors, 237 in Sabiá Park and 73 in the Caça e Pesca Reserve, from 37 colonies (18 from Sabiá Park and 19 from Caça e Pesca). The arthropods collected were from four orders of insects (Hymenoptera, Dermaptera, Hemiptera and Coleoptera) plus two individuals from the order Araneae (spiders). The most predominant prey were ants, with 286 individuals (Table 1). They comprised 92.26% of all individuals found, and their body size ranged from 1.73 to 15.87 mm in length and 0.49 to 5.69 mm in width ($\bar{x} = 6.84 \pm$

0.14 mm). The second most abundant type of prey was Coleoptera, with 15 individuals (4.84%), followed by three Hemiptera (0.97%). The Student's t-test showed that the mean length of prey items differed between the study areas, with prey found in the Sabiá Park being longer than those obtained from the Caça e Pesca Reserve ($t_{1,308} = 3.74$; $P < 0.001$; data transformed using logarithmic function), while our Mann-Whitney test showed no difference in prey width between the two study sites ($U_1 = 8,302.50$; $P = 0.60$; Table 1). The negative control collectors were empty most of the time during the study, indicating that our sampled arthropods were effectively captured and discarded by pseudoscorpion colonies.

Table 1. Number of prey found in each taxon (at the level of order, except for the Formicidae family) in the two study areas and the size of the prey items (in mm, ± the standard error of the arithmetic mean).

Taxon	Sabiá Park	Caça e Pesca	Total number of individuals
Formicidae	217	69	286
Coleoptera	11	4	15
Hemiptera	3	0	3
Hymenoptera	2	0	2
Araneae	2	0	2
Dermaptera	1	0	1
Other	1	0	1
Total	237	73	310
Mean length	7.78 ± 0.16*	6.08 ± 0.31*	6.84 ± 0.14
Mean width	1.47 ± 0.05	1.39 ± 0.08	1.45 ± 0.04
Δ width	1.08 ± 0.17	1.00 ± 0.26	1.04 ± 0.15

*Represents a statistically significant comparison ($\alpha = 0.05$)

In Sabiá Park, colonies contained 9–67 individuals in total, which consisted of 2–36 adults and 7–50 nymphs. At the Caça e Pesca Reserve, we found 5–32 individuals per colony, comprising 1–23 adults and 0–31 nymphs. We collected a total of 810 individuals in both areas combined (Table 2).

Table 2. Number of individuals of *P. nidificator* from the two studied areas and the size of the bark openings (in mm, ± the standard error of the arithmetic mean). We used 18 colonies from Sabiá Park and 19 from Caça e Pesca reserve.

	Sabiá Park	Caça e Pesca	Total
Total number of individuals	572	238	810
Adults	186	63	249
Nymphs	386	175	561
Opening	2.73 ± 0.17	2.26 ± 0.12	2.47 ± 0.11
Max opening	3.56 ± 0.27	2.66 ± 0.17	3.05 ± 0.17
Min opening	1.97 ± 0.12	1.86 ± 0.09	1.88 ± 0.07
Δ opening	1.55 ± 0.24	0.80 ± 0.12	1.14 ± 0.14

We did not find a relationship between the number of pseudoscorpions in the colony and the mean size of captured prey, both using the total number of individuals ($F_{1,30} = 1.79$; $P = 0.19$) and the number of adults ($F_{1,29} = 2.75$; $P = 0.11$). However, we found a positive relationship between the number of individuals and the variation in the width of prey (Δ width), both using the total number of individuals ($F_{1,29} = 8.26$; $R^2 = 0.22$; $P = 0.008$) and the number of adults ($F_{1,29} = 19.88$; $R^2 = 0.41$; $P < 0.001$; Figure 5). Likewise, the Δ opening was not related to the mean width of the captured prey, but was related to Δ width (maximum width - minimum width). However, the relationship was not linear and we found that a quadratic model was the best fit ($F_{2,27} = 5.61$; $R^2 = 0.29$; $P = 0.009$; Figure 6).

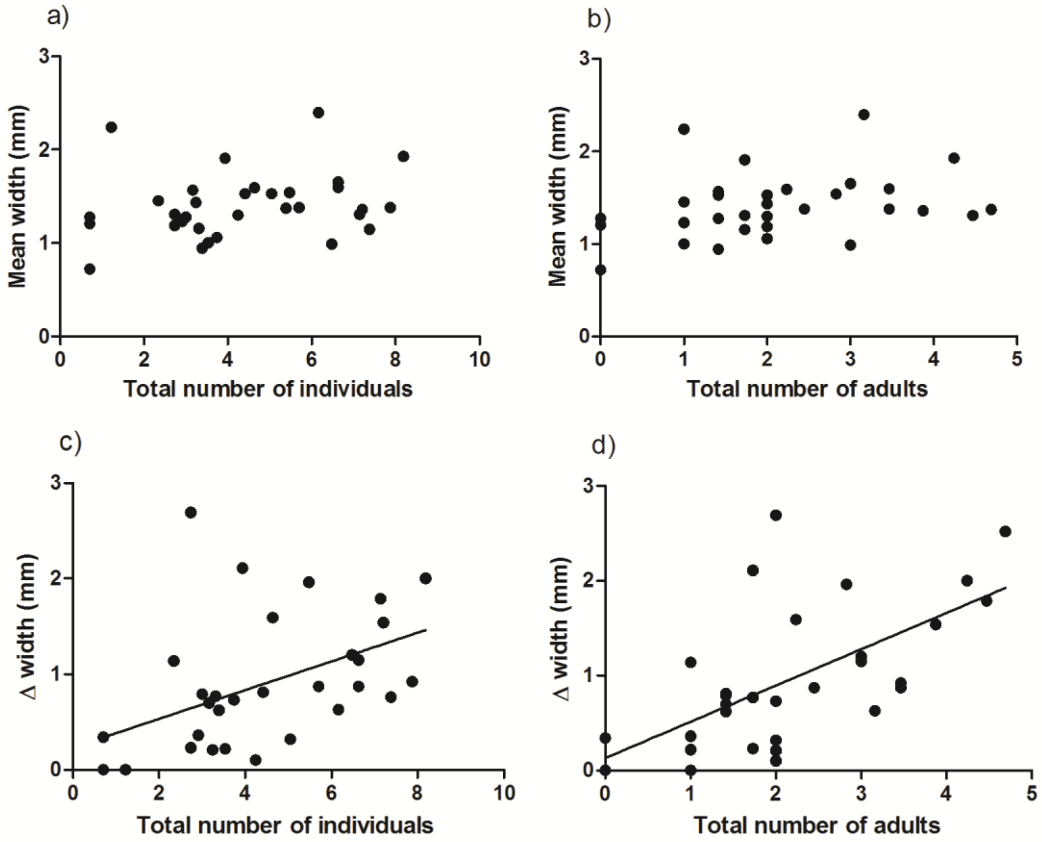

Figure 5. Relationship between the total number of individuals (a and c) and adults (b and d) of *Paratemnoides nidificator* and the mean width of their prey (a and b) and the variation in the width of the prey (c and d). A and B represent non-significant relationships at α = 0.05. The total number of individuals and adults were square root-transformed in order to normalize the data.

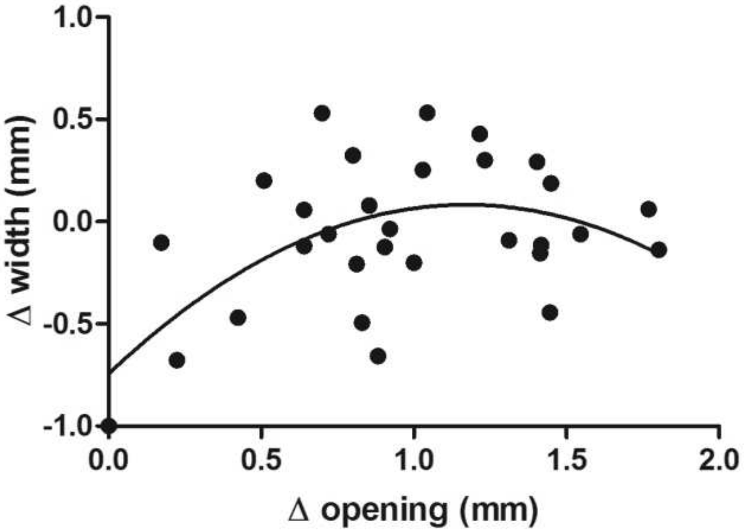

Figure 6. Relationship between the variation in the size of the bark openings (Δ opening) and the variation in the width of *Paratemnoides nidificator* prey items (Δ width). Δ width and Δ opening were transformed using log10 and square root, respectively, in order to normalize the data.

Prey size preference

We used 109 nymphs and 136 adults for tests with small prey and 122 nymphs and 77 adults for tests with large prey ($\bar{x} = 111$ individuals). Nymphs showed no preference for any offered prey; 55.06% fed on small prey while 67.2% fed on large prey ($\chi^2 = 0.86$; $P = 0.35$). Among the adults, only 25% fed on small prey, while 63.63% fed on large ants ($\chi^2 = 12.79$; $P < 0.001$). We found a difference between nymphs and adults considering small prey ($\chi^2 = 10.16$; $P = 0.0014$), but no difference concerning large prey ($\chi^2 = 0.06$; $P = 0.81$; Figure 7).

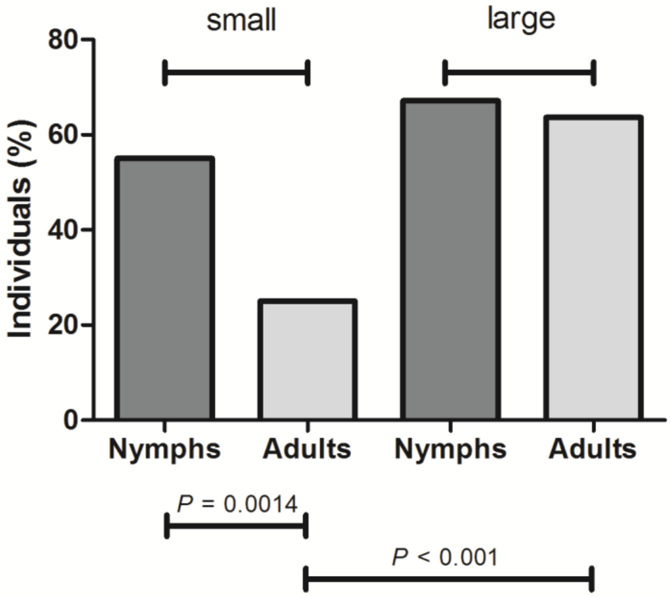

Figure 7. Percentage of individuals (nymphs and adults) that fed on small (*Tapinoma sessile*) and large (*Camponotus mus*) prey. Significant chi-square tests are indicated below the x-axis.

In the tests with small prey, we observed that both nymphs and adults were able to kill the ants. Despite the reduced interest the adults had in feeding on small prey, they still killed the ants whenever they approached them, and on many occasions, they also pursued them. Even when surrounded by dead ants, adults showed few interest in feeding on them; overall, nymphs showed more interest for the small prey. Both adults and nymphs were observed moving around while carrying a dead ant in their pedipalps. Very small nymphs (protonymphs, size < 1 mm) were not able to kill the ants due their size, but they fed on them when they encountered a dead one. We observed no difficulties in the handling of prey by adults when they decided to feed. We frequently observed the same ant being shared by two individuals, independent of their age. Eventually, the individuals competed for the same prey, and adults were able to take the prey from the nymphs easily. We also observed both nymphs and adults starting to feed but losing interest after a few moments. We did not consider this behavior as feeding. During the experiment with large ants, captures were started by one individual (usually an adult, although bigger nymphs were also able to capture prey many times bigger than themselves) and then one or more additional individuals from the colony joined the hunt. Even though we used small colonies, not all individuals were always able to feed at the same time, thus we observed an exchange of feeding individuals.

DISCUSSION

Habitat structure modulates prey access and preference of cooperative social predators. We confirmed this hypothesis using a social pseudoscorpion as a model system and showed that: a) larger groups of a social predator manage to capture a wider range of prey items; b) the habitat structure, here expressed by the bark openings of colonies, influences the size of prey captured, and the relationship between bark openings and prey width showed an optimum range for larger prey; c) adults of this pseudoscorpion have distinct preferences for prey of different sizes, while nymphs do not present prey size preference.

Our field survey corroborated Tizo-Pedroso and Del-Claro's (2007) findings. These authors found that *P. nidificator* feeds on prey of different sizes, including small insects (1–2 mm) and large Scarabaeidae bettles (13 mm), although in this study, we found even larger prey (a 15.7 mm ant). However, the variety of prey items we found was different from Tizo-Pedroso and Del-Claro (2007): they found that, in the dry season, 70% of *P. nidificator* prey was represented by ants, while in the wet season, ants comprised 28% of prey. Although we did not control the prey survey by season, the number of ants we found was clearly greater than that of Tizo-Pedroso and Del-Claro (2007), representing 92.8% of all prey items, and this pattern did not change between the two areas studied here. The numbers of prey items we found were considerably different to those in previous studies. Variation in the types of prey between these studies could be related to natural variation in arthropod abundances and prey availability in different areas, which suggests that *P. nidificator* colonies may adjust their use of prey according to availability.

In our study, colonies from Sabiá Park contained more individuals and the captured prey was, on average, longer and more abundant in comparison to Caça e Pesca Reserve. These findings were unexpected because Sabiá Park is a somewhat urbanized environment. This suggests that *P. nidificator* can benefit from impacted urban areas, and perhaps, as our data indicate, they can be more successful than in more natural environments. Some ant species can benefit from disturbances in urban areas, being more abundant in these areas. Also, trees in urban areas or in green urban areas can act as a refuge for ants and other arthropods (Yasuda and Koike 2009, Uno et al. 2010, Guénard et al. 2015, Ossola et al. 2015, Vonshak and Gordon 2015), which could also influence the occurrence of pseudoscorpions and food availability.

We found a relationship between Δ opening and Δ width that partially corroborated our second hypothesis. It seems that colonies of *P. nidificator* residing in trees with a greater variation in the size of their bark openings are able to capture prey of more variable sizes, as they can capture small prey in the smaller openings and large prey in the larger openings. However, this relationship is not linear; it appears that neither colonies with the smallest nor the greatest values of Δ opening are able to capture such a wide variety of prey. For example, colonies that live within small bark openings might be able to more often capture small individuals, therefore, the values of Δ opening should be low. Similarly, the extreme values of Δ opening reflect the challenge of colonies in capturing either the larger individuals or the smaller ones, as the openings are either too wide or too narrow to capture most prey.

We believe this foraging behavior, especially with regards to the capture of large prey by *P. nidificator*, is a case of extended phenotype. That is, the use of bark openings works as a trap and undoubtedly eases the process of prey subduing. We considered the extended phenotype to be any genetic effects capable of increasing the fitness of the organism (*sensu* Dawkins 1982, 2004, but see Bailey 2012). There are many examples of extended phenotype in nature, such as host manipulation by its parasite or trap-building animals (Zschokke et al. 2006, Hoover et al. 2011). In cases involving predation, predators experience a high catch rate (Vermeij 1982) but have a restricted range of prey types and quantity (Mayntz et al. 2003). It is not common to observe *P. nidificator* attacking prey outside of tree bark, so we highlight the importance of the bark in the predation process (Tizo-Pedroso and Del-Claro 2007). Additionally, the structure of bark openings of *C. peltophoroides* not only provides a predation advantage to *P. nidificator*, but also protects these animals from being attacked by their own predators, or by large and dangerous prey. Additional laboratory experiments showed that, when the bark opening is too wide, some ants like *Camponotus mus* are capable of turning and biting the attacking pseudoscorpion, which sometimes results in the mutilation of their pedipalps (unpublished data). Thus, the width of bark openings is critical and its heterogeneous distribution should enhance *P. nidificator* survival, as is the case for many species (Nelson and Bonsdorff 1990, Heck and Crowder 1991, Babbitt and Tanner 1998, reviewed by Kovalenko et al. 2012).

Furthermore, we expected that larger colonies would be able to capture larger individuals, on average; however, we did not found this relationship. We observed that larger colonies were able to capture individuals of different sizes (Δ width). This might occur simply because large colonies have a greater probability of capturing prey due to the number of potential predators. This also explains why the relationship was much stronger when we compared Δ width only with the number of adults in each colony, as they are the main force capable of capturing prey (Tizo-Pedroso and Del-Claro 2007).

It has also been observed that sit-and-wait predators have a tendency to capture large prey (Griffiths 1980, Greene 1986). This is because these predators are able to ambush the prey while avoiding a direct fight that would raise the chance of a predator being hurt, or even killed, by large prey (Forbes 1989, Dietl 2003, Rutten et al. 2006). Other studies about prey capture behavior in *P. nidificator* showed that larger colonies are able to capture large prey more frequently (Tizo-Pedroso and Del-Claro 2007, 2011). However, these studies were conducted under laboratory conditions and did not measure the effects of bark openings on subduing prey. It is therefore possible that, because of heterogeneity in bark structure, pseudoscorpion colonies experience physical restrictions in accessing some types and/or sizes of prey, which can limit the overall potential of large colonies to exploit the absolute prey availability. The preference for large prey is what we observed for *P. nidificator*, but still, as generalist predators, they also caught a reasonable range of prey sizes. We suggest that this range of prey sizes is the reason for the lack of relationship between the colony size and the mean prey size, as the high variety of prey items, particularly the small ones, might have diluted the mean size of captured prey. The positive relationship between the colony size and Δ prey width probably reflects this argument.

For our third hypothesis, we wanted to verify whether nymphs of *P. nidificator* have more interest in small prey items in comparison to adults, as smaller prey probably offer proportionally more energy to nymphs. Experimental results revealed that both nymphs and adults fed on small ants, although adults preferred larger prey. *P. nidificator* is known for collectively capturing large prey and sharing it among the colony; however, as revealed by Tizo-Pedroso and Del-Claro's (2007) surveys, *P. nidificator* feeds on a variety of items, including small insects (1–2 mm) and large Scarabaeidae beetles (13 mm), but they represented only a small fraction of their diet.

Furthermore, as Yip et al. (2008) argued, large colonies of *Anelosimus* spiders tend to capture less prey per spider in the colony than in small colonies. Still, this system is sustained because these colonies are able to capture larger prey. Considering this, it was expected that *P. nidificator* adults would prefer the larger ants offered as a diet option and this outcome indicates a relationship with the higher energy intake from larger prey, even considering the increase in time and energy that is needed to capture and subdue it. Small differences in prey size can be enough to substantially change the amount of energy a predator obtains (Conway et al. 1999), which may explain why they did not often feed on the small ants. However, we cannot discredit the intrinsic attributes of the *T. sessile* ants regarding their quality as prey. Although many generalist predators avoid toxic or low quality prey (Paradise and Stamp 1993, Bilde and Toft 1994, Mayntz and Toft 2000), there are many studies that have shown that invertebrate predators do not always develop an aversion to this kind of prey (Toft 2000, Fisker and Toft 2004, Stamp and Meyerhoefer 2004).

However, there still might be trade-offs regarding the preference of *P. nidificator* for larger prey. For example, when a colony succeeds in capturing a prey item, it is reasonable to assume that the most strong and hungry individuals will feed first and from the best parts of the prey. Then, the weaker individuals and the small nymphs will wait and feed from the remains of the item. Unequal distribution of food is very common in social carnivorous groups (Tilson and Hamilton 1984, Frank 1986, Gese et al. 1996). In *Anelosimus* spiders, Vollrath and Rohde-Arndt (1983) describe differences in the size of individuals as result of competition, and an experiment conducted by Gonzaga and Vasconcellos-Neto (2002) showed differential growth rates in spiders of the same genus, possibly attributed to intraspecific competition. Another possibility in *P. nidificator* colonies is that some individuals are simply unaware of the captured prey, if it occurs some distance away. Therefore, it is plausible that these drawbacks could be minimized if weak adults and nymphs were to capture small prey.

The small ants we used in this work (*T. sessile*) are occasionally found in the same tree as *P. nidificator*, and we observed in the laboratory that they easily sneak into the colonies, do not hesitate to approach the pseudoscorpions, and can be killed instantly by one individual, which can be either adult or nymph, but not newborns or very young nymphs. Hunting small prey is considered an alternative strategy for smaller and less competitive individuals, as they do not need the participation of others to perform the capture (Gese et al. 1996, Ebert 1998). For nymphs, the benefits might be greater, as they have a limited capacity to capture large prey and presumably have less energetic needs than an adult. Additionally, as Hamilton and Barclay (1998) argued, experience is one of the factors that drive age-shift diets. Nymphs of many species are not specialized to capture prey and they commonly have a generalized diet, learning what to eat or not eat by experience. In addition to this kind of experience, small prey can be a good start for nymphs acting as a predator and they might refine their hunting behavior while capturing small and harmless prey (Tizo-Pedroso and Del-Claro 2011). Small prey are often abundant, and as optimal foraging theory predicts, the density of prey types is a factor that influences an individual's decision on what prey to consume (Stephens and Krebs 1986, Kamil et al. 1987, Stephens 2008).

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CONSIDERAÇÕES GERAIS

Concluímos que a abundância e o tamanho das presas, além da estrutura de habitat, modulam a ecologia da predação das colônias do pseudoescorpião social *Paratemnoides nidificator*. Colônias mais numerosas foram encontradas na área de estudo onde as presas amostradas foram maiores e mais abundantes. Além disso, verificamos que colônias mais numerosas, principalmente em termos de indivíduos adultos, são capazes de capturar presas de tamanhos mais variados, provavelmente, por conta do maior número de indivíduos disponíveis para atividades de forrageio. A abertura das cáscas de árvore (onde residem as colônias) são utilizadas para capturar e imobilizar as presas de *P. nidificator*, porém, o tamanho das aberturas determina o tamanho das presas que podem ser capturadas: variações muito pequenas nas aberturas permitem a captura de presas muito pequenas ou muito grandes; variações intermediárias permitem a captura de presas de tamanhos mais variados; por fim, variações muito grandes permitem a captura apenas de presas muito grandes e muito pequenas. Portanto, acreditamos que a estrutura do habitat desses animais seja um exemplo de fenótipo estendido, favorecendo, em certos casos, a captura de indivíduos de maiores tamanhos, essenciais para a manutenção de espécies sociais. Em laboratório, concluimos que adultos e ninfas de *P. nidificator* apresentam distintas preferências quanto ao tamanho da presa: adultos demonstraram preferência por formigas maiores, enquanto que as ninfas se alimentaram de modo semelhante tanto das formigas grandes quanto das pequenas. Esse resultado pode estar relacionado à redução da competição entre adultos e ninfas, e/ou pode refletir uma relação de custo/benefício, pois a quantidade de energia disponível para as ninfas é proporcionalmente maior em comparação aos adultos.

A hipótese do tamanho da presa (*prey size hypothesis*) sugere que presas grandes são necessárias à manutenção do comportamento social em espécies de artrópodes. Neste estudo, demonstramos que *P. nidificator* tem preferência por presas grandes e é capaz de utilizar a estrutura do habitat para auxiliar em seu comportamento predatório. Portanto, nossos resultados indicam que a estrutura de habitat é um fator potencial, capaz interferir no surgimento e/ou na manutenção do comportamento social dos artrópodes.