Universidade Federal de Uberlândia

Instituto de Biologia

Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais

ECOLOGIA E EVOLUÇÃO DO COMPORTAMENTO SOCIAL EM PSEUDOESCORPIÕES NEOTROPICAIS: O EXEMPLO DE *PARATEMNOIDES NIDIFICATOR* (ATEMNIDAE)

Everton Tizo Pedroso

2011

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Ecologia e Evolução do Comportamento Social em Pseudoescorpiões Neotropicais: o exemplo de *Paratemnoides nidificator* (Atemnidae)

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

Orientador
Prof. Dr. Kleber Del Claro

UBERLÂNDIA

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APROVADA em 25 de Janeiro de 2011

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Uberlândia, janeiro de 2011

Dedicado a minha família, meus amigos e mestres.

"Se andarmos apenas por caminhos já traçados, chegaremos apenas aonde os outros chegaram."

Alexandre Grahm Bell

AGRADECIMENTOS

Agradeço sinceramente a todas as pessoas que, de algum modo, contribuíram para a realização deste estudo. A todos os amigos, colegas e companheiros que sempre me ajudaram nos momentos de dificuldade e também estiveram presentes nos momentos de gozo. Agradecimento especial aos amigos Marcela Yamamoto e Lourenço, Vanessa Stefani e Bruno Rossi, Denise Lange e Leandro, Estevão A. Silva, Pietro Kiyoshi Maruyama, pela grandiosa amizade e companheirismo. Também agradeço o amigo Célio Moura pelas sugestões no trabalho, por ceder cópias de suas imagens de pseudoescorpiões e de papers. Agradecimento especial ao amigo Jean Carlos Santos pelo valoroso apoio e incentivo, especialmente, nos primeiros anos de pesquisa. Seu apoio foi fundamental para que esta tese chegasse à etapa final. Aos amigos "LECIanos" pela cooperação em laboratório. Agradeço também aos meus amigos do Programa de pós-graduação em Ecologia e Conservação de Recursos Naturais, UFU.

Não poderia deixar também de agradecer à amiga Profa. Dra. Solange Cristina Augusto pelo incentivo, todas as sugestões e nossas discussões sobre a evolução da socialidade. Agradeço também a Profa. Dra. Alejandra Ceballos por sua atenção sempre excepcional, pelo incentivo no estudo dos pseudoescorpiões e por ter me recebido tão bem em seu país e em sua casa. Desde já agradeço também aos professores Alejandra Ceballos, Fernando Barbosa Noll, Helena Maura Torezan Silingardi, Marcelo de Oliveira Gonzaga, Natália Oliveira Leiner e Vanessa Stefani Sul Moreira, membros da comissão avaliadora, pelos comentários e sugestões que contribuirão para refinar este estudo e para a elaboração de projetos futuros. Agradecimentos sinceros também aos professores e colaborados da PPG-ECO-UFU por todo apoio durante muita graduação, mestrado e doutoramento.

Deixo também meus agradecimentos a toda minha família. Vocês sempre estiveram presentes em todos os momentos. Sinceros agradecimentos ao meu pai e minha mãe, e irmã. À minha amada esposa Alinne (e Filipe). Como amiga, companheira e cúmplice, você sempre esteve ao meu lado e abraçou minhas lutas para superar as dificuldades. Serei eternamente grato ao seu amor. Agradeço também a José do Carmo, Elizabete e Tatiane, por me receberem em sua família com muito amor, como um filho. O amor, carinho e dedicação de todos sempre estará presente em minha vida!

Faço meu sincero e eterno agradecimento aos amigos e mestres Kleber e Maura! Sou muito grato por terem me recebido como um filho e acreditarem um jovem, muito disposto a aprender e que necessita de preparação para iniciar sua caminhada por esta vida. Vocês sempre serão exemplos singulares de vida profissional, pessoal e familiar.

Agradeço também à Fundação de Amparo à Pesquisa do Estado de Minas Gerais pelo suporte financeiro como bolsa de incentivo a pesquisa de doutoramento de março de 2007 a outubro de 2010, e também pelo suporte ao projeto de pesquisa CRA 2841/07 entre os anos de 2008 e 2010. Presto meus agradecimentos ao PPG-ECO-UFU pelo suporte na realização do doutoramento, com apoio nas coletas e materiais, processamento do material e participação em eventos.

Ao meu Pai Celeste, Senhor da minha vida, que renova minhas forças e alegria a cada amanhecer!

RESUMO GERAL

Pedroso, Everton T. 2011. Ecologia e evolução do comportamento social em pseudoescorpiões neotropicais: o exemplo de *Paratemnoides nidificator* (Atemnidae). Tese de Doutorado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 87p.

Nas últimas duas décadas foram descobertas novas espécies vivendo em complexas organizações sociais, além dos himenópteros e isópteros. Exemplos como ratos-toupeira, camarões, afídeos, pulgões e besouros foram adicionados às listas de espécies eussociais. Estágios intermediários de socialidade também foram descritos em novos aracnídeos como as aranhas, amblipígeos e uropigídeos, opiliões, escorpiões, e agora pseudoescorpiões. Embora ainda existam grandes ressalvas no uso das classificações do comportamento social, que geralmente privilegiam as espécies eussociais, não se pode negar que muitas espécies tomaram caminhos convergentes. Independentemente do grau de complexidade social, cada espécie tem um poder único de abrir novas perspectivas na compreensão da evolução dos comportamentos cooperativos, em especial as espécies intermediárias. Neste manuscrito apresento a história de um pequeno aracnídeo social obrigatório, capaz de constituir grandes colônias mantidas pelo trabalho coletivo e complexos comportamentos cooperativos. Embora não seja novo para a ciência, ainda conhecemos muito pouco sobre seu comportamento social. Atualmente, sabemos que apenas duas dentre as mais de três mil espécies conhecidas de pseudoescorpiões vivem em complexas sociedades permanentes. Neste volume apresentaremos a história natural de *Paratemnoides nidificator* (Balzan, 1888) (Atemnidae) e suas diferenças em relação aos pseudoescorpiões solitários, comportamento cooperativo de forrageio e de dispersão e sua implicação para a manutenção da socialidade neste grupo; discutiremos a existência e a evolução da divisão de trabalho; também a existência que um segundo modo de vida social baseada em parasitismo em outra família; por fim, uma revisão sobre o comportamento social na ordem pseudoescorpiões e uma avaliação dos principais fatores na seleção deste modo de vida. Estes pequenos e discretos animais podem nos contar uma surpreendente história, e nos ajudar a compreender melhor a evolução do comportamento social em artrópodes.

Palavras-chave: Aracnídeos, Pseudoescorpiões, Cooperação, Divisão de Tarefas, Parasitismo Social.

ABSTRACT

Pedroso, Everton T. 2011. Ecology and evolution of social behavior in Neotropical pseudoscorpions: the example of *Paratemnoides nidificator* (Atemnidae). Doctoral thesis. UFU. Uberlândia-MG. 87p.

In the last two decades new species were discovered living in complex social organizations, besides the hymenopterans and isopterans. Examples as the naked mole-rat, coral-reef shrimps, aphids, thrips and beetles were added to the lists of eusocial species. Intermediate degrees of sociality were also described in arachnids as the spiders, amblypygids and uropygids, harvestmen, scorpions, and now pseudoscorpions. Although there is great resistance in the use of social behavior' classifications, which usually privilege the eusocial species, we cannot deny that a lot of species took convergent pathways. Independently of the degree of social complexity, each species has unique perspectives in understanding the evolution of cooperative behaviors, especially the intermediate species. In this manuscript I present the natural history of a small social-permanent arachnid, capable to live in large colonies maintained by collective work and complex cooperative behaviors. Although it is not a new species for the science, we know very little about it social behavior. Now, we know that only two among the more than three thousand known pseudoscorpion species live in complex obligate societies. In this study we will present the natural history of *Paratemnoides nidificator* (Balzan, 1888) (Atemnidae) and their differences in relation to solitary pseudoscorpions; cooperative forage and dispersion and it implications for the maintenance of sociality in this group. We will discuss the existence and the evolution of division of labor; and also the existence that a second way of social life based on parasitism; and finally, a revision about the social behavior in the Pseudoscorpiones order and an evaluation of the main factors in the selection this way of life. These small and discreet animals can tell us a surprising history and help us to better understand the evolution of the social behavior in arthropods.

Keywords: Arachnida, Pseudoscorpiones, Cooperation, Division of Labor, Social Parasitism

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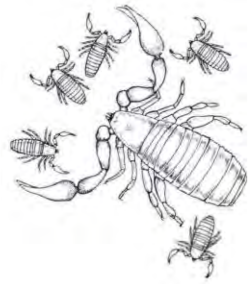
INTRODUÇÃO GERAL

NATURAL HISTORY AND SOCIAL BEHAVIOR IN NEOTROPICAL PSEUDOSCORPIONS

(Encyclopedia of Life Support Systems, 2008)



NATURAL HISTORY AND SOCIAL BEHAVIOR IN NEOTROPICAL PSEUDOSCORPIONS

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Keywords: arachnids, ecology, evolution, sociality, tropical.

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Summary

Pseudoscorpions (false scorpions) are small arachnids that in a quick look resemble small scorpions, although, without the "tail" having a sting. They have the body divided in cephalothorax and abdomen and six pairs of appendixes. Nowadays are known more than 3,200 species of pseudoscorpions in the world, grouped in 425 distinct genera and 24 families. Although widespread through the Earth, they are poor known in terms of biology and behavior, especially in the tropics. In the Amazon forest are expected more than 100 of new species, completely unknown by the science. These animals can live in a wide variety of conditions and environments, like the leaf litter; under the bark of live or dead trees; under stones; cavern walls; on the bat's guano; and also in extreme conditions like rocky crevices of some coastal regions. Pseudoscorpions are predators of small animals that they found in their territories. The reproductive behavior of pseudoscorpions is also very interesting and curious. Although the fecundation is internal, they do not perform direct transference of spermatozoids. The spermatophore is a small structure formed by a type of flagpole that is glued in the soil having in the top, in the position of the flag, a small package full of sperm in its interior. This package has appendices that are responsible to attach in the genital

opening of the female and to bomb the sperm to the female genital chamber.

The lack of information about the natural history of pseudoscorpions is a grave problem in the comprehension of importance in trophic chains, life histories and biology of this diversified group of arachnids. Indeed, for several decades in the last century natural history studies in almost all taxonomic groups, especially of animals, were neglected by referees of the main journals. Here we will present full data about the biology, development, reproduction and life system of the Neotropical pseudoscorpion Paratemnoides nidificator. After this previous presentation we will discuss why these small creatures, P. nidificator, live in a type of society and cooperates each other in prey capture? How it life system can be evolved and how are the advantages? The social behavior and causes of its evolution, details of ecology that pointed out this species in direction of sociality will be discussed here as an important issue that can reveal much more than we can figure out about the evolution of eusociality in tropical arthropods.

1. Introduction

1.1. What we know about the Order *Pseudoscorpiones*?

Like the name suggests, pseudoscorpions (false scorpions) are small arachnids that in a quick look resemble small scorpions, but without the extended metasoma (without the tail and sting). In fact they are very small, not longer than five to eight millimeters (Figure 1). Even all arachnids, the pseudoscorpions have the body divided in cephalothorax and abdomen and six pairs of appendixes: the chelicerae (associated to the mouth chamber); the pedipalps (like tweezers similar to that from scorpions) and four pairs of legs used to locomotion. Like other arthropods the body is segmented and in this case the segments of cephalothorax are melted giving them an aspect sometimes flat and in other times lumpy. Nowadays are known more than 3,200 species of pseudoscorpions in the world as a whole and they are grouped in 425 distinct genera and 24 families. Although widespread over the Earth, the major part of studies about biology, ecology or simple natural history and taxonomy of pseudoscorpions are concentrated on European, North American and Australian species. Although specialists pointed out South America as belonging to the richest fauna in this group, some researches await more than 150 new species only in Brazil; its pseudoscorpion fauna is almost unknown. Some parts of the Amazonian forest are the most studied regions of Brazil and the initial studies revealed the existence of 75 species.

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Figure 1. A solitary tropical pseudoscorpion from the Brazilian savanna. This species belongs to Chernitinae sub-family and probably is a new species that lives under the bark of trees.

Ones can easily perceive that due its small size the observation of pseudoscorpions in natural conditions is very difficult. However, there are a good group of naturalists working and showing that these animal can live in a wide variety of conditions and environments, like the leaf litter; under the bark of live or dead trees; under stones; cavern walls; on the bat's guano; and also in extreme conditions like the species *Neobisium maritmum* that can live on rocky crevices of some coastal regions of Europe. The beauty can be found in the most unexpected places of nature. Additional facts made the study of pseudoscorpions very difficult: furtive habits, cryptic coloration (camouflage), agility and the use of hidden environments as home. Some of the best known species are cosmopolite and well adapted to urban conditions. A good example is the species *Chelifer cancroides* (Linne, 1758) commonly found in house cracks. This pseudoscorpion discovered a "secure environment" among sheets of old books stored and forgotten in bookcases, a good place to build their silk nests. Opening a book like that some people get scared with the disturbed pseudoscorpions, now running and searching for a place to hide. These occurrences with time ended with people naming and recognizing these animals like Book-scorpions or false-scorpions.

1.2. Predatory Behavior and Feeding Habits

Peudoscorpions are predators of small animals that they find in their territories, as larvae and adults flies (Diptera) and beetles (Coleoptera), springtales (Collembola), mites (Acari), ants (Formicidae) and other false-scorpions too. Due to their small size, these arachnids are limited to attack and prey on animals of also small size, similar to them or preferentially smaller. In fact, pseudoscorpions are in general solitary animals, very aggressive, especially one with each other. In this sense, cannibalism of youngest (infanticide) or of small ones is not rare.

The most important sense to prey location is vibration (mechanorrecpetion). The body of these arachnids, mainly the chelicerae, legs, abdomen apical portions and, mainly, the pedipalps, are covered by long sensorial hairs, the trichobotria. These structures are able to detect a minimal air vibration nearby the predator. Thus so, when a prey moves by the environment, it produces an air disturbance and substrate vibration at the point where it is. These signals act as cues to the pseudoscorpion locate and to direct the attack. Vision is not an important sense in this world, serving mainly to determine variations between day and night. Several species are blind or can present up to two pairs of composed eyes, or a pair of ocelli, small structures able to detect changes in luminosity. It is possible that pseudoscorpions are also be able to locate and identify prey to chemical signals.

The pedipalps and chelicerae are strong weapons used to capture and subjugate preys. The capture and way to kill are variable according to the suborder. For example, the suborder Epiocheirata did not present poison glands associated to the chaela of pedipalps, as is common in this animal group (taxa). The Epiocheirata species present more delicate pedipalps; they can be long and fine, in some cases short, but rarely robust. In these species the pedipalps are very important in prey manipulation after the capture. The chelicerae are responsible for maceration. In the suborder Iocheirata, the arthropods can present a poison gland associates with both fingers of pedipalps, or in special cases present only in the immovable or in the movable finger, depending on the family; it is a very important taxonomic character to species determination. The Iocheirata species firmly and quickly grasp on the prey with the pedipalps, while they inoculate the poison that has functions both, digestive and paralyzing (neurotoxic and proteolitic).

1.3. Reproductive Behavior

The reproductive behavior of pseudoscorpions is also very interesting and curious. Although the fecundation is internal, they do not perform direct transference of spermatozoids. However, it does not mean that there is no structure to penetration, copulation and to produce the spermatozoid transference. The indirect transference of gametes is a common behavior among arachnids with the exception of Opiliones (Harvestmen) and some Acari. In the case of pseudoscorpions the male produces a small structure that stores the spermatozoid (the spermatophore) that will later be transferred to the female. The spermatophore is a small structure formed by a type of flagpole that is glued in the soil having in the top, in the position of the flag, a small package full of sperm in its interior. This package has appendices that are responsible to attach in the genital opening of the female and to bomb the female genital chamber with the sperm. The morphology of spermatophore is widely varied among species. Thus so, the fit in between the spermatophore and female genital opening is something like a key-lock mechanism, therefore, there is no connection between different species.

In the major part of species of Neobisoidea superfamily it is believed that males never found a female along their whole life. It happens probably due to the natural conditions in what they live, the litter fall. In the forest ground the leaf litter that covers the ground can be compared to an enormous ocean in the point of view of so small creatures like these arachnids. In this taxa, the males put the maximum number of spermatophores in the environment, randomly, and during almost their whole life. Females probably are attracted by chemical signals of these spermatozoid packages, a sensual and irresistible odor. Finding the structure the female puts her body upon it producing the fecundation. The reproductive behavior is very distinct in another superfamily, the Cheliferoidea. These pseudoscorpions generally are found in bark crevices of live and dead trees, under stones and rocky cracks. After finding a female, the male produces an elaborate repertory of behavioral acts, using mainly his pedipalps; it is courtship. If the female accepts and is receptive to copulate, both will enlace the pedipalps and they will initiate a movement similar to a dance. During the dance the male fixes the spermatophore on the ground and now, he will direct the female to the package that will fit in the female genital opening. The male will grasp the female over the spermatophore for a good length of time to enable the total transference of his genetic material.

1.4. Development, Life Cycle and Parental Care

Pseudoscorpions are viviparous animals. Egg development and larvae emergence occur still inside the mother's body, where one can find embryos in distinct stages. In the following phase, the embryos or larvae, both names are valid names in this case, are deposited by the mother in the interior of a delicate and membranous sac. This bag is secreted and produced by the reproductive organs and annex glands, having the general appearance of a transparent small sphere of side by side cloves. This special structure is named brood sac and it can be more or less elaborate depending on the species and of the type of glands related in its production.

The brood sac remains attached to the female's genital opening and can be carried under the mother's womb while she walks about searching for food and better shelters through the environment (Figure 2). The embryos are fed by a nutritive fluid produced in the interior of reproductive channels of the mother and thrown inside the brood sac. Larvae do the first molt still inside the sac. During the second molt, in the ecdysis the larvae cut the old cuticulae and the sac opens like it was composed by several capsules. Now the young, named nymphs, yet resembling a small pseudoscorpion go out. The ontogenetic aspects, like developmental time, were investigated in a few species.

The first described pseudoscorpion was initially classified as an animal belonging to the Acari taxonomic group. For this reason and until nowadays, researchers maintained that the three stages of initial development of pseudoscorpions must receive the same names used in the study of arachnids: Protonymph, Deutonymph and Tritonymph, respectively to the first, second and third instar. Besides size differences, each instar can be differentiated by the clearest exoskeleton in the youngest. The post-embryonic developmental time was studied in detail in a very limited number of species. These studies pointed out that in some North American and European species, like *Chelifer cancroides* (Levi 1948), the whole post-embryonic development can delay one year.

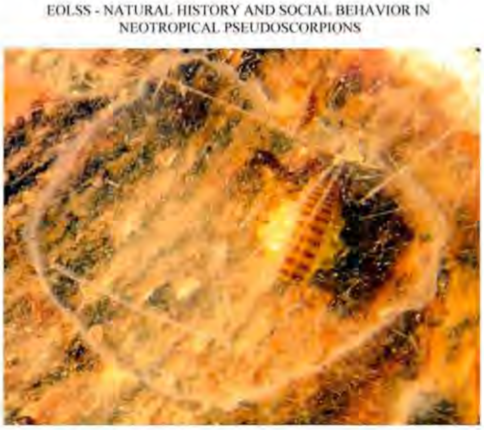

Figure 2. Female of the Neotropical pseudoscorpion *Americhernes bethaniae* carrying on a brood sac, full of second instar embryos. The female is building her silk chamber in the bark tree where their brood will develop.

1.5. Living Together

Living together is not an easy thing to do in nature. Animals living together have to be adapted to share food, space, mates, shelters, and several other resources and possibilities. Perhaps, due to this and other factors, species in general prefer to live alone. We can not say that one life strategy, alone in sociality, is superior. We can say that species were selected through hundreds or thousands of millions of years to live in one or another way, better to each one in each time and space circumstances. Like the great majority of other arachnids, pseudoscorpions are predominantly solitary animals. Arachnids are known by their aggressive behavior against co-specifics, they can be cannibals or necrophagous. Tolerance, an initial step in the evolution of sociality is almost nonexistent in this group. Some males have problems to control females during the reproduction.

Thus, it is extremely rare to find examples of arachnids, including pseudoscorpions that live together in aggregations or cooperate in some way during their life cycles. However, we have to consider

that these animals are small, cryptic, freak and that they scare humans with facility and that there are a reduced number of researchers studying the social behavior of arachnids in the world. In fact, there is only one pseudoscorpion genus where social behavior was described and in the following sections we will present and discuss the case study involving the fascinating *Paratemnoides nidificator*.

2. The Social Pseudoscorpions

2.1. Distribution and Occurrence of the Social Pseudoscorpion Species

The lack of information about the natural history of pseudoscorpions is a grave problem in the comprehension of importance in trophic chains, life histories and biology of this diversified group of arachnids. Indeed, for several decades in the 20th century natural history studies in almost all taxonomic groups, especially of animals, were neglected by referees of the main research journals. But luckily in the end of twentieth century and in recent years, these studies were recognized again as basic and important to our real understanding of the natural world. However, as a result of poverty in studies about natural history of pseudoscorpions, despite the fact that there are more than three thousands of species, in almost all parts of the continents, there are fewer than ten articles describing in detail the behavior of this taxa, and in particular their social behavior. Published papers describe only three social species of Atemnidae, all belonging to the *Paratemnoides* genus, as presenting some degree of sociality in pseudoscorpions: *P. nidificator*, *P. minor* and *P. elongatus*. The three species are distributed in the Americas, mainly in the tropical regions. Nevertheless, the taxonomic resolution of this species is until now unclear. Recently, the researcher Finn Erik Klausen from Norway published a detailed analysis of male genital structures in Atemnidae family that revealed a possible synonymy between *P. nidificator* and *P minor*. This is important information, which reveals that also in terms of taxonomy hard work is needed.

The available data in the current literature show that the social species of *Paratemnoides* genera occur from the south part of North America up to the south of South America. Field collections in several countries suggest that these animals were able to adapt to the life in a wide variety of environments. However, these animals appear to be limited to the life only under the bark of live trees. The pioneer studies were done by Brach in 1978 and later by Zeh and Zeh in 1990 that investigated respectively, the social organization and cooperative predation inside populations of *P. elongatus*. This species lives under the bark of Florida pine trees. More recently, other authors communicated that this species can be also found in tropical forests of Central America and also in Sao Paulo, state, Brazil. *P. minor* is described from the Brazilian Amazon forest, Paraguai, Uruguai, Argentina and also Sao Paulo state, in Brazil.

Figure 3. Distribution of Atmenidae genus of pseudoscorpion, *Paratemnoides*, in the Americas and inside Brazil.

Although, there are no quantitative studies about distribution and population density of *Paratemnoides*, several authors reported evidences of sociality in this genus in distinct countries of South America and in a variety of Brazilian states. The present authors began to study this animal in 2001, and were able to collect colonies of *P. nidificator* in five states of the Brazilian federation (Figure 3). Their field observations are mainly qualitative, but enable us to predict that this species is adapted to live in different environments subjected also to different ecological pressures, possibly resisting strong changes in climate, predator and prey presence and also anthropomorphic perturbation.

Despite its wide distribution and presence in forest areas, *P. nidificator* has also been found to be a common species associated to the trees of Cerrado vegetation. They are found in natural areas such as in the urban perimeter where they are easily observed. The Cerrados, Brazilian tropical savannas, are seasonal upland vegetation on deep and well-drained soils, with a permanent, usually very deep water table. This situation is quite unique and usually does not occur in tropical American savannas. Cerrado also does not develop when the soil becomes flooded or saturated for any appreciable period in the rainy season. Another difference between most northern tropical American savannas and the Central Brazilian cerrados is the richness of species per unit area (alpha diversity). Cerrados may contain between 250 and 350 (-450) vascular plant species per hectare, whereas in South American savannas this number is very significantly lower, usually only a quarter as much by area or by number of trees/shrubs counted. Originally the Cerrados covered 25-27% of the Brazilian territory. Nowadays, it is on of the most endangered ecosystems of the Earth, resting on less than 8% of the original area. This rich biome is being increasingly surrounded by agricultural fields and cities; it represents the last agricultural frontier to the expansion of sugar cane in Brazil, so there is an enormous priority in the study of its animals and plants and also in the elaboration of proposals of conservation to set up preserved areas. The study with pseudoscorpions in this environment can represent a modest, but very important step in the understanding of the intricate ecological web present in this vegetation.

2.2. Colony Structure, Growth and Division

Carefully looking under the bark of Cerrado trees, in the summer, winter or anytime, you can find one of the greatest terrors of this miniaturized world: colonies of pseudoscorpion *Paratemnoides nidificator* searching for their preys. The aggregations are composed by numerous silk chambers attached (Figure 4). The chambers are built by the nymphs (so called molt chambers), to have a shelter during the torpor phases that occurs for a short time before the ecdysis. Adult females can also build the chambers to reproduce (so named reproductive chambers). These shelters, nests or chambers are placed side by side, performing a type of interconnecting labyrinth that can be formed by the minimal number of one to twenty or more chambers, depending on the number of individuals in the colony. Most of the time, the pseudoscorpions are inside the chambers, going out only top forage.

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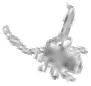
Figure 4. An example of *Paratemnoides nidificator* (Pseudoscorpiones: Atemnidae) aggregation in a bark of a Caesalpinoidea tree, in the Brazilian Tropical Savanna (Cerrado). In the figure, adults are surrounding three silk chambers with nymphs and females inside.

Thus, the size of a common nest and the number of chambers are a direct result of the local population. Then, the colonies present a strong variability in their structure and composition. In the nature we find from one isolated female and her brood, or a small group of adults and few young, groups formed only by adults, to an enormous aggregations with more than two hundred individuals including males, females, and young. So far the authors were not able to detect any pattern in the dynamics of colony organization in this social pseudoscorpion.

The colony composition is influenced by the number of resident reproductive females. The higher the number of females, the more growth the colony will have and more diverse will be the structure and composition of the group. But, we have to remember that colony size is also affected by colony's age (settling time), food access, energy allocation to reproduction, support capacity of the environment, available area below the bark tree where the nest can expand. Among all these factors, food availability



shows be the most important regulator factor to population increase in colonies of *P. nidificator*.

When food is more abundant, be it due to major or better quality of a determined environment or due to seasonal variation, the aggregations of *P. nidificator* reproduce intensively and each female can generate two, three, four or more offspring per year with a mean number of 13 nestlings in each one. Colonies having a large number of females will produce a large quantity of new individuals, which in turn can generate an explosive number that will double or treble in size in an interval of one year. Growing and becoming new adults, these new individuals will engage in tasks such as prey capture or reproduction. Thus, the success and chances in prey capture will be proportional to the number of individuals fit to hunt.

However, the relatively rapid increase in population size has a reversal. The population can surpass the environment's support capacity causing intense competition, both intraspecific and inside a colony, resulting in hunger and death. Low food availability or intense competition for a specific resource can break or weaken the cooperative behavior in the aggregations. Hunger can cause cannibalism. Thus, in large populations with tendency to increase further, the pseudoscorpions *P. nidificator*, found a solution to reduce their numbers in the same colony by division. Colony division or fission reduces the number of individuals taking part in the same group and, consequently, drops the level of competition between its members.

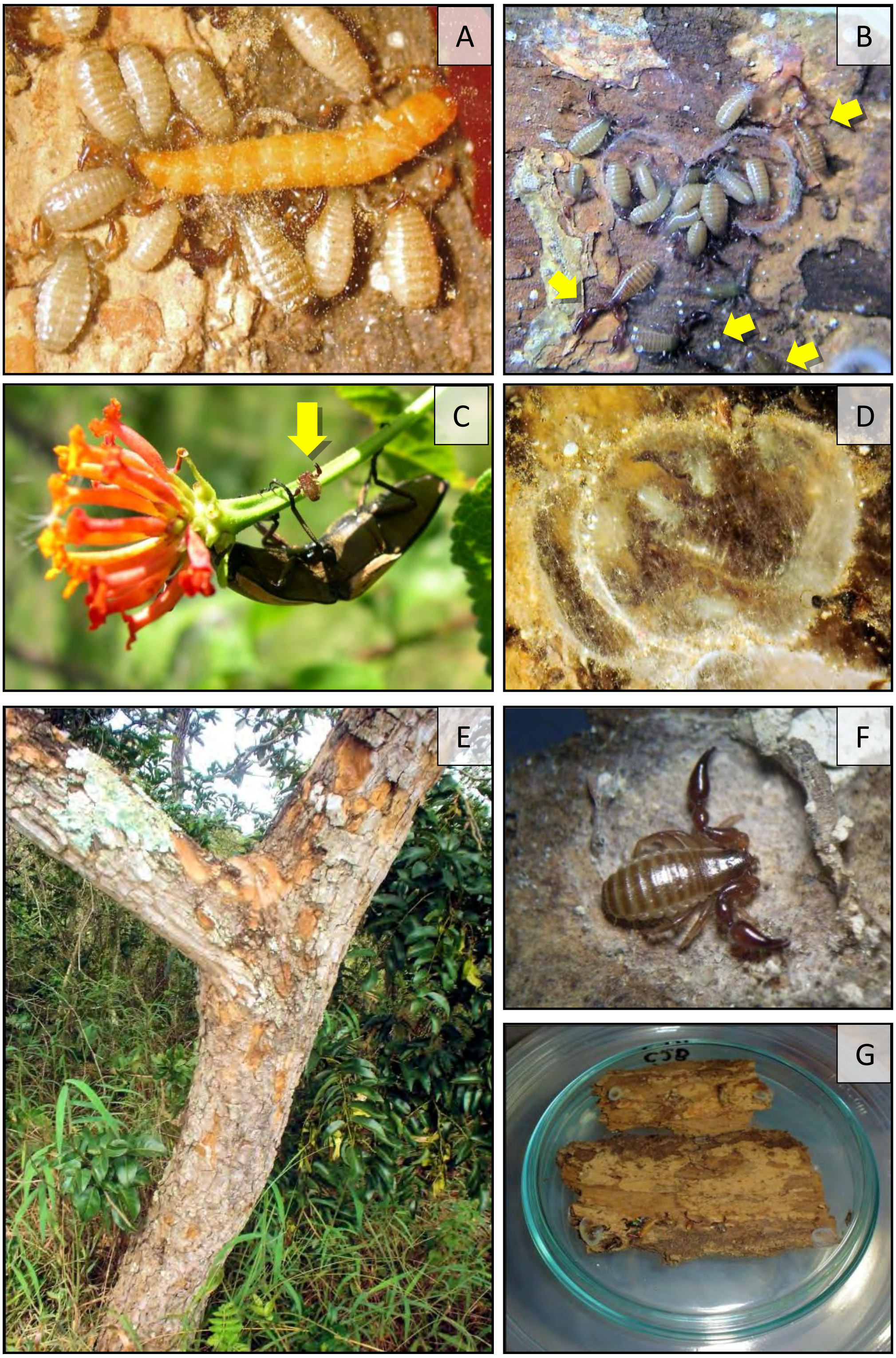
The main mechanism of dispersion is called multiple phoresy. In this case, adult pseudoscorpions, four, five or more individuals, are able to attach themselves to the body of a larger insect that is walking nearby the colony. Generally they attach to the legs (Figure 5) or hindwings, but sometimes also to the antennas. When the vector insect leaves the tree, it will leave together with the pseudoscorpion to a totally new place, another tree, passing by flowers and several other places never visited before by the phoretics. The colony fission is characterized by the formation of one small new aggregation, formed by a few individuals that leave the original colony searching for a new place to live, to found another aggregation. Although this dispersion mechanism, shows a reduced power of locomotion, it can involve a large number of individuals increasing the chances for prey catch and consequently the survival of the new pseudoscorpion colony.

Figure 5. Pseudoscorpion attached to the leg of an Elateridae beetle. Photo by. J.C. Santos.

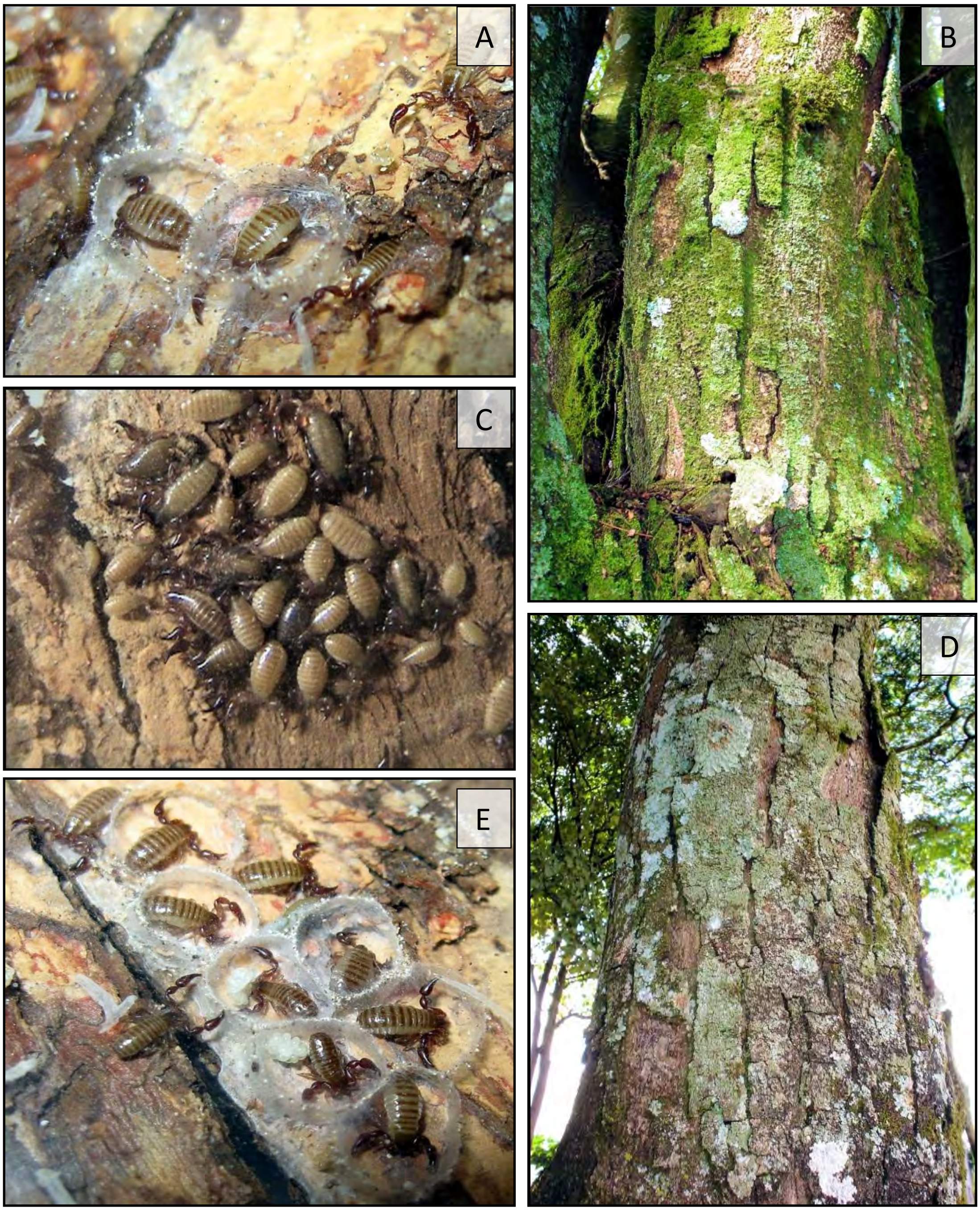
2.3. Forage and Feeding Habits of Social Pseudoscorpions

The social species of pseudoscorpions present a very interesting variation in forage and feeding habits when compared with the solitary individuals. Although very small in size (three to five millimeters), *Paratemnoides nidificator* and *P. elongatus* are able to hunt and kill their prey in group. For example, in *P. elongatus* aggregations the individuals can pursue and hunt as workers as soldiers of ant species *Cephalotes attratus* that can be over thirty times the body mass of a single pseudoscorpion. In South America, the authors have been studying *P. nidificator* for more than five years, in field and laboratory work, and they can point out that this species has similar skills to prey on bigger arthropods. Additionally, this arachnid is also able to feed on a very wide range of distinct arthropods found in barks of trees, several times larger than any other studied group, possibly due its most aggressive behavioral strategy of group hunting.

In general, *P. nidificator*, is a sit-and-wait predator, or else, they "rest" in a place beside the way of their preys, hidden and waiting for the right moment to attack for the highest chances of success. In general, these hidden places are the borders of barks of trees. Below them, the pseudoscorpions direct the pedipalps with open fingers to the area immediately



Prancha 1. (A) Os pseudoescorpiões *Paratemnoides nidificator* (Atemnidae) exibem comportamentos altamente sociais, e dentre eles, a capacidade de abater cooperativamente presas de grande porte. Nesta foto, jovens compartilham uma larva do besouro *Palembus dermestoides* (Tenebrionidae); (B) Detalhes de uma colônia de *P. nidificator*. As setas apontam os indivíduos adultos. Note as câmaras de seda e os jovens em seu interior; (C) Pseudoescorpião em forésia em um besouro Elateridae (fotografado por Jean Carlos Santos); (D) Fêmea de *P. nidificator* na câmara de seda com seus filhotes. A espécie exibe elaborados comportamentos parentais; (E) No Cerrado, os pseudoescorpiões sociais geralmente são encontrados vivendo sob as cascas de árvores suberosas, principalmente das Caesalpinaceae; (F) Detalhes de um pseudoescorpião adultos no interior de sua câmara de seda (fotografado por Célio Moura) (G) Detalhes do método de criação e observação dos pseudoescorpiões em laboratório. Os animais eram mantidos em placas de Petri.



Prancha 2. (A) Detalhes do início do estabelecimento de uma colônia, as fêmeas estão iniciando a construção de suas câmaras de seda para reprodução; (B) Em áreas naturais os pseudoescorpiões sociais podem ocorrem sob as cascas de árvores suberosas, mais comuns em cerrado sentido restrito ou cerradão; (C) Comportamento defensivo de agregação de *P. nidificator*, mantendo os jovens no centro do grupo; (D) Na área urbana, os pseudoescorpiões são comuns nos troncos das sibipirunas (*Caesalpinia peltophoroides*, Caesalpinaceae); (E) Colônia de *P. nidificator* em fase reprodutiva. As fêmeas constroem câmaras de seda dispostas lado a lado, onde se abrigam com as bolsas embrionárias.

outside the shelter, looking for movements, vibrations produced by other small animals walking nearby. Thus, *P. nidificator* avoids exposing the most vulnerable part of its body, the abdomen, to injury.

When an insect, for example, is coming closer to the entrance of the colony, marked by a crack in the wood, this movement causes substrate vibration and air disturbance, cues that are quickly perceived and recognized by the pseudoscorpions. At the right moment when the animal steps on the crack, its legs are grasped and the animal is pulled under the bark of the tree. In a few seconds, several adults of the colony hold the legs and other appendixes, such as antennas or tip wings, searching by articulations, where they will inoculate the venom. The prey remains practically immobilized with the body between the crack and the bark attempting to free its legs. The needed time to subjugate and paralyze a prey depends on the size and the number of pseudoscorpions involved in the attack. To kill a large prey needs a very good job by a very coordinated team to inoculate the exact amount of venom, not more, not less, because each choice will have a cost and benefit ratio.

Using such sit-and-wait strategy, the individuals of *P. nidificator* are able to prey not only on large beetles and bugs, but also on very aggressive and dangerous animals, like ants and spiders. Sometimes, living on trees, ants like the tropical Ponerinae *Pachycondyla villosa* (Figure 6), with more than ten millimeters and a strong sting are caught and immobilized between the cracks of the bark of a tree. After the victim is dead, the pseudoscorpions search for the joints and articulations where they insert the chelicerae injecting the digestive juice. It is important to remember that like other arachnids the food digestion is extra-corporeal, or else, the pseudoscorpions wait for the action of the digestive juice inside the body of the dead prey to suck the tissues.

However, will this strategy be the unique one to capture prey in *P. nidificator*? Indeed, the true answer is, no. Still it is possible to verify other common prey capture strategies depending on the prey body size. Some victims are larger than the pseudoscorpions, but not enough to stay and remain tied up to the crack of the tree bark. Insect larvae for example, although big compared with a pseudoscorpion, generally are able to invade the space under the tree bark. Preys that are quickly attacked by the pseudoscorpions and are pulled to nearby silk chambers or, sometimes, to the interior of the chambers where they are killed in a cooperative way by the predators. The predation behavior is totally different when the prey is short, smaller than a single pseudoscorpion. In this case, as the prey is small in size and is unable to offer resistance, it is captured and served as food only to the animal that found it first.

Figure 6. Ponerinae ant, *Pachycondila villosa*, tied up in the crack of a bark tree by the action of *Paratemnoides nidificator* pseudoscorpions.

These diversified prey capture strategies suggest that the tropical pseudoscorpion *P. nidificator* shows a generalist feeding habit, unlike the large majority of all known pseudoscorpions. So, it is possible that most arthropods that have tropical trees like feeding habitat, hiding place, reproductive encounter point, or like a simple resting place for some moments, are recognized as a potential prey to this special species of pseudoscorpion, and have a tragic end.

Although, people in general knew very little about the diversity of animals associated with the bark of cerrado trees, they can assert that the flexibility of predator behavior of *P. nidificator*, in cooperative or solitary ways, allows this animal to explore a wide range of invertebrates as feeding resources. It is surprising to know that these small animals are able to prey on more than 60 distinct species of tropical tree bark visitors, including large predators and herbivores arthropods like: jumping spiders (Salticidae); ants (Formicidae); beetles (Coleoptera), bugs (Heteroptera) and harvestman (Opiliones); all of them larger than one centimeter. The Figure 7 illustrates the number of morpho-species the authors observed in each

taxonomic group that serve as prey to *P. nidificator* in the tropical savanna and how much each one represents in terms of percentage.

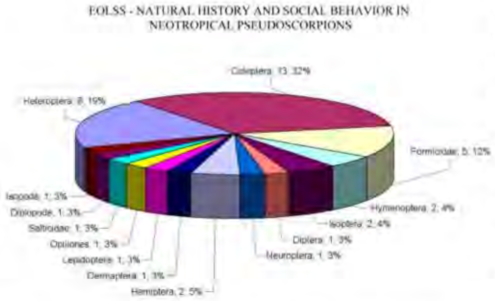


Figure 7. Diversity of taxonomic morpho-species and the percentage of each taxonomic group represented in the diet of the pseudoscorpion *Paratemnoides nidificator* in the tropical savanna.

2.4. Cohesion and Cooperation

After all that was said about these creatures so far, some questions arise: Why these small creatures, *P. nidificator*, live in a type of society and cooperate with one another in prey capture? How its life system could have evolved and what are the advantages? Well, these questions are the main objective of our investigation line and remain being researched. In fact, we know very little about pseudoscorpions' life history and it is especially true in the case of Neotropical species. The social behavior and causes of its evolution, details of ecology that led this species in the direction of sociality are important issues that can reveal much more than we can figure out about the evolution of eusociality in arthropods. The authors have been publishing their recent discoveries in scientific journals, listed in the bibliography of this chapter and available on www.leci.ib.ufu.br

We must bear in mind that for the maintenance of social behavior in a species, the benefits of sociality are in fact exceed its costs. However, it does not mean that the skills of a social species to explore the available environmental resources are greater than those of solitary species. Comparing it in a direct way we will see that solitary or social strategy only reflects the final result of a long process of decision based on a cost-benefit comparison in the evolution of a species. Social or solitary, the final strategy should be the best final result to a species if it has to survive in a temporal-spatial scale. Going ahead we investigate the effects of parental care in the grouping life of tropical pseudoscorpion *P. nidificator* and how this behavior can increase cohesion among individuals. We remember now that, fundamentally, arachnids are the most aggressive animals in relation to their co-specifics and that hunger or territoriality can often result in cannibalism. So, perhaps the first step to cross the bridge to sociality is to carry this stage on avoiding hunger and territoriality, in other words, reducing the chance of occurrence of cannibalism. *P. nidificator* attained this goal through an elaborate and diversified strategy of parental care.

2.5. Parental Care

In several invertebrate species, the females place their eggs in a special site, with ideal temperature and humidity, where they will develop and remain on their own. This is the maximum of maternal care offered by most invertebrates. In a few species, the maternal care is not limited to the selection of a shelter for the siblings and the mother remains with the brood till the eclosion of juveniles. This period of intensive care can delay from days to weeks or months, sometimes reaching the second or third stage of development.

Theories on parental care indicated that direct care provided by females (mother) to her brood is a basic condition to the evolution of social behavior (in a natural selection way). This principle also can be applied in the same way to pseudoscorpions. All species of this special arachnid exhibit some type of parental care. However, the complexity level in these behaviors, varies according to the family and species as previously discussed in reproductive behavior. Indeed, we know very little about the parental behavior and behavior in a general way of the majority of pseudoscorpion species. Those studied in detail belong mainly to the temperate climates and in general, it is not an easy task to identify the differences among the studied species. Perhaps, it will be relatively an easy task to focus attention on more conspicuous differences, thereby, looking for the most complex strategies of parental care. In some members of Atemnidae family we observe a long period of aggregation between adult females and nymphs (e.g. *Atemnus politus* in a pioneer study of Weygoldt). During this period the nymphs remain inside the nest with the female (mother) for two or three weeks. But there is no evidence of additional care in this case, like food offering and protection against predators. The most complete and well known reports of a developed social behavior in pseudoscorpions are those on the Neotropical species *Paratemnoides nidificator*, recently studied by the authors in the tropical savannas of Brazil. The authors previously commented that this animal is found below of the bark of live and dead trees in colonies of few (5-10) to hundred of individuals (100-200). In general adults, males and females, and nymphs of different stages can be found together and most of these individuals are genetically related. The adults of *P. nidificator* take care of their brood until the young become adults, and females remain inside the nest protecting their descendants. Other males and females remain outside the nests (silk chambers), where they are able to catch and kill prey that is offered to the colony. In this case, all individuals of the colony can take care of the young, offering food and defense without paternity discrimination. The post-embryonic development of nymphs can delay for seven months. When isolated from the colony, by chance or other reason, mothers hunt and feed their brood until the adult phase. In extreme situations, with prolonged food restriction, cannibalism occurs or death in the brood is high. So, in this case, this species present an amazing way of parental care called matriphagy, or the act of feeding on the mother's body. The mother offers her body to her brood to avoid their death or to avert cannibalism. The young now are on their own. So, they pass to prey on small insects in bands of brothers

The complex cooperative parental care in *P. nidificator* can be a very important strategy for the survival of the colony. All females of the colony are able, morphologically and physiologically, to reproduce generating a large number of new individuals to whom they are able to offer care for several months. Thus, the cooperation of immature males and females is fundamental to the hunt of enough prey to satisfy a normal development of nymphs. Despite this fact, the cooperation increases the chance of tolerance among individuals, increasing also the cohesion of the group and the chance of the evolution of a more sophisticated social behavior.

3. New Directions

The study of tropical biodiversity is one of the main steps human beings have to improve to save the planet. Knowing life forms and their function in the ecosystems we will be able to maintain still conserved communities and in other cases to re-build disturbed areas. Arachnids are one of the most important groups of second level consumers in trophic cascades and due to their cryptic habits and freak appearance and behavior, are still evading science. Pseudoscorpions in particular are very poorly known animals. We barely know about their taxonomy and biology. What concerns us is that they are very interesting and important animals to reveal to us basic steps and primordial steps in the evolution of sociality. Perhaps, discovering a bit more about the cryptic world and evolution of sociality in this group, we will be able to better understand ourselves, the most intriguing and developed social species in the future.

Acknowledgements

We thank CNPq – Brazilian Council of Research and Fapemig – Minas Gerais State agency of research and Technology for financial support to our work. We also thank the Graduate Program in Ecology and Natural Resources of Federal University of Uberlandia for all support provided by the doctoral thesis of Tizo-Pedroso. We specially thank the Clube de Caca e Pesca Itororo de Uberlandia for authorization to work in its cerrado reserve. We thank too Helena Silingardi and Marina Mineo for reviewing the original version of the manuscript.

Glossary

Camouflage	: An animal is cryptic or in camouflage coloration, when its color and shape confound this animal with the environmental background to a visually oriented predator.
Co-specific	: Member of the same species, and in some cases, of the same population.
Eclosion	: The process by which young individuals (e.g. nymphs or larvae) break their egg shells and go outside to complete their development.
Eusociality	: Term used to the more derivate level of social behavior mainly found in hymenopterans (ants, some wasps and bees) and termites, Eusocial organisms present several special features: overlapping generations; cooperative brood and cooperative care of youngs, division of labor with the existence of a caste system with distinct workers and reproductive individuals, the queen(s).
Guano	: The excreta of animals, especially birds and bats that are commonly used as fertilizers.
Leaf litter	: The tiny decompsoing layer of leaves and stems covering the floor of the forest.
Matriphagy	: When the mother offers her body as food to the young. A special case of cannibalism.
Morpho-species	: A distinction between species without the need of to classification.
Necrophagy	: To feed on dead body of co-specific.
Phoresy	: Dispersion mechanism, common in insects and other arthropods in what the phoretic (dispersed animal) will attach itself to the body of another and major insect (vector), getting locomotion.
Sit-and-wait strategy	: When the predator to wait in a hidden position by a prey that pass nearby to attack.
Spermatophore	: Structure to store and transfer sperm.
Trichobotria	: Small hairs able to detect sound and air and substrate vibration. Present in the legs and other articulate appendix of arachnids.

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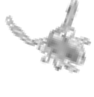
Biographical Sketch

Everton Tizo-Pedroso is a biologist, graduate in Ecology from the Federal University of Uberlandia (UFU) in 2007 and developing his doctorate thesis in the Ecology and natural history of tropical pseudoscorpions. He is also member of Biotic Interactions and Behavioral Ecology Research Group from the Brazilian Council of Science and Technology (CNPq) and member of the project sponsored by the FAPEMIG (Research council of Minas Gerais State) to investigate ecology, diversity and Natural history of pseudoscorpion in the cerrados (tropical savannas) of Minas Gerais, Brazil.

Kleber Del-Claro is a biologist with doctorate in Ecology by State University of Campinas (Unicamp) in Brazil. Since 1992 is a teacher at Federal University of Uberlandia (UFU), where between 2003 and 2007 Ecology. Kleber is the coordinator of the international cooperation agreement between UFU and the University of Missouri, St. Louis (UMSL), USA. He is a researcher from the Brazilian Council of Research, Science and Technology (CNPq) since 1996. At UFU and other Brazilian universities he was instructor of several master and doctoral thesis in ecology and animal behavior developed in the tropics. His scientific history, books and publications are available in: www.leci.ib.ufu.br. In 2005 he was the president of the "Frontiers in Tropical Biology and Conservation" meeting, settled in Brazil (Uberlandia), the annual meeting of Association for Tropical Biology and Conservation (ATBC) and supported by the Brazilian Society of Ethology (SBEt, now President for the second time).

To cite this chapter

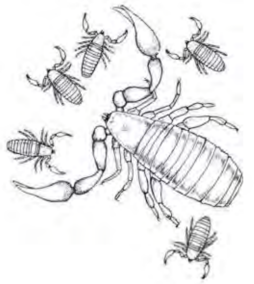
E. Tizo-Pedroso & K. Del-Claro, (2008), NATURAL HISTORY AND SOCIAL BEHAVIOR IN NEOTROPICAL PSEUDOSCORPIONS, in *International Commission on Tropical Biology and Natural Resources*, [Eds. Kleber Del Claro, Paulo S. Oliveira, Victor Rico-Gray, Ana Angelica Almeida Barbosa, Arturo Bonet, Fabio Rubio Scarano, Francisco Jose Morales Garzon, Gloria Carrion Villarnovo, Lisias Coelho, Marcus Vinicius Sampaio, Mauricio Quesada, Molly R.Morris, Nelson Ramirez,Oswaldo Marcal Junior, Regina Helena Ferraz Macedo, Robert J. Marquis, Rogerio Parentoni Martins, Silvio Carlos Rodrigues,Ulrich Luttge], in *Encyclopedia of Life Support Systems (EOLSS)*, Developed under the Auspices of the UNESCO, Eolss Publishers, Oxford, UK, [http://www.eolss.net] [Retrieved July 18, 2008]



CAPÍTULO 1

COOPERATION IN THE NEOTROPICAL PSEUDOSCORPION, *PARATEMNOIDES NIDIFICATOR* (BALZAN, 1888): FEEDING AND DISPERSAL BEHAVIOR

(Insectes Sociaux, 2007)



Insect. Soc.
DOI 10.1007/s00040-007-0931-z

Insectes Sociaux

Research article

Cooperation in the neotropical pseudoscorpion, *Paratemnoides nidificator* (Balzan, 1888): feeding and dispersal behavior

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Received 10 August 2006; revised 17 November 2006; accepted 23 January 2007

Abstract. Social behavior is rare among arachnids, and "permanent-sociality" is a strategy documented only in a few spider species. Here we describe the feeding and dispersal behavior of *Paratemnoides nidificator*, a Neotropical pseudoscorpion presenting "non-territorial permanent-sociality". Field and laboratory observations (100 hours and 200 sessions over four years) and manipulative experiments revealed that *P. nidificator* is a generalist predator that lives in rough bark of trees, in groups of 2 to 175 individuals (42.62 ± 28.27; N=35 colonies; solitary individuals were never found), including reproductive adults and nymphs. Individuals in groups cooperatively capture prey four times larger than solitary individuals. Adult hunters share food with siblings. Reproduction in natural conditions occurs during the hot/wet season, when food availability is high. Prey diversity and abundance seem to be the main factor limiting reproduction in this species. Phoresy (attachment to a transporter animal) is the basic mode of dispersion in *P. nidificator*. Grouped individuals use large animals as vectors for dispersal, and once established they use the vector as the first food item of the new colony. However, they can also disperse by colony fission, newly documented herein for this taxon. The elaborate, cooperative behavior in *P. nidificator* is unique among pseudoscorpions and represents an excellent model for studies on the evolution of sociality in invertebrates.

Keywords. Arachnida, social behavior, cooperation, cooperative prey capture, phoresy.

Introduction

Pseudoscorpions are small arachnids living below litter, stones, tree bark, inside dead tree trunks, caves and other similar habitats (Weygoldt, 1969; Harvey, 1986). Most studies of this group focus on taxonomy and distribution, and the group presently includes 3240 recognized species, 425 genera and 24 families (Harvey, 2002). Despite their abundance in nature, there are few studies about their biology, ecology and natural history, probably due to their small size and furtive habits (e.g. Levi, 1948; Harvey, 1986; Muchmore, 1990). Pseudoscorpions prey on animals generally smaller than themselves, with feeding and hunting behaviors that vary depending on the chelicera morphology and presence of poison glands (e.g. Feio, 1945; Gilbert, 1951; Weygoldt, 1969; Andrade and Gnaspini, 2002).

Dispersion and colonization of new habitats is difficult because of the small size of these arachnids (2–8 mm). However, several species engage in phoresy, a dispersion process by which the phoretic (dispersing animal) attaches itself to the body of a vector (transporter animal). This behavior is known in at least ten pseudoscorpion families worldwide (Weygoldt, 1969; Piomar et al., 1998). The most recent study reviewing phoresy in pseudoscorpions suggests advantages and disadvantages of this behavior, and points to Diptera, Lepidoptera and Coleoptera as main vectors (Piomar et al., 1998). Information about vector-phoretic specificity and benefits to the transporter are rare. Zeh and Zeh (1997) described a complex interaction between the pseudoscorpion *Cordylochernes scorpioides* and its vector, the beetle *Acrocinus longimanus*, reporting interference of phoresy with sexual selection mechanisms, reproduction and ecology of the arachnid. Concerning this same species, Santos et al.

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(2005) suggested that pseudoscorpions can bring benefits to the vector through predation upon parasitic mites.

The pseudoscorpions of Neotropical regions, and especially those from Brazil, are practically unknown in terms of their biology, ecology, behavior and natural history. The studies in Brazil, conducted in the Amazon forest, concern mainly taxonomy and phoresy, (e.g. Adis and Mahnert, 1985; Aguiar and Bührnheim, 1998). Generally, pseudoscorpions are solitary animals, but there are a few social species (Weygoldt, 1969). Recently, Tizo-Pedroso and Del-Claro (2005) described social behavior in *Paratemnoides nidificator* (Atemnidae), a species from the Brazilian tropical savanna (Cerrado), which included cooperative hunting and elaborate parental care. They suggested matriphagy as an important step toward the evolution of social behavior in arachnids. Due to its abundance in savanna habitats, easy maintenance and reproduction in laboratory conditions, *P. nidificator* is a suitable model species to investigate the general characteristics of social pseudoscorpions. The main objectives of the present study were to explore the natural history of this Atemnidae directly in nature, its feeding behavior and the occurrence of phoresy.

Material and methods

Field studies were conducted between October 2001 and November 2005. The field site included the experimental garden of the Umuarama campus of the Federal University of Uberlândia (UFU), Uberlândia, Minas Gerais State, Brazil (48°17' W; 18°58' S) as well as some nearby natural vegetation (Cerrado *sensu stricto:* savanna woodland, Oliveira and Marquis, 2002). The climate in the region features distinct dry (June to September) and rainy (October to May) seasons (Reu and Del-Claro, 2005). Laboratory maintenance of pseudoscorpions, observations and experiments took place in the Behavioral Ecology and Interactions Laboratory of the Biology Institute, UFU.

Natural history observations

We searched for *P. nidificator* in barks of trees within the field sites and recorded the following data: a) tree species and characteristics (height, trunk diameter, bark type); b) size and composition of the colony (number and age of individuals); and c) development stage of the colony (presenting or not molting chambers, reproductive chambers, reproductive individuals, juveniles, females with brood sacs). We also identified and measured any prey items being consumed or attacked. The activity pattern of the animals was monitored during the dry and wet season of the first year of the study to assess daily activity patterns. The reproductive season was recorded directly in the field during the four years of the study. Additionally, we collected and maintained 25 colonies in the laboratory for four years, offering prey of different species and sizes. The rearing and maintenance methods in laboratory followed Tizo-Pedroso and Del-Claro (2005). Food was offered twice weekly between 2002 and 2003 and only once weekly between 2004 and 2005. We collected data weekly on the development of these aggregations, reproductive activities (number of new brood sacs) and feeding behavior. To avoid that any experimental colony would feed on a test animal just for lack of options or because of starvation, whenever we tested a food item we also introduced simultaneously a common prey (termite nymphs or Tenebrionidae larvae).

Experiments and phoresy observations

We performed two experiments in the laboratory. In the first one we tested possible vectors for phoresy, offering distinct options (insects, spiders, isopods and millipedes) to the colonies. We conducted 30 min observation sessions (all occurrences sampling, *sensu* Altmann, 1974) to assess the reactions of the pseudoscorpions to each item. Three types of reaction were expected relative to the introduced animals: a) refusal; b) attack and/or consumption; and c) use as phoretic vector. This experiment also provided data about potential food items.

In natural conditions we performed 100 hours of observations ("all occurrences sampling", *sensu* Altmann, 1974) divided into 200 sessions of 30 minutes, equally distributed throughout the seasons of the four years of study, involving around 50 colonies per year. These observations yielded data about natural predation and phoresy.

The second experiment tested whether colonies can disperse not only through phoresy but also by colony fission (*sensu* Avilés, 1997, 2000). We collected three colonies in the field (78, 93 and 104 individuals) and transported them to laboratory. Each of these aggregations, contained within a 40 cm^2 piece of bark, was placed in the center of a plastic box (60 x 50 x 5 cm), in which four other similar pieces of the bark of the same tree were placed at each corner. Each of the three colonies was fed and observed weekly for two years (2002–2004).

Results

Five different plant species in the families Caesalpiniaceae (*Copaifera langsdorffii,* and *Caesalpinia pelthophoroides*), Fabaceae (*Vatairea macrocarpa* and *Pterodon pubenscens*), and Vochysiaceae (*Vochysia tucanorum*) hosted colonies of *P. nidificator.* Only one of these species, *C. pelthophoroides*, was available within the campus. The host plants have the same general aspect, being tall trees (5–10 m) with thick trunks (15–25 cm radius at the base) and rough bark. We found that there are spaces in several points between the bark and the trunk itself, which are used by the colonies. The colonies are generally composed by nymphs and adults, and occur in the field year-round, presenting peaks of activity around midnight. However, the colonies presented asynchronous development over the four years of study, exhibiting heterogeneous proportions of developmental stages (Fig. 1). The number of males and females of each colony was compared by a paired *t*-test. The results indicated that the colonies of *P. nidificator* were female-biased (t =3.09; df=34; $p<0.004$; N = 35 colonies), with an average sex ratio of 2:3 (males:females).

Paratemnoides nidificator used a large variety of prey items, primarily insects but also arachnids, isopods, and myriapods (Fig. 2, Appendix 1). The size of the prey also varied widely, including small bugs (1–2 mm) and Scarabaeidae beetles, larger than 13 mm. Depending on the size and agility of the prey, the pseudoscorpions exhibited solitary or cooperative hunting. We observed that smallest prey (smaller than or as large as an isolated pseudoscorpion) were usually attacked and consumed by a single pseudoscorpion ($x = 1.46 \pm 0.72$ individuals; N=24; Fig. 3A), whereas large prey were captured and consumed cooperatively ($x = 2.50 \pm 0.78$ individuals; N=24; Fig. 3B). These results are significantly different

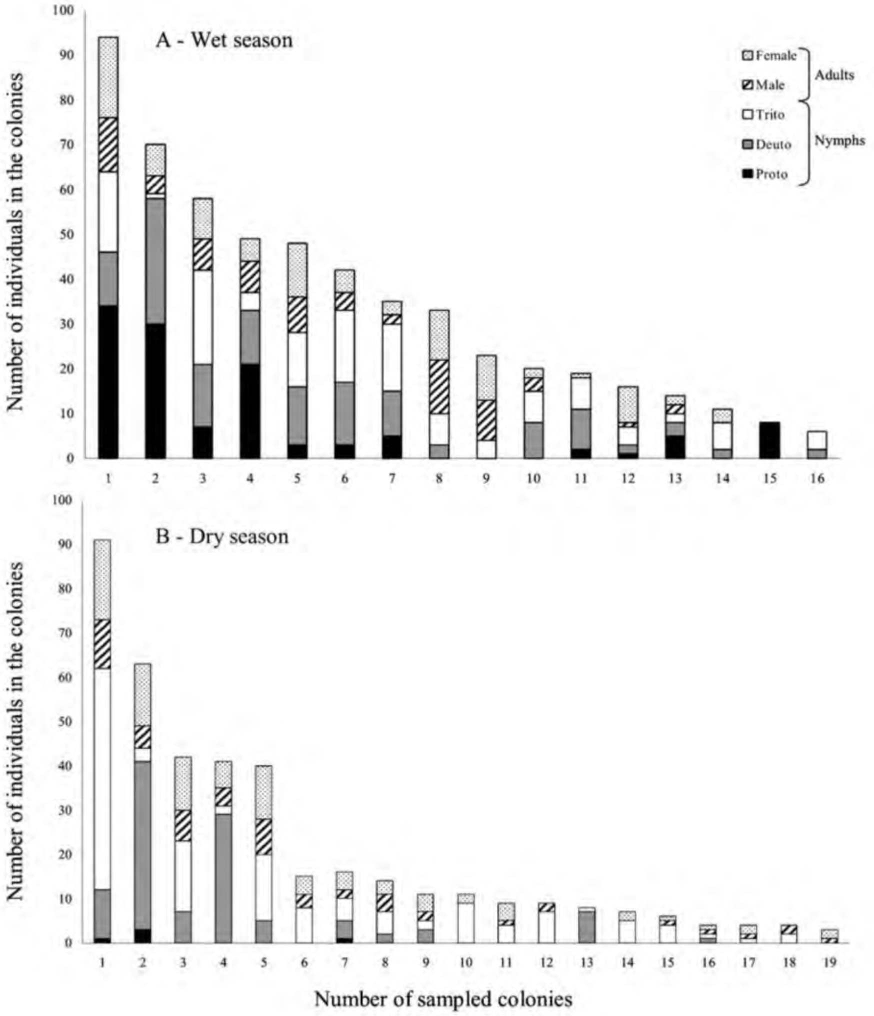

Figure 1. Characterization of the *Paratemnoides nidificator* colonies investigated in the Cerrado vegetation from 2001 till 2005, denoting individual colony composition in the wet and dry seasons. Proto = protonymphs; Deuto = deutonymphs and Trito = tritonymphs.

(U=478; N=48; $p<0.001$). The hunters in the colonies are adult male and female, and after the prey is dead nymphs gather to feed together with the adults. During feeding, they generally attach their chelicerae to the prey's appendages, mainly at the level of leg joints.

The reproductive period of *P. nidificator* in the Cerrado is centered on the wet season, between October and April, peaking in early December. Our data showed that it is adjusted not only according to higher humidity and heat in the field, but is also strongly influenced by prey diversity and availability (Fig. 4). In laboratory conditions, with no food restriction (prey offered twice weekly), the pseudoscorpions presented reproductive activities (evidenced through the presence of new brood sacs) year-round, but also with a peak in the early wet season (Fig. 4A). When we restricted food, offering prey once weekly, the results were similar to what was observed in the field, with reproduction restricted to the wet season (Figs. 4A and B; interaction effect between food level and months, $F=10.30$; df=11; $p<0.001$).

We observed 12 different insect species and one harvestman serving as transporter to the phoretic *P. nidificator* (Table 1). Solitary as well as grouped pseudoscorpions may present phoresy, which involves only adults. In multiple phoresy, up to seven individuals, both males and females, can attach themselves to the body of the same vector. Legs and antennae are the structure generally used by the phoretic individuals.

We found a positive correlation between colony size and intensity of phoretic events (Fig. 3C), but not between the number of attached pseudoscorpions and the size of the vector (Fig. 3D). We also observed that the

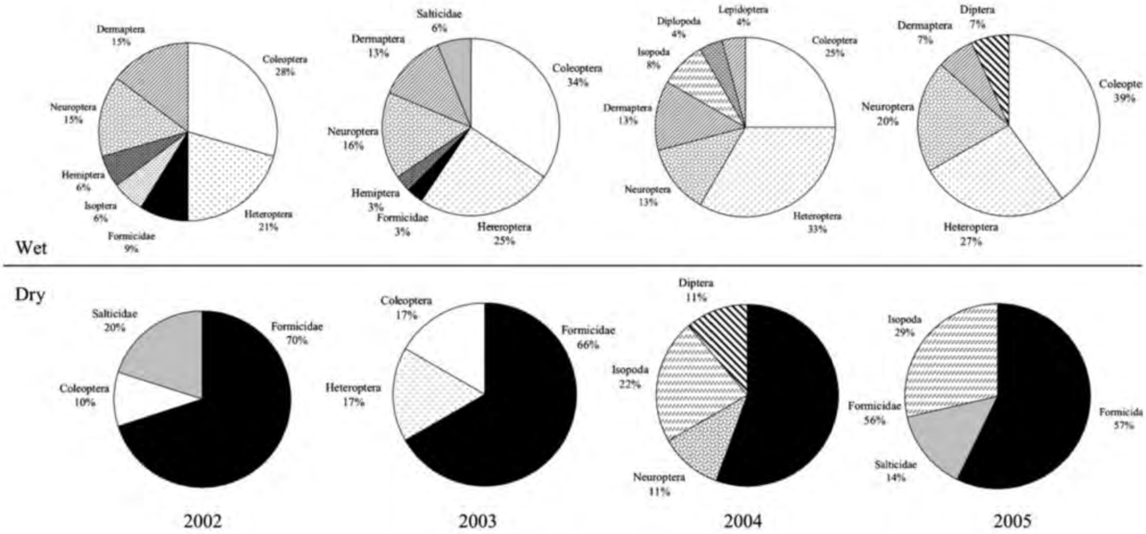

Figure 2. Effect of seasonality on prey consumed by *Paratemnoides nidificator* in the Cerrado biome of central Brazil during four years of observations.

same arthropod species could be used both as a vector to phoresy as well as a food item in different circumstances. Under natural conditions we collected eight insect species (Hemipterans: six Pentatomidae and two Reduviidae) with pseudoscorpions (both males and females) attached to their bodies. These vectors were transported to the laboratory and maintained in Petri dishes together with a piece of tree bark. After the vectors died, they were eaten by the pseudoscorpions which, subsequently, founded a new colony.

The three colonies maintained in the laboratory grew successfully with the constant offering of food items. In the end of the first year of observations, the colony with 93 individuals produced a new small colony in one of the bark pieces offered, composed exclusively of adults, four females and two males. The colony with 104 animals gave rise to two new small aggregations also composed exclusively of adults, the first with six females and four males and the second with five females and four males. The third colony with 78 individuals did not present fission.

Discussion

Pseudoscorpions are generalist predators limited in their hunting abilities by their small size, and preying on animals smaller than themselves (Gilbert, 1951; Weygoldt, 1969; Andrade and Gnaspini, 2002). *Paratemnoides nidificator* is a sit-and-wait generalist predator feeding on a wide variety of prey items, and contrary to most other pseudoscorpions, this species includes animals larger than itself in its diet. Some *Paratemnoides* species are known for cooperative behavior in the capture of large prey (Brach, 1978; Zeh and Zeh, 1990; Hahn and Matthiesen, 1993). The feeding plasticity of *P. nidificator* is clearly related to the presence of cooperative hunting. Our results showed that groups of *P. nidificator* were able to subdue prey almost four times larger than each individual. Similar patterns of cooperative hunting, including prey sharing, have been registered in social spiders (reviewed in D'Andrea, 1987; Avilés, 1997; Kim et al., 2005a, b), and the advantages of this type of behavior have been widely discussed for social vertebrates (e.g. Giraldeau and Caraco, 2000). Within a group the food intake per individual is smaller than that of a solitary predator; however, cooperative hunting can increase not only the chance to obtain a larger prey, but simply the chance of obtaining any prey (Schneider, 1996; Ulbrich and Henschel, 1999; Kim, 2000; Amir et al., 2000, Kim et al., 2005). In subsocial spiders cooperative hunting not only enables the group members to hunt larger prey, but they do it more quickly and reduce the chances of cannibalism and aggression among siblings (Kim et al., 2005a; Whitehouse and Lubin, 2005). In *P. nidificator* cooperative hunting abets mutual tolerance, group cohesion and maternal care, and matriphagy appears as an important step in the evolution of "non-territorial permanent social behavior" (Tizo-Pedroso and Del-Claro, 2005).

The female-biased sex ratio was similar to that found in another social *Paratemnoides* (Zeh and Zeh, 1990) and in social spiders (Avilés, 1997; Avilés et al., 2000). However, it was not possible to determine whether or

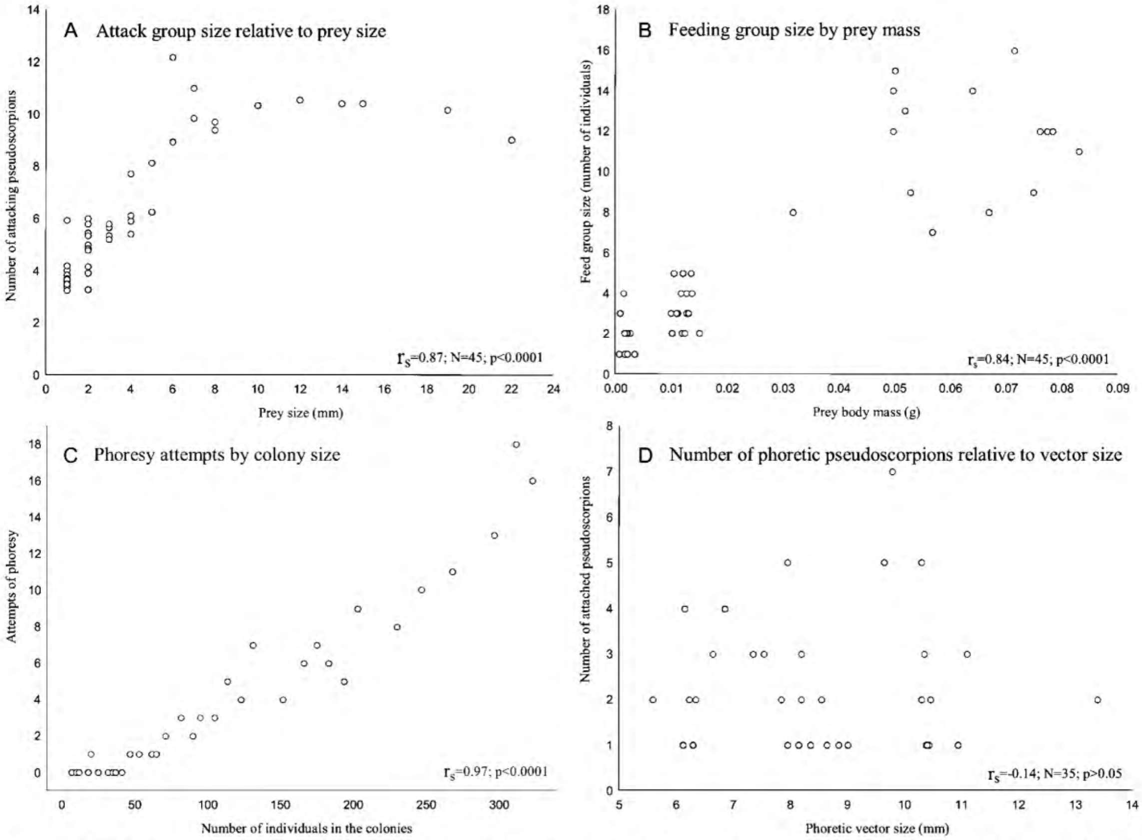

Figure 3. Correlations analyses involving colony size. (A) The size of pseudoscorpion hunting group increase by function of the prey size; (B) The number of pseudoscorpion composing the feed group was restricted by the prey size; (C) Relationship between the number of individuals in colonies of *Paratemnoides nidificator* maintained in the laboratory and the number of phoresy attempts; (D) Relationship between the size of phoresy vectors and the size of phoresy groups.

not the adult sex ratio reflected a female bias among nymphs, because sex in this species can only be identified in adult individuals. Our results do not show the existence of a demographic pattern among *P. nidificator* colonies: there is great variation in the number of individuals per instar. This suggests that the colonies reproduce and increase asynchronously, probably because the number of juveniles that a colony can produce is dependent of the number of mature females present. However, climatic conditions influence female reproduction, as shown by the extremely reduced number of protonymphs observed during the dry season. Living organisms present adjustments to maximize their fitness through cost-benefit relationships that directly depend on physical and biological characteristics of the environment. Insects and other arthropods in the tropics tend to reproduce and grow in numbers when food and climatic conditions are not limiting factors (e.g. Marquis and Braker, 1994; Gullan and Cranston, 2005). Our results concerning brood sac production through time in *P. nidificator* clearly suggest that food, or prey availability, is a strong limiting factor in the reproduction of these animals. During four years of observations conducted under natural conditions in Cerrado, no reproduction occurred during the dry season, a period where the main prey items are scarce and represented mostly by relatively dangerous prey such as ants and spiders (Fig. 2) (see Del-Claro and Oliveira, 2000; Oliveira and Marquis, 2002). For many predators, energy allocation to reproduction is directly dependent on prey availability (Krebs and Davies, 1993; Barbosa and Castellanos, 2005; Wise, 2006). Low temperatures and mainly hydric stress during the dry season in the Cerrado can also have an important role in the reproductive strategy of *P. nidificator.* However, tree bark can offer protection against unfavorable climatic conditions and water can be obtained from prey items.

Phoresy is the unique way of dispersion described for pseudoscorpions (e.g Weygoldt, 1969; Piomar et al., 1998), and several species of animals have been reported as vectors (Piomar et al., 1998; Zeh and Zeh, 1992).

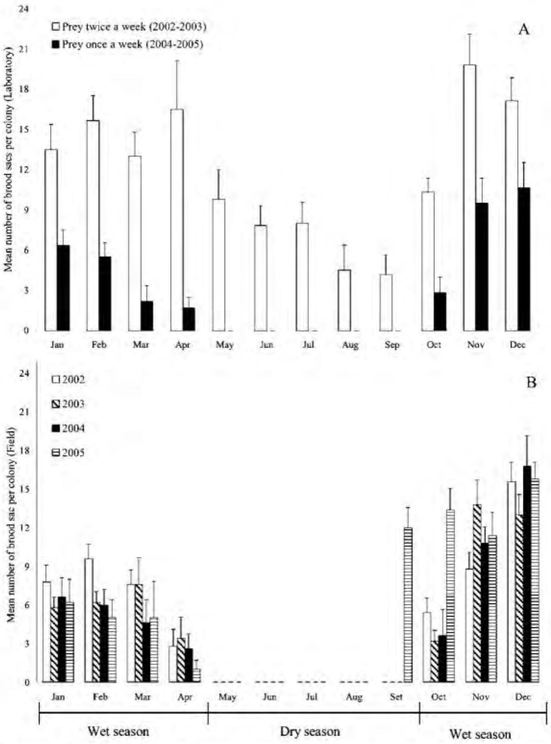

Figure 4. Effect of feeding frequency in the mean number of brood sacs produced by colonies of *Paratemnoides nidificator* for: (A) Reproduction of colonies maintained in laboratory; bars indicate the mean brood sac produced by colonies offered food twice (open bars, years 2002 and 2003) or once (closed bars, years 2004 and 2005) a week. (B) Mean number (x ± SD) of brood sacs produced by colonies in the field (2002–2005).

Table 1. Phoresy, vectors and composition of multiple phoresy group of *Paratemnoides nidificator* in a study conduced in the Cerrado biome, central Brazil. Observations in parentheses indicate multiple phoresy, and without parentheses, single phoresy. The asterisk indicates several number of combinations.

Taxonomic group	Number of occurrences	Events of single phoresy	Composition of groups of multiple phoresy	Mean size (mm)
Heteroptera				
Coreidae sp.1	2	1♀, 1♂	–	8.90
Coriscidae sp.1	2	–	(3♂), (1♀)	11.05
Pentatomidae sp.1	1	–	(2♀, 3♂)	10.30
Pentatomidae sp.3	2	–	(2♀, 1♂), (3♂)	11.25
Pentatomidae sp.5	2	–	(3♀, 2♂), (4♀, 3♂)	9.75
Reduviidae sp.1	2	1♀, 1♀	–	10.30
Coleoptera				
Coccinelidae sp.1	3	1♂, 1♂	(1♀, 1♂)	6.20
Crysomelidae sp.1	2	–	(2♀, 1♂), (3♀1, ♂)	6.75
Crysomelidae sp.3	2	–	(1♀, 3♂), (1♀, 1♂)	6.25
Crysomelidae sp.5	1	–	(2♀)	5.60
Family 2	2	1♀, 1♀	–	13.40
Neuroptera				
Chrysopidae sp.1	18	*	*	8.30
Dermaptera				
Family 1	6	1♀, 1♀, 1♂, 1♂	(1♀, 2♂), (2♂)	10.45
Opiliones				
Discocyrtus oliveroi	2	–	(1♀, 2♂), (3♂)	7.45

Accordingly, we identified a large number of different arthropods acting as vectors for *P. nidificator* both in the field and in the laboratory. The specific or opportunistic nature of the association between the phoretic and the vector in pseudoscorpions has not been clearly defined due to lack of information, thus not allowing a firm and final conclusion. Our data suggested casual associations in *P. nidificator*, but did not enable us to confirm or reject specific relations. Conclusively, we can point out that the number of individuals in a colony enhances phoresy attempts, independently of the vector size or of the number of successfully attached pseudoscorpions.

Colonies of *P. nidificator* presented a new way of dispersion besides phoresy, i.e., colony fission, which is common in social spiders (Lubin and Robinson, 1982; Rayor and Uetz, 1990; Avilés, 1997). Phoresy and colony fission are solutions to the same problem, however, they can present different results, and the efficiency of each one remains to be tested. We suggest that fission can represent a more secure and very useful way to occupy new sites at short distances. This option is more secure because the individuals disperse in groups, but in a furtive way through the crevices of the tree bark, with the additional benefit of being able to change host trees across branches and avoiding the ground. However, it limits the distance of dispersion which, when using vectors, can be of hundreds of meters. An additional problem is that fission increases the chances of inbreeding (see Avilés, 1997; Keller and Waller, 2002; Bilde et al., 2005). Alternatively, the major problem in phoresy is that the arachnids may have little time to attach strongly to the legs of the vector, they have no input into the decision concerning destination, and the vector may disperse individuals of only one sex, which reduces the chances of success in founding a new colony, especially if they disperse only males or virgin females. An advantage of phoresy, in addition to wide-ranging dispersion, is that the vector, once dead, can be promptly consumed by the pseudoscorpions, an outcome that occurred in all of our field and laboratory observations. However, according to Zeh and Zeh (1992), there is no evidence that phoretic behavior could have evolved from failure to capture prey. Vectors reported in the literature are generally large animals that can hardly be attacked and killed by a few or a single pseudoscorpion (Piomar et al., 1998).

Our study is the first broad investigation of the natural history of a social species of pseudoscorpion, encompassing several years of study, and involving distinct and general aspects of the animal's biology. We believe that this type of basic information, using both naturalistic and experimental data, will allow the elaboration of more accurate hypotheses about the evolution of permanent social behavior in arachnids.

Acknowledgements

We thank Regina H. F. Macedo for her critical review of the manuscript and English. We also thank Ingi Agnarsson and an anonymous reviewer for suggestions on the manuscript. K. Del-Claro thanks CNPq and Fapemig for a research grant and financial support. E. Tizo-Pedroso thanks CNPq for a graduate fellowship.

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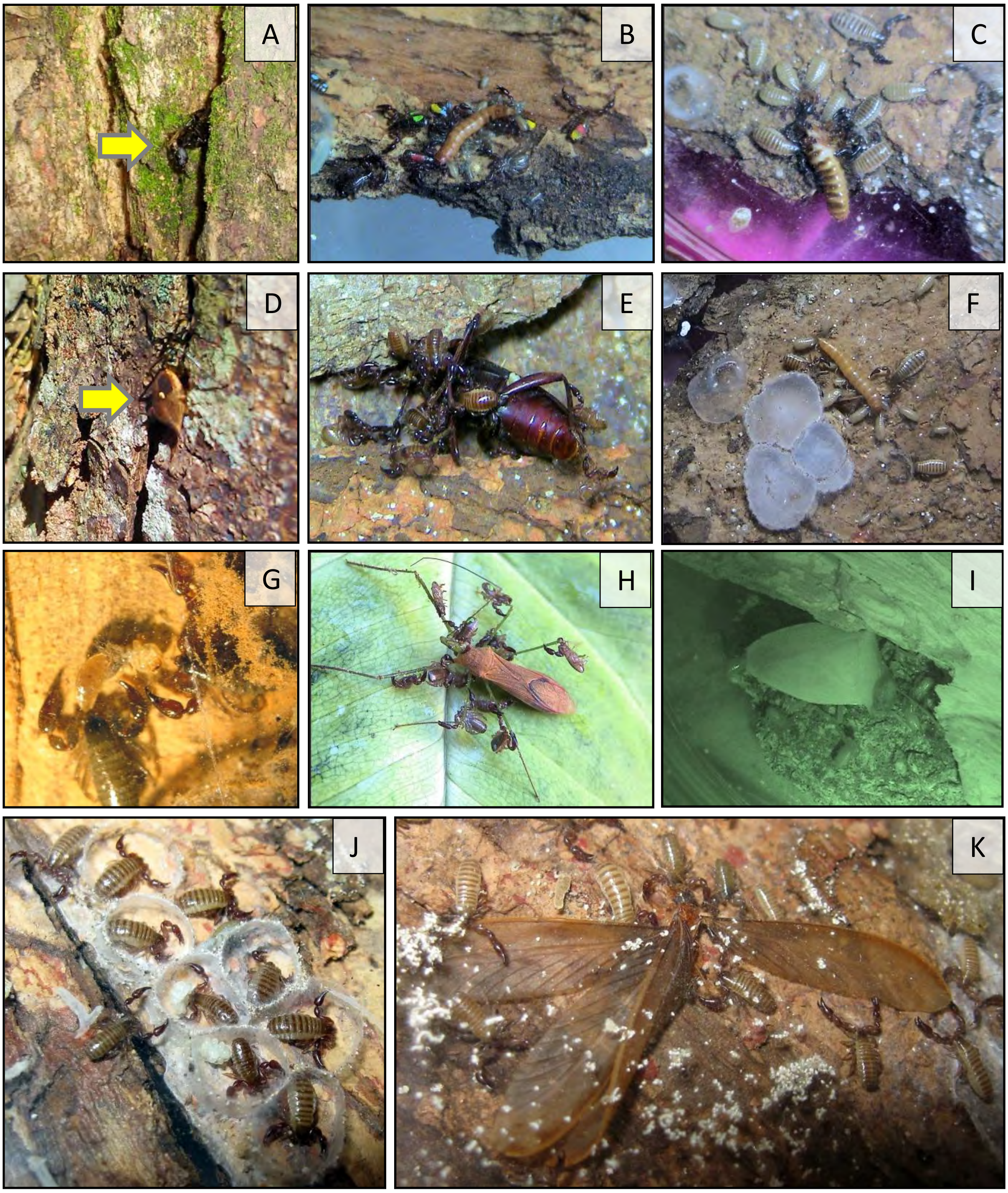
Appendix 1. Records of field and laboratory successfully captured preys by colonies of *Paratemnoides nidificator*. (†=unidentified family; a=mean size calculated in cases of three or more occurrences of the prey).

Prey taxonomic group identity	Number of observation in laboratory	Number of observation in field	Mean size (mm) ±SD^a
Heteroptera			
Coreidae 3 spp.	5	8	9.03±2.36
Corimelaenidae sp.1	3	1	8.05±1.23
Coriscidae sp.1	2		11.45
Enicocephalidae sp.1	1	1	9.55
Pentatomidae 5 spp.	12	6	10.84±3.38
Pyrrhocoridae sp.1	2	1	5.00±0.76
Reduviidae 2 spp.	3	1	10.5±1.27
Family 1	1		4.00
Coleoptera			
Anobiidae sp.1	10		2.10±0.52
Bruchidae			
Acanthodcelides obtectus	10		3.10±1.12
Zabrotes subfaciatus	10		2.35±1.03
Coccinelidae sp.1 adult	2	14	4.85±1.78
Coccinelidae sp.1 larvae	1	10	6.35±1.58
Cucujidae sp.1	2		3.75
Chrysomelidae 5 spp.	8	6	6.69±1.18
Meloidae 2 spp.	2	3	10.95±1.94
Mycetophagidae sp.1	1	2	4.60±2.03
Scarabeidae 3 spp.	11		13.55±1,35
Tenebrionidae 2 spp. adult	22		6.10±0.95
Tenebrionidae 2 spp. larvae	21		9.50±1.03
Family 1	1		11.53
Family 2	2		13.40
Family 3	2		6.35
Hymenoptera			
Formicidae			
Acromyrmex sp.1	15	12	8.35±1.34
Camponotus 3 spp.	15	13	4.92±1.98
Chephalotes sp.1	10	6	3.60±0.63
Pseudomyrmex sp.1	3	2	5.60±0.96
Pachycondyla sp1	1	3	13.65±1.16
Evaniidae sp.1	1		7.10
Family 1	1		11.90
Isoptera			
Armitermes 2 spp.	42		3.75±1.91
Diptera			
Muscidae sp.1	1	4	11.35±1.76
Musca domestica	2		5.25
Neuroptera			
Chrysopidae sp.1	15		8.55±1.31
Hemiptera			
Membracidae sp.1	2	6	1.00±0.98
Cicadellidae	1	7	8.70±1.06
Dermaptera			
Family 1	10	6	10.60±1.67
Lepidoptera			
Family 1	1	2	3.75±0.89
Opiliones			
Discocyrtus oliveroi	3		7.65±2.39
Araneae			
Salticidae sp.1	2	4	5.85±1.54
Diplopoda			
Family 1	1	5	17.65±1.26
Crustacea			
Isopoda			
Family 1	3	8	6.40±0.46

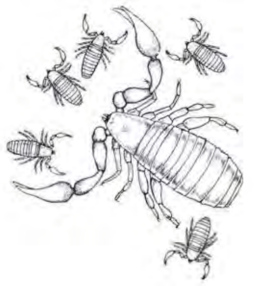


Prancha 3. (A) Operária da formiga *Pachycondyla vilosa* capturada por adultos de *P. nidificator*. O abdome e as pernas da formiga foram puxados para baixo da casca; (B) Ilustração do método de observação do comportamento de predação dos pseudoescorpiões. Na foto, indivíduos adultos marcados atacam uma larva de *Palembus dermestoides* (Coleoptera: Tenebrionidae); (C) Jovens e adultos de *P. nidificator* se alimentam um indivíduo reprodutivo de Isoptera; (D) Imagem de um Hemiptera Pentatomidae sendo atacado por uma colônia de pseudoescorpiões. O percevejo está preso nas frestas da casca de sibipiruna; (E); Adultos de *P. nidificator* atacando cooperativamente um besouro Carabidae. (F) Comportamento parental cooperativo: fêmeas de *P. nidificator* capturaram coletivamente uma larva de *P. dermestoides*, a transportaram para a colônia e ofereceram como alimento aos filhotes; (G) Dois pseudoescorpiões adultos compartilham um operário do cupim *Armithermes* sp.; (H) Comportamento de dispersão coletiva, a forésia múltipla, em um Hemiptera: Reduviidae; (I) Imagem noturna de um ataque cooperativo a um percevejo adulto (Hemiptera: Pentatomidae); (J) Detalhes de uma colônia reprodutiva de *P. nidificator*. As fêmeas estão construindo suas câmaras de seda enquanto cuidam das bolsas incubadoras. Os machos permanecem do lado externo as câmaras; (K) Adultos de *P. nidificator* capturando um indivíduo alado de Isoptera.

CAPÍTULO 2

IS THERE DIVISION OF LABOR IN COOPERATIVE PSEUDOSCORPIONS? AN ANALYSIS ON THE BEHAVIORAL REPERTOIRE OF A TROPICAL SPECIES

(Ethology, 2011)



ethology international journal of behavioural biology

Ethology

Is There Division of Labor in Cooperative Pseudoscorpions? An Analysis of the Behavioral Repertoire of a Tropical Species

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Received: March 23, 2010
Initial acceptance: June 24, 2010
Final acceptance: March 10, 2011
(D. Zeh)

doi: 10.1111/j.1439-0310.2011.01906.x

Abstract

Division of labor is a strategy that maximizes the foraging and reproductive success of eusocial insects. Although some arachnids exhibit colony structure and social organization similar to that of hymenopterans, temporal polyethism has only been demonstrated in few species. The social organization of cooperative pseudoscorpions *Paratemnoides nidificator* is similar to that of social spiders, but it involves a clear division of labor. Work allocation was experimentally investigated in colonies composed of only one developmental stage (young or adults) or by one sex (males or females), through laboratory manipulation. During 44 h of observation, more than 14 000 behavioral repetitions were quantified, distributed in 95 different types of behavioral acts, and grouped in 10 behavioral categories. The results showed that reproductive colonies of *P. nidificator* are maintained by gender- and age-based activities. Males and non-reproductive females performed the external cleaning of the colony and prey capture. Reproductive females take care of the juveniles and build reproductive silk chambers. Nymphs build most of the molt chambers and perform internal cleaning. In the absence of nymphs, male colonies survived 1–2 mo, while female colonies survived 3–4 mo. In nymph colonies, work is readjusted so that all maintenance tasks are executed. This is the first study clearly demonstrating division of tasks in arachnids. It suggests that specialization is an adaptative and evolutionarily old trait in this species. Unlike cooperative spiders, *P. nidificator* possesses physiological (e.g. reproduction, ecdysis, lifespan) and behavioral (e.g. behavioral synchrony or self-organization) characteristics that allow task specialization.

Introduction

Division of labor is defined as a repeatable pattern of activity variation among workers in a group-living population (Beshers & Fewell 2001). Division of tasks based on different morphological castes on age and/or sex is well known among insects (Oster & Wilson 1978). Its main advantage is more efficient foraging and resource exploitation (Wilson 1971; Beshers & Fewell 2001). Although division of labor is well studied in Hymenoptera and termites (Gordon 1996; Franks et al. 1997; Robson & Beshers 1997; Traniello & Rosengaus 1997), there is little information on this phenomenon in other arthropods.

The most complex forms of sociality in arachnids are observed in cooperative social spiders and pseudoscorpions. These species exhibit cooperative prey capture and food sharing, cooperative nest and/or capture web building, overlapping generations, and cooperative parental care (D'Andrea 1987; Avilés 1997; Uetz & Hieber 1997; Lubin & Bilde 2007). No published studies have provided compelling evidence

that division of labor occurs in social spiders (Lubin & Robinson 1982; Avilés 1993, 1997; Lubin 1995; Ainsworth et al. 2002; Avilés et al. 2006), although social spiders do exhibit some behavioral and ecological traits similar to those found in social insects (D'Andrea 1987; Avilés 1997). Despite the lack of empirical data on morphological castes, some cooperative spiders display behavioral differences in task allocation according to sex and age. Young or adult females can participate with greater or lesser intensity in such colony activities as prey capture, building nests and/or cobweb maintenance (behavioral attributes defined as task specialization) (Avilés 1993, 1997; Lubin 1995; Evans 2000; Lubin & Bilde 2007). According to Lubin (1995), several factors, such as inbreeding, which reduces the spread of rare alleles determining extreme reproductive altruism, may have acted to constrain the evolution of task specialization in arachnids.

A level of social organization very similar to that of social spiders has been observed in two pseudoscorpion species of the genus *Paratemnoides*. This rare form of sociality among pseudoscorpions involves cooperative prey capture and food sharing, cooperative nest building, cooperative parental care and matriphagy, and collective dispersal through phoresy or colony fission (Brach 1978; Zeh & Zeh 1990; Hahn & Matthiesen 1993a,b; Tizo-Pedroso & Del-Claro 2005, 2007). In this study, we investigated whether division of labor could be a factor favoring colonial existence in *Paratemnoides*. Specifically, we evaluated the hypothesis that the social structure of the cooperative pseudoscorpion *Paratemnoides nidificator* (Balzan, 1888) (Pseudoscorpiones, Atemnidae) is maintained by task specialization.

Methods

Study Species, Collection, and Maintenance

Paratemnoides nidificator lives under the bark of Neotropical trees, particularly *Caesalpinia pelthophoroides* (Caesalpinaceae). Between Oct. 2003 and Oct. 2007, 35 colonies were collected around Uberlândia, State of Minas Gerais, Brazil. Colonies varied in size from five to 170 individuals and in total included more than 700 pseudoscorpions. The colonies were transported to laboratory and each one was housed in a separate Petri dish (experimental colonies). These containers were covered with red cellophane to reduce the stress caused by light. Each box also received the bark fragment from the colony collection site. The pseudoscorpions were fed in captivity every 3 d with termites (*Armithermes* sp.) and beetle larvae (*Palembus dermestoides*; Tenebrionidae).

Behavioral Repertoire and Activity Schedule

A behavioral repertoire is a detailed description of all the behavioral characteristics of one species (Lehner 1996). To describe the repertoire of *P. nidificator*, one large colony (94 individuals: 30 adults, 18 tritonymphs, 12 deutonymphs, and 34 protonymphs) was housed in a Petri dish (25 cm in diameter, 3 cm high). Observation and quantification were performed under a stereomicroscope, following the 'all occurrence sampling' method, *ad libitum* (Altmann 1974), in 40-min sessions separated by 15-min intervals. The pseudoscorpions were first submitted to 10 h of qualitative observations to describe their behavioral acts and categories. Then, 42 quantitative observation sessions, totaling 28 h, were performed to describe the entire repertoire. After that time, the nymphs had totally covered the silk chambers with silk, hiding the animals, which impeded further quantitative data collection.

The number of models to assess whether a behavioral repertoire documented in laboratory conditions includes most behaviors that could be observed in nature is limited. One of them is the 'sample coverage' analysis, which verifies the likelihood that next behavioral act in a repertoire is a new behavior (Fagen & Goldman 1977; Lehner 1996). The 'sample coverage' is calculated through the expression: $\theta = 1 - \left(\frac{N_1}{i}\right)$, in which N_1 is the number of behaviors observed only once, and i is the number of total behavioral acts observed. When θ is close to 1, the probability that the next behavioral act will be a new behavior is relatively low. The repertoire can be considered virtually complete when θ ranges between 0.90 and 0.99.

A very recent model, adapted from the species richness accumulation curve, was proposed by Dias et al. (2009) as an alternative to evaluate the behavioral repertoire by contrast with the expected values yielded by Clench equation (see Soberón & Llorente 1993). Here, we generated the behavioral curve according to Dias et al. (2009) and compared it with sample coverage analysis (Lehner 1996).

The activity schedule of *P. nidificator* (foraging period preference) was also determined by counting the number of animals moving (engaging in any kind of movement lasting at least 2 min) or at rest during 10 min every 2 h, throughout 48 h first in the wet season (April–Sept.), then in the dry season (Oct.–Mar.), to verify differences in behaviors frequency in relation to seasons.

Table 1: Behavioral repertoire of *Paratemnoides nidificator* described from 34 h of observation of one reproductive colony with 94 individuals (30 adults, 18 tritonymphs, 12 deutonymphs, and 34 protonymphs) maintained in laboratory. Details of each behavioral type compounding the behavioral categories can be found in Table S1

Behavioral categories	Adults (%) (n = 30)	Tritonymphs (%) (n = 18)	Deutonymphs (%) (n = 12)	Protonymphs (%) (n = 34)	Number of distinct behavioral acts in category
1 – Self-grooming	4.27	2.54	1.50	0.69	4
2 – Social interaction and communication	9.43	3.21	2.88	4.10	36
3 – Forage	7.76	7.86	6.61	5.10	18
4 – Parental care	7.74	0	0	0	13
5 – Exploratory	11.40	7.02	12.30	9.71	8
6 – Rest and immobility	58.10	71.80	56.20	65.30	5
7 – Silk chamber building	0	7.17	19.90	13.70	4
8 – Defense	0.24	0.09	0.15	0	1
9 – Matriphagy	0	0	0.27	1.09	1
10 – Other	0.96	0.35	0.20	0.24	5
Total	100	100	100	100	95
Number of distinct behavioral acts of each age	81	60	42	44	–
Sample coverage (θ)	0.9986	0.9977	0.9946	0.9992	–

Division of Labor and Activity Patterns

To examine task distribution among colony individuals, the pseudoscorpions were divided into four experimental groups, with eight replications each, thus comprising 32 colonies manipulated to contain a specific set of individuals: Control – non-manipulated colonies composed by individuals of all ages and sexes; Male only – colonies composed only of adult males; Nymph only – colonies composed only of nymphs; and Female only – colonies composed only of adult females. Each experimental group was maintained in 10-cm-diameter Petri dishes containing one bark fragment and 7–10 individuals. Despite the fact that experimental colonies had a small number of individuals relative to the colony assayed for behavioral repertoire analysis, it is common to find in the field colonies of 5–10 individuals, with all ages and sex represented. These small colonies in field conditions behave typically like a colony in initial phase of establishment. Under laboratory conditions, small colonies enable more accurate observation of behaviors.

The colonies were kept in the laboratory for 3 wks, time enough for the pseudoscorpions to build their silk chambers. After this time, each colony was observed during 10 h, following the 'all occurrence samples' method (Altmann 1974). These 10 h of observation were divided into sessions of 30 min. Observations were carried out in a maximum period of 3 mo in each colony, totaling 80 h for each treatment. The behaviors observed were classified into new groups of tasks that were behaviors related to colony maintenance, i.e. behaviors directly related to the basic tasks of colony maintenance such as cleaning, prey capture, building of silken chambers, and parental care. The frequencies of each of these tasks were quantified for each experimental colony, and a flowchart was developed from the mean values of task performance (behavioral sequences) for each treatment. The mean values of task performance were compared using a G test to assess possible treatment effects on maintenance tasks.

Results

Activity Schedule and Behavioral Repertoire

The 14 431 behavioral repetitions for all the developmental stages (protonymphs, deutonymphs, tritonymphs, and adults) yielded a behavioral repertoire of the reproductive colony of *P. nidificator* comprising 95 distinct behavioral acts, classified into 10 behavioral categories, (Table 1). The most diversified category was communication with 36 different behaviors based on large variation of pedipalps vibration (see fully detailed repertoire in Table S1).

The animals exhibited foraging activities throughout the day, with a small increase between 21:00 and 03:00 h in both the dry and wet seasons (Fig. 1). Each developmental stage performed a different number of behavioral acts: adults were the most active group, followed by tritonymphs, deutonymphs, and protonymphs, respectively. The sample coverage values were all close to the maximum expected (Table 1). Clench's equation fitted to the original data

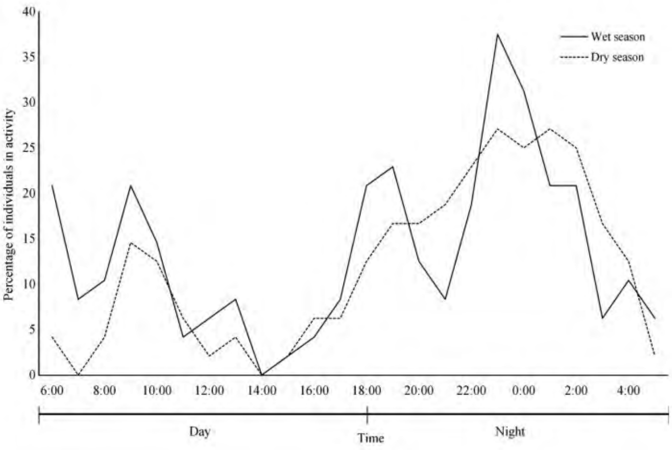

Fig. 1: Activity schedule of reproductive colonies of *Paratemnoides nidificator*. The *y*-axis indicates the percentage of individuals performing behaviors lasting more than 2 min. The solid line indicates wet season observations and the dotted line dry season observations.

distribution pattern yielded an $r^2 = 0.998$, $a = 21.847$, and $b = 0.206$. The total behavioral acts recorded fitted 89% of the estimated behaviors; the behavioral estimation was 106 behavioral acts and would require 43 observation sessions to reach 90% of the estimated behaviors. The frequencies of each behavioral category for the juvenile and adults were organized in Table S1.

Division of Labor in Reproductive Colonies

Males and non-reproductive females (young or old females, inseminated or not, but for some reason did not reproduce) execute similar tasks, mainly prey capture and external silk chamber maintenance (debris removal) (Fig. 2a). Males and non-reproductive females also provide direct and indirect parental care by allowing immatures to feed on their prey or by directly offering food to nymphs. Reproductive females engage in parental care and provide protection (against natural enemies), nursing, and food to their brood. Reproductive females also contribute to colony physical growth by building new reproductive chambers, which might later serve as communal chambers, but this production is smaller than that of nymphs (around 35% of the colony chambers). Because the young individuals build most of the colony chambers, they are mainly responsible for the physical expansion of the colony. They also cooperate to internally maintain the nest by removing exuvia and prey remains (Fig. 2a). Tritonymphs rarely contribute to prey capture. Details of tasks performance and its mean values in each experimental age and gender groups can be found in Tables S2 and S3.

Experimental Colonies and Task Organization

Experimental colonies behaved differently from the control colonies. There was a highly significant treatment effect on task performance ($G = 201.57$; df = 12; $p < 0.0001$). Non-control colonies lacked some maintenance behaviors. In the Male-only colonies, the animals were unable to build or clean chambers. Thus, pre-existing chambers (built by nymphs) were littered with feces and prey carrion, facilitating the proliferation of fungi (Fig. 2b). Male-only colonies only survived 2 mo (67 ± 33 d, n = 8). In Female-only colonies, few silk chambers were constructed (2 ± 1, n = 8). Only previously inseminated females were able to build chambers, but only to shelter their embryos and nymphs. Colony stability was only reached after protonymphs emerged (Fig. 2c). Adult females did not perform nest maintenance behaviors, and Female-only colonies survived an average of 3 mo (92 ± 38 d, n = 8).

By contrast, Nymph-only colonies performed all the maintenance behaviors observed in normal reproductive colonies, but with some differences. They exhibited activity adjustments and assumed functions that they do not normally perform; they captured prey cooperatively, built silk chambers, and engaged in both forms of debris removal (inside and outside of chambers) (Fig. 2d).

Discussion

The hypothesis that *P. nidificator* colonies display division of labor and that the colonies are organized through an age-based system of labor division was confirmed by this study. This pseudoscorpion has

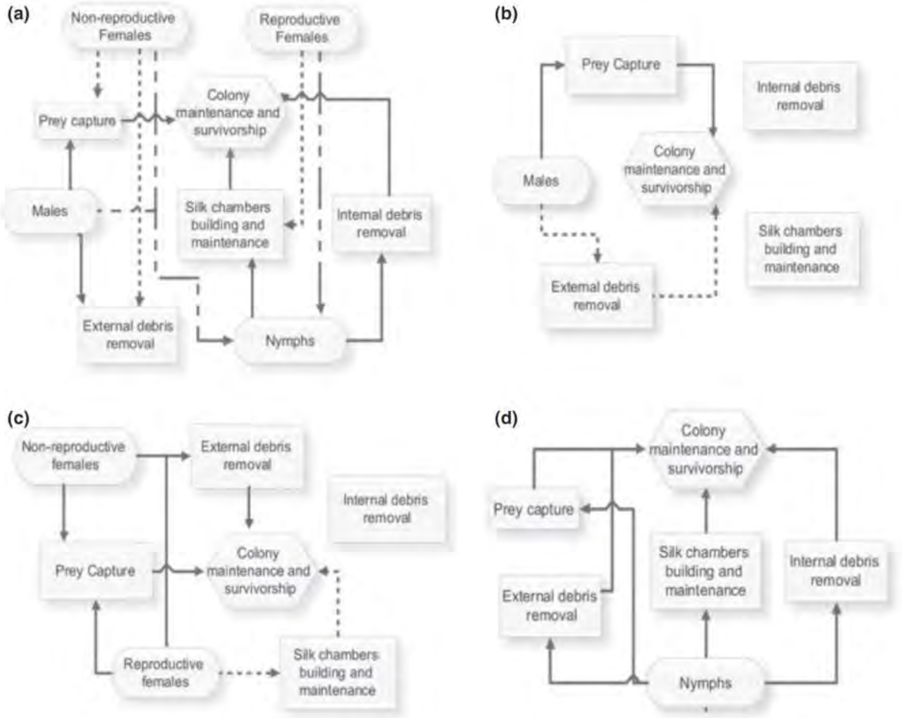

Fig. 2: (a) Division of labor in reproductive colonies of *Paratemnoides nidificator*. The rounded rectangles represent sexes or developmental stage. Rectangles indicate tasks essential to colony maintenance and survivorship. Solid lines represent tasks performed by a sex or age class, and dotted lines indicate tasks occasionally performed by a sex or age class (see mean values of maintenance tasks performance in Table S3). The central hexagon represents the ultimate colony stability attribute supported by the essential maintenance tasks. We defined colony stability as the function of all essential tasks to maintenance of individuals' behaviors and colony survivorship. It was pointed out with five attributes: parental care, prey capture, silk chamber building, internal debris removal, and external debris removal. (b) Task performance in colonies composed only by males. Males are unable to build silk chamber and do not carry out chamber cleaning. (c) Task performance in colonies composed only by females. Females build reproductive chambers but not the communal rest chambers; they also lack chamber cleaning behaviors. (d) Task organization in nymph colonies. Nymphs show very plastic behaviors and rapidly readjust their behaviors to substitute for the essential maintenance behaviors executed by adults. Nymph colonies have lower extinction rates.

one of the most elaborate behavioral repertoires known among social invertebrates, and our study provides the first clear evidence of division of labor in arachnids. The observation of division of labor in *P. nidificator* provides new information not only on the Pseudoscorpiones order, but also on sociality in arachnids. The analysis of the behavioral repertoire revealed that *P. nidificator* has a very complex behavioral structure. It was expected that the diversity of behavioral acts would be related to the species social complexity (Lehner 1996). Among South American arachnids, behavioral repertoire studies in species of Opiliones and Scorpiones also revealed the occurrence of some degree of sociality. Scorpions *Tityus serrulatus* Lutz & Mello, 1922 (Buthidae) constitute larger aggregations, but have a lower social relation and a poorly diversified behavioral repertoire (Mineo et al. 2003). The gregarious harvestmen *Discocyrtus oliverioi* (Gonyleptidae) and *Mischonyx cuspidatus* (=*Ilhaia cuspidata*) (Gonyleptidae) constitute groupings with richer repertoires and more extensive social relationships (Elpino-Campos et al. 2001; Pereira et al. 2004). The social amblypygi *Damon diadema* have a more complex social organization than scorpions, harvestmen, and several other spiders (Walsh & Rayor 2008). In relation to these species, *P. nidificator* had a more diversified repertoire, especially with regard to the number of behavioral acts related to social interactions.

The sample coverage analysis confirms that the behavioral repertoire of *P. nidificator*, in all its development stages, can be considered complete. The analysis based on the behavioral accumulation curve corroborated these results. According to the model by Dias et al. (2009), the asymptote was not reached and the estimated value was slightly higher. The final analysis indicated that 89% of the estimated behavioral acts were observed, which allows us to consider the repertoire as nearly complete.

Pedipalp Signaling as Communication Behavior

In his classic study of pseudoscorpion biology, Weygoldt (1969: 25) postulated 'It seems probable, therefore, that they have some behavioral device by which they recognize each other or, more scientifically expressed, by which the predatory aggression is suppressed in members of the same species.' In fact, the pedipalps have some communication function. Previous research has established that body, leg, and mainly pedipalp vibrations function in courtship and in mediating aggressive interactions among adults (Weygoldt 1969; Zeh & Zeh 1997; Andrade & Gnaspini 2003). Communication behavior based on pedipalp vibrations was the most diversified behavioral category exhibited by *P. nidificator* (Table 1 and Table S1), possibly with purposes other than courtship and reproduction. For example, the signaling among nymphs could be related to non-aggressive contests for access to food.

Division of Labor in Spiders

Division of labor is well studied in eusocial insects (Wilson 1971; Hölldobler & Wilson 1990; Beshers & Fewell 2001), but has not previously been unambiguously demonstrated in social arachnids. In Araneae, task specialization appears not to occur, and all colony members are able to perform the tasks needed for colony maintenance (Whitehouse & Lubin 2005). D'Andrea (1987) suggested that the social complexity of some spider species would provide the conditions required for the evolution of task specialization. Studying *Achaearanea wau* (Theridiidae), Lubin (1995) did not observe evidence of division of labor, and Ainsworth et al. (2002) did not find differences in prey capture behavior of *Stegodyphus mimosarum* (Stegodyphus) in relation to the size of the spiders. Evans (2000) obtained suggestive evidence for division of labor showing that subadult males of *Diaea ergandros* (Eresidae) contributed to the building of capture webs.

Although division of labor is not very clear in spiders, evidence of task partitioning exists. For example, in the cooperative spider, *Anelosimus eximius* (Theridiidae), competition for food can result in reproductive and non-reproductive females in the same nest. Several authors have reported that tasks that involve more risks and performance outside the nest are preferentially executed by adult females (e.g. foraging), while juveniles usually repair webs, a less vulnerable activity (Christenson 1984; Avilés 1993; Lubin 1995).

According to Lubin (1995), inbreeding would be a factor restricting the evolution of division of labor. Endogamic reproduction, as occurs in cooperative spiders, would favor low genetic variation and contribute to homozygosity, limiting the expression of genes for extreme altruism that would only be expected to occur in heterozygotes (Michod 1980, 1993; Lubin 1995). Beside these reproductive and genetic constraints, task specialization could diminish individual reproductive success in cooperative spiders (Lubin 1995).

In spider colonies, all females are totipotent. However, there are traces of reproductive asymmetry that could result in reproductive skew (Rypstra 1993; Gonzaga & Vasconcellos-Neto 2002; Whitehouse & Lubin 2005; Avilés et al. 2006). Thus, the absence of division of labor can result from the selection for a 'strategy of colony growth' and not for specialization in work. Division of labor would reduce the number of reproductive females and consequently the foundation of new colonies (Avilés 1993; Lubin 1995).

Division of Labor in *Paratemnoides nidificator*

Communication and individual recruitment are key elements for the division of tasks among social hymenopterans (Wilson 1971; Beshers & Fewell 2001). Our findings demonstrated a great diversity of communicative behaviors, but do not clarify how communications mediate the division of labor. However, tasks do not appear to be regulated by recruitment mechanisms. Rather, the synchrony among individuals, without clear communication during tasks, suggests that work can be regulated by self-organization. In other words, similar traits, added to the physiological and behavioral characteristics of the development stage or sex, stimulate similar behavioral responses (Hemelrijk 2002a,b). Although communication behaviors have been the most frequent and diversified ones, they possibly are not related to the division of tasks.

There are some similarities and differences between the task distribution of *P. nidificator* and that of social spiders. In the case of *Aebutina binotata*, there is also an asymmetrical performance of colony tasks (Avilés 1993). Nymphs also perform maintenance tasks more frequently than adults. However, Avilés (1993) did not evidence division of labor among individuals of the same age. By contrast, *P. nidificator* have an elaborate organization with groups of individuals performing group of tasks based on their morphological or physiological limitations. The reallocation of tasks by nymphs, when no adults are present, reinforces both the adaptative importance of this organization and nymph behavioral plasticity, allowing colony survival.

Our findings show that the behavioral flexibility of *P. nidificator* nymphs is an important attribute in colony maintenance and stability. However, we still need to explain what mechanisms cause the behavioral restrictions or stimulate the changes in task performance by nymphs. The role of juveniles in colony work and their capability to adjust task in absence of a caste also occurs in termites. In experimental colonies of lower termite *Reticulitermes fukienensis* (Rhinotermitidae), in absence of large workers, medium-sized workers adjusted their behaviors to perform tasks mainly performed by large workers (Crosland & Traniello 1997). In the absence of workers, nymphs of *Coptotermes formosanus* (Rhinotermitidae) are capable of feeding and surviving by themselves, despite the existence of soldiers specialized for feeding (Crosland & Su 2006). In social Hymenoptera, age polyethism is common and early instars have morphological and physiological characteristics that predispose them to carry out colony tasks not performed by adults (Wilson 1971; Robinson 1992). Similar to termites (Noirot & Pasteels 1987), pseudoscorpion nymphs are small version of adults with little morphological limitations to task cooperation. However, the small size of nymphs, shortened palp segments, and body fragility make juveniles less efficient in all tasks compared with adults. Variation in task performance is therefore expected, and we suggest that behavioral flexibility has important consequences for the maintenance of colony cohesion in *Paratemnoides*.

Why do Male *Paratemnoides nidificator* Share Work and Take Care of Brood?

Only exceptionally do males of invertebrate social species participate in colony work. Their sole contribution to the colony is gene transmission (Wilson 1971; Beshers & Fewell 2001; but see also Santos & Del-Claro 2009). Some factors that could limit male work include lower lifespan than females, premating dispersion when they reach adult age, and significant deviation of sex ratio in favor of females.

Isopterans are among the few examples of animals whose male work. In this group, both sexes engage in similar tasks in the colony. The sex ratio in isopteran species is typically close to one (Roisin 2001). Males and females have similar longevity, morphology, and behaviors (Thorne 1997). Males of the wasp *Ropalidia marginata* can contribute to feeding nestlings in the period of colony growth, before dispersion, but not as efficiently as females (Sen & Gadagkar 2006). Among spiders, young males of *Diaea* sp. can help weave the web that shelters the colony (Evans 2000).

Paternal care is also uncommon among invertebrates and is generally correlated with paternity assurance (Zeh & Smith 1985). Males providing care could increase their chances of being selected by females and their paternity rates (Queller 1997; Whittingham & Dunn 1998; Kvarnemo 2005). Among arachnids, parental care is more frequent and best understood in harvestmen (Machado et al. 2004; Requena et al. 2009). However, several factors could favor the evolution of parental care and the division of labor in *P. nidificator*. Among them are a close to one sex ratio (2♂/3♀); equal male and female life expectancy (approximately 3 yrs of adult life); similar body size in males and females; and ability of both sexes to produce poison, enabling males to be nearly as successful as females in hunting, defending, and maintaining the colony, and dispersion of both sexes is very limited and males can remain in the mother colony during their entire life (Tizo-Pedroso & Del-Claro 2007; Del-Claro & Tizo-Pedroso 2009). All these features constitute a complex system in which each characteristic interacts with the others to offer favorable conditions for the development of a division of labor that includes males making a significant contribution to colony maintenance (Fig. 3).

The same factors that have favored the evolution of male work could also favor the development of male brood care. Paternity uncertainty does not seem to be a fundamental requirement in the evolution of paternal care in this system, because the colonies have restricted flux of individuals among them. Thus, high relatedness among males and between males and nymphs in a colony is likely. Therefore, males can obtain indirect fitness benefits by taking care of related nymphs. The participation of males in colony work and cooperative parental care appears to be a strategy to organize and maximize colony productivity. As a consequence,

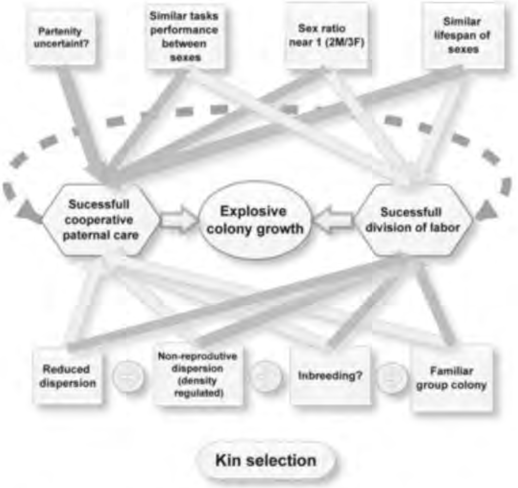

Fig. 3: Schematic view of the interactive direct and indirect factors that appear to be fundamental to the maintenance of male work and paternal care, all related to the increase in colony size and production of new propagules.

reproductive females can concentrate their effort on reproductive activities, which increases colony growth and originates new propagules to disperse and found new colonies.

Acknowledgements

We thank Ana Paula Marques Costa for her help with repertoire observation and animal maintenance. We also thank M. Yamamoto, J. Byk, S. Augusto, S. Powell, P. S. Oliveira, and an anonymous referee for their suggestions and comments on the early version of the manuscript. We thank to D. W. Zeh and L. S. Rayor for extensive English review, criticism, and suggestions in the three final versions of the manuscript. K. Del-Claro thanks CNPq/FAPEMIG for research grant and E. Tizo-Pedroso thanks FAPEMIG for granting him a scholarship.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Behavioral repertoire of *Paratemnoides nidificator* (Pseudoscorpiones, Atemnidae), based on 34 h of observations of a colony with 94 individuals (30 adults, 18 tritonymphs, 12 deutonymphs and 34 protonymphs) maintained in captivity.

Table S2. Mean value of maintenance tasks performance in experimental colonies of *Paratemnoides nidificator*.

Table S3. Mean value of maintenance tasks performance in experimental colonies of *Paratemnoides nidificator* in activities of age and gender division of labor. The abbreviations indicate respectively: (M) males; (RF) reproductive females; (nRF) non-reproductive females; (N) nymphs.

Table 2. Mean value of maintenance tasks performance in experimental colonies of *Paratemnoides nidificator*.

Maintenance tasks	Control colonies (n=8)	Male colonies (n=8)	Female colonies (n=8)	Nymphs colonies (n=8)	Task description
1– Prey capture	23	27	63	53	Basic foraging activities, involving single or cooperative location and subdue of prey
2 – Internal debris removal	18	23	37	26	Behaviors related to maintenance of silk chambers, i.e. transport of exuvia and prey remains that are inside silk chamber to outside of it.
3 – External debris removal	15	18	0	0	Removal of exuvia and prey remains that were left outside of silk chambers. Individuals actively transporting it away from the nests and drop it out of bark fragments.
4 – Parental care	27	0	0	0	Involving all direct and indirect behaviors related to nymphs care, i.e. defense, food offering and food share.
5 – Silk chamber building	17	32	0	21	Building of essential structures that act as physical limits of colony and important shelter to all individual, especially to nymphs during torpor phase and ecdysis. Chambers are also important to reproduction sheltering the female and it brood sac.
Total	100%	100%	100%	100%	

Table 3. Mean value of maintenance tasks performance in experimental colonies of *Paratemnoides nidificator* in activities of age and gender division of labor. The abbreviations indicate respectively: (M) males; (RF) reproductive females, (nRF) non-reproductive females; (N) nymphs.

Maintenance tasks	Control colonies (n=8)				Male colonies (n=8)	Female colonies (n=8)		Nymphs colonies (n=8)
	M	RF	nRF	N	M	RF	nRF	N
1– Prey capture	69±1.94%	-	31±2.16%	-	60.88±1.81	17±1.44%	36±2.07%	26.00±1.3%
2 – Internal debris removal	-	-	-	100%	-	-	-	21.25±2.25%
3 – External debris removal	75±0.96%	-	25±1.03%	-	39.13±1.81	8±1.87%	17±1.83%	22.38±1.06%
4 – Parental care	10±1.02%	78±1.21%	12±0.98%	-	-	-	-	-
5 – Silk chamber building	-	40±1.67%	-	59±1.32%	-	22±1.69%	-	30.37±1.51%

Supplementary material 1. Behavioral repertoire of *Paratemnoides nidificator* (Pseudoscorpiones, Atemnidae), based on 34 hours of observations of a colony with 94 individuals (30 adults, 18 tritonymphs, 12 deutonymphs and 34 protonymphs) maintained in captivity

	Adults		Tritonymphs		Deutonymphs		Protonymphs	
Behavioral categories	Frequency	Proportion	Frequency	Proportion	Frequency	Proportion	Frequency	Proportion
1-Grooming								
1.1 Grooming pedipalps with the chelicera	238	4.09	83	2.4	20	1.35	19	0.52
1.2 Removing remains of food from the colony	5	0.09	2	0.06	0	0	0	0
1.3Rremoving exuvia from the colony	3	0.05	3	0.09	2	0.15	6	0.17
1.4 Removing dead prey from the colony	2	0.03	0	0	0	0	0	0
Total		4.27		2.54		1.5		0.69
2 – Communication and social interaction								
2.1.1.1 Protonymph touching (--) on abdomen	2	0.03	4	0.12	2	0.15	5	0.15
2.1.1.2 Protonymph touching (--) on pedipalps	8	0.14	6	0.17	5	0.34	13	0.35
2.1.2.1 Deutonymph touching (--) on abdomen	1	0.02	1	0.03	2	0.15	2	0.06
2.1.2.2 Deutonymph touching (--) on pedipalps	2	0.03	2	0.06	4	0.28	3	0.09
2.1.3.1 Tritonymph touching (--) on abdomen	4	0.07	2	0.06	1	0.08	2	0.06
2.1.3.2 Tritonymph touching (--) on pedipalps	12	0.21	13	0.38	2	0.15	7	0.2
2.1.4.1 Adult touching (--) on abdomen	27	0.46	5	0.14	1	0.08	0	0
2.1.4.2 Adult touching (--) on pedipalps	68	1.17	13	0.38	1	0.08	9	0.25
2.2.1 Protonymph performing horizontal vibration signaling with right pedipalp to…	1	0.02	2	0.06	2	0.15	7	0.2
2.2.2 Protonymph performing horizontal vibration signaling with left pedipalp to…	1	0.02	5	0.14	3	0.21	7	0.2
2.2.3 Protonymph performing horizontal opposite vibration signaling with both pedipalps to…	0	0	1	0.03	0	0	8	0.23
2.2.4 Protonymph performing horizontal simultaneous vibration signaling with both pedipalps to…	2	0.03	6	0.17	5	0.35	57	1.55
2.3.1 Deutonymph performing horizontal vibration signaling with right pedipalp to…	0	0	1	0.03	0	0	0	0
2.3.2 Deutonymph performing horizontal vibration signaling with left pedipalp to…	0	0	1	0.03	0	0	0	0
2.3.3 Deutonymph performing horizontal opposite vibration signaling with both pedipalps to…	0	0	1	0.03	0	0	0	0
2.4.1 Tritonymph performing horizontal opposite vibration signaling with both pedipalps to…	0	0	3	0.09	0	0	0	0
2.4.2 Tritonymph performing horizontal simultaneous vibration signaling with both pedipalps to…	0	0	5	0.14	0	0	2	0.06
2.5.1 Adult performing vertical vibration signaling with right pedipalp to…	3	0.05	0	0	0	0	0	0

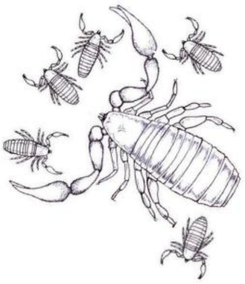
2.5.2 Adult performing vertical vibration signaling with left pedipalp to...	4	0.07	0	0	0	0	1	0.04
2.5.3 Adult performing vertical opposite vibration signaling with both pedipalps to…	2	0.03	0	0	0	0	0	0
2.5.4 Adult performing vertical simultaneous vibration signaling with both pedipalps to…	1	0.02	0	0	0	0	0	0
2.5.5 Adult performing horizontal vibration signaling with right pedipalp to…	116	2	0	0	0	0	0	0
2.5.6 Adult performing horizontal vibration signaling with left pedipalp to…	121	2.08	0	0	0	0	0	0
2.5.7 Adult performing horizontal opposite vibration signaling with both pedipalps to…	49	0.84	0	0	0	0	0	0
2.5.8 Adult performing horizontal simultaneous vibration signaling with both pedipalps to…	19	0.33	0	0	0	0	0	0
2.5.9 Adult aggregate signaling	4	0.07	0	0	0	0	0	0
2.6 Pushing other individuals to pass out	17	0.29	3	0.09	1	0.08	2	0.06
2.7 Move way when touched for other individual	11	0.19	4	0.12	3	0.21	9	0.25
2.8 Individual using one of it pedipalp to grasp one pedipalp of another individual	1	0.02	3	0.09	0	0	0	0
2.9 Individual using one of it pedipalp to grasp one pedipalp f another individual and drag it	2	0.03	0	0	0	0	0	0
2.10 Individual using both pedipalps to grasp one pedipalp of another individual	13	0.22	1	0.03	0	0	0	0
2.11 Individual using both pedipalps to grasp one pedipalp of another individual and drag it	44	0.76	4	0.12	0	0	0	0
2.12 Individual using both pedipalps to grasp both pedipalp of another individual	1	0.02	5	0.14	0	0	0	0
2.13 Individual using both pedipalps to grasp both pedipalp of another individual and drag it	2	0	5	0.14	2	0.15	0	0
2.14 Individuals moving to the individual that performed a vibration	9	0.15	1	0.03	0	0	0	0
2.15 Signaling with both pedipalps while feeding on prey carrion	3	0.05	14	0.4	6	0.42	13	0.35
Total		9.43		3.21		2.88		4.1
3 – Forage								
3.1 – Attack								
3.1.1 individual attacking the prey alone	21	0.36	1	0.03	0	0	0	0
3.1.2 individual attacking the prey in group	77	1.32	12	0.35	5	0.35	3	0.09
3.1. Individual investing quickly against the prey	27	0.46	1	0.03	0	0	0	0
3.1.4 Individual investing slow against the prey	10	0.17	0	0	0	0	0	0
3.1.5 Receiving help to transport the prey	78	1.34	25	0.72	4	0.28	5	0.15

3.1.6 Individual investing against one captured prey	1	0.02	0	0	0	0	0	0
3.1.7 Abandoning the captured prey to attack another prey in movement	2	0.03	1	0.03	1	0.08	0	0
3.1.8 Unsuccessful attack against the prey	7	0.12	1	0.03	0	0	0	0
3.1.9 Abandoning prey in thanatosis	5	0.09	0	0	0	0	0	0
3.2-Feeding								
3.2.1 Feeding on live prey	28	0.48	16	0.46	9	0.62	17	0.46
3.2.2 individuals sucking the preys isolated of the other individuals	5	0.09	9	0.26	0	0	3	0.09
3.2.3 Only adults feeding together	40	0.69	0	0	0	0	0	0
3.2.4 Adults and nymphs sucking the prey together	72	1.24	59	1.7	30	2.03	49	1.33
3.2.5 Only nymphs sucking the prey together	0	0	53	1.53	14	0.95	27	0.73
3.2.6 Individuals feeding pushing the newcomers	5	0.09	2	0.06	0	0	2	0.06
3.2.7 Fighting for the prey	1	0.02	1	0.03	0	0	4	0.12
3.2.8 Individuals moving around the prey	70	1.2	91	2.63	34	2.3	76	2.06
3.2.9 Abandoning the captured prey	2	0.03	0	0	0	0	0	0
Total		7.76		7.86		6.61		5.1
4 – Parental care								
4.1 Female building reproductive silk chamber	179	3.08	0	0	0	0	0	0
4.2 Female occupying an old chamber	5	0.09	0	0	0	0	0	0
4.3 Female excluding conspecific of it new built nest	4	0.07	0	0	0	0	0	0
4.4 Female resting inside the nest	76	1.31	0	0	0	0	0	0
4.5 Female moving inside the nest	19	0.33	0	0	0	0	0	0
4.6 Female touching the nest walls with pedipalps	10	0.17	0	0	0	0	0	0
4.7 Female touching it embryos with pedipalps	84	1.45	0	0	0	0	0	0
4.8 Female touching it protonymphs with pedipalps	29	0.5	0	0	0	0	0	0
4.9 Female transporting wood fragments for interior of the nest	4	0.07	0	0	0	0	0	0
4.10 Female inserting wood fragments in nest walls	4	0.07	0	0	0	0	0	0
4.11 Female resting inside the nest with second instar embryos	4	0.07	0	0	0	0	0	0
4.12 Female resting inside the nest with it protonymphs	29	0.5	0	0	0	0	0	0
4.13 Female excluding cospecific of an old nest	3	0.05	0	0	0	0	0	0
Total		7.74		0		0		0
5 - Exploratory								
5.1 Moving out of the nests	466	8.02	178	5.14	153	10.4	256	6.95
5.2 Moving inside of the nests	25	0.43	21	0.61	19	1.29	88	2.39
5.3 Moving out of the wood fragment	83	1.43	4	0.12	0	0	0	0
5.4 Turn around 180 degrees	27	0.46	19	0.55	2	0.15	4	0.12
5.5 Moving backward	24	0.41	6	0.17	0	0	0	0
5.6 Investigating the prey	10	0.17	5	0.14	3	0.21	4	0.12

5.7 Entering in the nest	18	0.31	7	0.2	2	0.15	2	0.06
5.8 Leaving the nest	11	0.19	3	0.09	2	0.15	2	0.06
Total		11.4		7.02		12.3		9.71
6 - Immobility								
6.1 Resting alone	18	0.31	0	0	0	0	0	0
6.2 Resting on the cotton ball	186	3.2	3	0.09	10	0.68	5	0.15
6.3 Resting inside of the nest	468	8.05	680	19.6	287	19.4	1094	29.7
6.4 Resting out of the nest	2707	46.6	1755	50.7	491	33.2	1273	34.6
6.5 To stay in the torpor state that precedes the ecdysis	0	0	46	1.33	42	2.84	33	0.9
Total								
7 – Weaving molt chamber								
7.1 Nymphs weaving alone	0	0	225	6.5	244	16.5	360	9.78
7.2 Protonymphs silking with	0	0	0	0	0	0	63	1.71
7.3 Deutonymphs silking with	0	0	9	0.26	41	2.78	41	1.11
7.4 Tritonymphs silking with	0	0	14	0.4	9	0.62	40	1.09
Total		0		7.17		19.9		13.7
8 - Defense								
8.1Quick backward due the prey aggressions	14	0.24	3	0.09	2	0.15	0	0
Total		0.24		0.09		0.15		0
9 – Matriphagy								
9.1 Nymphs feeding on the mother body	3	0	0	0	4	0.27	25	1.09
Total		0		0	4	0.27	25	1.09
10 – Other non-classified behaviors								
10.1 Ecdysis	0	0	8	0.23	1	0.07	4	0.12
10.2 Individual rubbing it the abdomen in the wood fragment	34	0.58	0	0	0	0	0	0
10.3 Phoresy attempts	16	0.28	0	0	0	0	0	0
10.4 Individual touching it venter with one a pedipalp	4	0.07	0	0	0	0	0	0
10.5 Individuals practicing cannibalism	2	0.03	4	0.12	2	0.14	4	0.12
Total		0.96		0.35		0.2		0.24
Summation of behavioral repetitions	5812	100	3461	100	1477	100	3681	100

CAPÍTULO 3

PARASITISMO SOCIAL ENTRE OS PSEUDOESCORPIÕES *PARACHERNES MELANOPYGUS* (CHERNETIDAE) E *PARATEMNOIDES NIDIFICATOR* (ATEMNIDAE)



RESUMO

Quando espécies parasitas desenvolvem atributos que as capacitam a invadir e explorar as colônias de espécies sociais, as espécies hospedeiras são forçadas a reagir. A interação estabelecida, denominada parasitismo social, representa uma estratégia antagônica e rara de coevolução. Este modo de vida é melhor conhecido nos parasitas de himenópteros sociais, que se infiltram na colônia hospedeira e exploram seus recursos e também todo seu sistema social. Em 2003 foram descobertas colônias de pseudoescorpiões constituídas por duas espécies, *Paratemnoides nidificator* (Atemnidae) e *Parachernes melanopygus* (Chernetidae). Assim, o presente estudo analisou: (1) o papel ecológico das espécies de pseudoescorpiões em colônias mistas e simples manipuladas em laboratório; (2) se a segunda espécie (*P. melanopygus*) pode ser identificada pelo hospedeiro (*P. nidificator*) como invasora, em um experimento de identificação; (3) se o parasito utiliza camuflagem química para burlar as defesas do hospedeiro, em um novo experimento expondo indivíduos parasitas e hospedeiros a odores de outras colônias por 24h e 48h. Os resultados mostraram que o Chernetidae *Parachernes melanopygus* estabelece uma relação parasitária com seu hospedeiro *Paratemnoides nidificator* (Atemnidae), baseada na exploração do sistema social. A sobrevivência do hospedeiro foi significativamente menor na presença do parasita (53%) do que na sua ausência (85%). Enquanto o parasita obteve maior sobrevivência na presença do hospedeiro (80%), do que em sua ausência (22%). Os experimentos de identificação demonstraram que *P. nidificator* é capaz de identificar com maior frequência os parasitas oriundos de outras colônias (82%), em relação aos parasitas de sua própria colônia (23%). Na segunda etapa do experimento, parasitas expostos a odores da nova colônia hospedeira, durante 24hs, obtiveram menor sucesso na invasão (60%), em relação ao grupo controle (53%). Entretanto, quando expostos à 48hs, os parasitas alcançaram maior sucesso (80%), em relação ao grupo controle (20%). Ao contrário dos modelos de evolução do parasitismo social em himenópteros, a relação parasitária entre pseudoescorpiões não se enquadra no modelo simpátrico de Emery, compondo um cenário evolutivo distinto, agregando estratégias presentes nas formigas parasitas, bem como algumas vistas nas aves parasitas.

INTRODUÇÃO

O parasitismo é reconhecido como uma relação especializada e antagônica, amplamente difundida entre os seres vivos, forte o suficiente para gerar diversidade e extinção (e.g. Thomas et al., 2005). Este tipo de interação baseada na exploração direta da espécie hospedeira, ou de seus recursos, provavelmente constitui o modo de vida mais difundido no planeta (Thompson, 1994), compreendendo enorme variedade de estratégias. Recentemente, duas raras formas de parasitismo têm sido intensamente estudadas como modelos para compreendermos as perspectivas na coevolução entre parasito-hospedeiro: o parasitismo de ninhada e o parasitismo social (Brandt et al., 2005a).

Estas duas formas de parasitismos constituem uma impressionante relação entre parasitos e seus hospedeiros, envolvendo complexos mecanismos adaptativos e contradaptativos, como uma corrida armamentista (Dawkins & Krebs, 1979). O parasitismo de ninhada é mais frequente entre as aves (Davies, 1989; Davies & Brooke, 1989; Rothstein, 1990) e entre os insetos (Muller et al., 1990; Brockmann, 1993; Zink, 2003). Aves parasitas, como os cuckoos e os 'cowbirds', são capazes de se aproximar dos ninhos e colocar seus ovos, deixando-os aos cuidados do hospedeiro. Outra forma de parasitismo de ninhada ocorre entre os insetos, especialmente nos himenópteros solitários, vespas e abelhas (Wilson, 1971; Bourke & Franks, 1991; Cervo et al., 2004; Smith & Schwarz, 2006). Nestes casos as espécies parasitas burlam os custos inerentes à construção do ninho e do cuidado à prole, deixando seus filhotes aos cuidados de outro indivíduo (em casos intraespecíficos) ou outras espécies (Tallamy & Horton, 1990; Field, 1992; Zink, 2000).

O segundo tipo de parasitismo é melhor conhecido entre os himenópteros e envolve não somente a exploração do cuidado parental, mas de todo o sistema social do hospedeiro. Os parasitos sociais constituem várias formas intermediárias de parasitismo, podendo ser inter ou intraespecífico, temporário ou obrigatório. Em todos os estados, os parasitas burlam os custos de vários comportamentos sociais, explorando outras características do seu hospedeiro além do trabalho de seus operários e cuidado parental (Miller-III, 2004; Wang et al., 2008). No caso mais extremo de parasitismo social, o inquilinismo em formigas, as rainhas se infiltram na colônia hospedeira e coexistem com a rainha hospedeira, produzindo apenas indivíduos reprodutivos (Hölldobler & Wilson, 1990; Stuart, 2002; Huang & Dornhaus, 2008). Embora o parasitismo social seja mais freqüente entre os himenópteros, formas paralelas do parasitismo social têm sido encontradas em afídeos (Miller-III, 2004; Wang et al., 2008), proporcionando novos cenários para se investigar as pressões seletivas deste modo de vida e suas estratégias adaptativas.

Entre os aracnídeos encontramos exemplos de espécies que constituem sociedades complexas especialmente em Araneae (Avilés, 1997; Gonzaga, 2007; Lubin & Bilde, 2007), estas espécies poderiam atuar como hospedeiros para espécies parasitas sociais. Entretanto, as informações existentes a respeito de formações de agregados multiespecíficos e da presença de parasitas capazes de explorar esses sistemas são poucas ou inexistentes. A formação de agregados constituídos por duas ou mais espécies é bem conhecida entre os Opiliões (Machado & Vasconcelos, 1998; Elpino-Campos et al., 2001). Neste grupo, sabe-se que a relativa tolerância interespecífica, com baixa frequência de comportamentos agressivos e uso de microhabitats similares permitem que algumas espécies constituam agregados multiespecíficos sem bases cooperativas, porém mediados por outros benefícios, como manutenção de umidade e proteção contra predadores (Machado & Vasconcelos, 1998; Elpino-Campos et al., 2001; Machado & Raimundo, 2001; Machado et al., 2000; Pereira et al., 2004). Entre os pseudoescorpiões, o comportamento social é uma característica muito rara (Weygoldt, 1969; Del-Claro & Tizo-Pedroso, 2009) e a formação de grupos mistos (constituídos por duas ou mais espécies) ainda não foi documentada.

Os pseudoescorpiões constituem o quarto grupo mais diversificado entre os aracnídeos (Harvey, 2002), possuindo mais de 3350 espécies conhecidas (Harvey, 2009). Apesar de sua diversidade, a carência de estudos sobre a ecologia e comportamento ainda é muito grande. Entretanto, publicações recentes revelaram características muito peculiares (Zeh et al., 2005; Zeh & Zeh, 2005, 2006a, b, 2007), que tornam este grupo especialmente interessante para a experimentação e testes de hipóteses. Uma destas questões se refere aos raros casos de socialidade extrema, possibilitando o desenvolvimento de modelos sobre evolução da socialidade (Del-Claro & Tizo-Pedroso, 2009) e de outros aspectos ecológicos relacionados a este modo de vida.

A recente descoberta de colônias compostas por duas espécies de pseudoescorpiões (*Paratemnoides nidificator* e *Parachernes melanopygus*) em 2003, na região sudeste do Brasil, nos instigou a avaliar o comportamental e a ecologia das espécies na formação e manutenção destes raros agregados. Assim, o presente estudo investigou o papel ecológico de cada espécie nos agregados, por meio de manipulações de colônias em laboratório, buscando responder as seguintes perguntas: 1) as espécies em questão são comensais? 2) Existe interferência entre ambas resultando em variação na sobrevivência para as espécies? 3) Quais são as estratégias para que permaneçam agregadas? 4) Como se caracteriza o ciclo de vida de *Parachernes melanopygus*? Buscamos com estas questões confirmar ou refutar a hipótese de que *P. melanopygus* é um parasita social das colônias de *P. nidificator*.

MATERIAL E MÉTODOS

Espécies do estudo, coleta e manutenção das colônias

O pseudoescorpião *Paratemnoides nidificator* (Balzan, 1888) (Atemnidae, Chamberlin 1931) (3 a 7mm de comprimento) se distribui amplamente pelas Américas Central e do Sul, sendo encontrado em diversos estados brasileiros (Harvey, 2009). A espécie constitui grandes colônias sob as cascas de árvores suberosas, coexistindo em um modo de vida social permanente (Tizo-Pedroso & Del-Claro, 2008). Estes pseudoescorpiões sociais são abundantes em áreas urbanas do sudeste brasileiro, sendo encontrados em cascas de leguminosas, como as sibipirunas (*Caesalpinia peltophoroides*, Caesalpinaceae).

O gênero *Parachernes* Chamberlin 1931 (Chernetidae, Menge 1855) (1 a 2mm de comprimento) é exclusivamente neotropical e compreende mais de 30 espécies documentadas. Entretanto, se conhece muito pouco ou absolutamente nada sobre a ecologia e comportamento do gênero. A espécie-objeto deste estudo pertence ao gênero e subgênero *Parachernes* (*Parachernes*), mas sua identificação ainda não foi confirmada. Os indivíduos aqui analisados se aproximam muito da espécie *P. melanopygus* apresentada por Beier (1959). Entretanto, a morfometria dos seguimentos dos pedipalpos e de outras estruturas nos apêndices ultrapassou as medidas descritas por Beier. Apesar disto, faltam evidências robustas para considerar a espécie deste estudo como sendo uma espécie ainda não descrita ou pertencente a um grupo distinto de *P. melanopygus*. Além disso, inconsistências nominais neste gênero são esperadas por causa da grande variação fenotípica de suas espécies, fazendo necessária uma extensa revisão taxonômica. Por isto, a espécie deste estudo será considerada *Parachernes* cf. *melanopygus*. Deste ponto em diante o indicador cf. será omitido (Prancha 4).

As 47 colônias utilizadas nos experimentos deste estudo foram provenientes de coletas em três estados e cinco cidades: estado de São Paulo [cidade de Ribeirão Preto (21°10’53.61”S e 47°47’36.96”O, 570m)], estado de Minas Gerais [cidades de Uberlândia (18°52’56.98”S e 48°15’56.98”O, 930m), Uberaba (19°45’24.74”S e 47°56’34.41”O, 780m) e Araguari (18°39’24.01”S e 48°11’41.50”O, 940m)] e estado de Goiás [cidade de Caldas Novas (17°45’00.25”S e 48°38’06.40”O, 710m)] (Tabela 1). Todas as colônias foram coletadas com auxílio de um pincel nº 1 e acondicionadas em potes plásticos transparentes de 500mL, juntamente com os fragmentos de casca da árvore onde as colônias estavam localizadas. Um pedaço de algodão umedecido foi adicionado aos potes para manutenção da umidade durante o transporte.

As colônias foram preparadas posteriormente em laboratório, para observação e experimentação. Como alimento, os pseudoescorpiões receberam operários de cupim (*Armithermes* sp.) ou larvas de besouros tenebrionídeos (*Palembus dermestoides*), na proporção de um cupim para cada dois pseudoescorpiões, e uma larva para cada quatro pseudoescorpiões, duas vezes por semana. Eventualmente outras presas foram oferecidas, como besouros, percevejos e formigas *Camponotus*. Pedaços de algodão umedecidos foram incluídos em cada colônia uma a duas vezes por semana durante o período chuvoso e de duas a quatro vezes no seco.

Efeito de interação das espécies

Para avaliar o comportamento e as interações de cada espécie na manutenção das colônias mistas (contendo as duas espécies), realizou-se um experimento baseado na manipulação da composição específica das colônias mantidas em laboratório. O grupo controle 1 foi formado por 16 colônias constituídas apenas por *P. nidificator*, de 20 a 30 indivíduos entre adultos e ninfas (indivíduos de *P. melanopygus* foram removidos durante a preparação das colônias, logo após a coleta). O grupo controle 2 era formado por 12 colônias compostas de ambas as espécies (30 a 45 indivíduos); e grupo tratamento formado por 13 colônias compostas apenas por *P. melanopygus* (8 a 23 indivíduos; todos os indivíduos de *Paratemnoides* foram removidos destas colônias). Cada colônia foi alimentada com larvas de tenebrionídeos ou operários de cupins. Estas colônias foram monitoradas diariamente ao longo de 45 dias. Os comportamentos dos animais foram observados registrando-se o número de indivíduos vivos de cada espécie ao final dos 45 dias, calculando-se, posteriormente, a taxa média de sobrevivência para cada grupo com base no número inicial e final de indivíduos por colônia. Foram feitas também observações sobre reprodução, forrageio e dispersão. Ao final, os valores (obtidos em proporção) foram então transformados em Arco seno da raiz quadrada de X+0,5 e a distribuição normal destes valores foi avaliada pelo teste de Kolmogorov-Smirnov para uma amostra, para distribuição Liliefors. A homocedasticidade foi verificada dividindo a variância da amostra 1 pela variância da amostra 2. Os valores de sobrevivência obtidos após a transformação foram contrastados por ANOVA para dois fatores (relacionando as espécies *versus* o tipo de agregação uniespecífica ou mista).

Identificação interespecífica

Para avaliar a dinâmica da identificação dos indivíduos de *P. melanopygus* foi elaborado um experimento considerando-se as características específicas de cada colônia. Neste experimento, de cada colônia (*n*=10) foram removidos quatro pseudoescorpiões adultos (sendo dois de cada espécie, totalizando 30 indivíduos de *P. nidificator* e 26 de *P. melanopygus*), cada indivíduo foi retirado com tempo mínimo de 24h de diferença do anterior. Os indivíduos foram acondicionados separadamente em um frasco de acrílico de 15mL e mantidos isolados por 24h (Figura 1). Destes, dois indivíduos foram sorteados como controle (sendo um indivíduo de cada espécie) e os outros dois como tratamentos. Os indivíduos do grupo controle foram reintroduzidos na colônia original

e os indivíduos do grupo tratamento foram introduzidos em uma nova colônia (já parasitada). A ordem de reintrodução seguiu a sequência em que os animais foram retirados de suas colônias de origem, sendo que cada animal foi inserido na colônia com 24h de diferença do anterior. Os comportamentos foram observados durante 15 minutos com intervalo de três horas, durante 72h, seguindo a metodologia animal focal (detalhes da metodologia em Del-Claro, 2010). Os resultados foram analisados com o teste binomial.

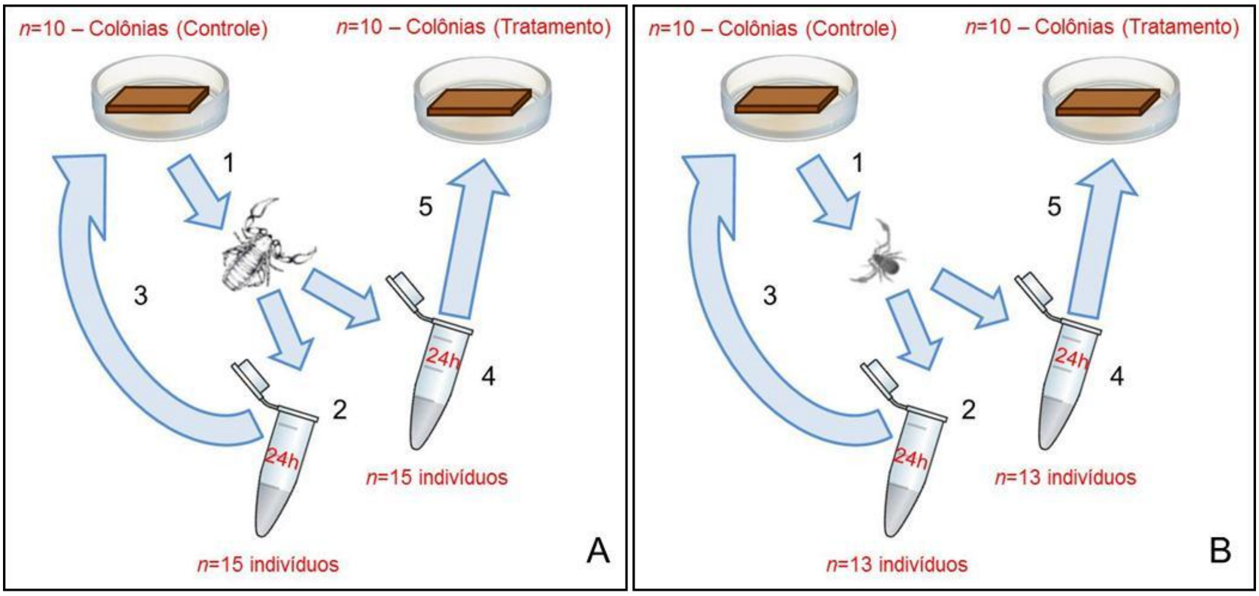


Figura 1. Diagrama do experimento de identificação inter e intraespecífica. Representação do experimento com (A) *Paratemnoides nidificator* e (B) com *Parachernes melanopygus*. A numeração indica a sequência de cada etapa no experimento, sendo: (1) remoção do indivíduo de sua colônia de origem; (2) inclusão em um frasco de acrílico vazio por 24h; (3) após este tempo, o animal foi reinserido em sua colônia de origem ou (4) após o tempo de 24h foi (5) introduzido em uma nova colônia parasitada.

Estratégias para burlar a identificação e invadir a colônia hospedeira

Com base na informação prévia que os pseudoescorpiões *P. nidificator* são capazes de identificar coespecíficos e também indivíduos não aparentados (dados não-publicados), um experimento adicional foi realizado para avaliar como os indivíduos de *P. melanopygus* trapaceiam os mecanismos de detecção de *P. nidificator* e invadem a colônias com sucesso. Para isto, um experimento baseado em impregnação por odor, sem contato físico, foi realizado. O experimento contou com um grupo constituído de 60 indivíduos de *P. nidificator*, e o segundo grupo constituído de 60 indivíduos de *P. melanopygus.* Cada grupo experimental foi dividido em dois subgrupos baseados no tempo de exposição, sendo 24h e 48h (os dois grupos de *Paratemnoides* foram constituídos por 7♂ e 8♀; enquanto os dois grupos de *Parachernes* foram compostos por 6♂ e 8♀; 7♂ e 8♀, respectivamente). Cada indivíduo foi inserido em um eppendorf esterilizado de 2mL, cuja tampa fora substituída previamente por um invólucro de malha de nylon, suficientemente fina para que os animais não pudessem sair. Cada tubo foi inserido em uma colônia parasitada, sorteada ao acaso, excluindo-se a colônia de origem de cada animal para o evento de inclusão do mesmo (Figura 2). Os tubos foram posicionados no interior da placa de Petri com a abertura, agora coberta pela malha de nylon, voltada para a fresta da casca de árvore, ficando assim o mais próximo possível dos pseudoescorpiões residentes. Os tubos foram expostos às novas colônias hospedeiras, por 24 ou 48 horas. Após este período, os animais foram liberados no interior da mesma colônia, e foram observados a cada 15 minutos de cada três horas durante 72h. Os resultados obtidos foram analisados com o teste binomial.

Um teste adicional avaliou a mesma resposta de identificação interespecífica com um pseudoescorpião externo à relação. O pseudoescorpião *Americhernes bethaniae* (Mahnert, 1979) é um pequeno Chernetidae que se distribui amplamente pela América do Sul. Ao longo dos anos de coleta, adultos deste pseudoescorpião foram frequentemente encontramos nas mesmas árvores que os *P. nidificator*, porém nunca dentro das colônias. Esta observação permitiu estabelecer um paralelo comparativo com a aceitação dos indivíduos de *P. melanopygus* nas colônias dos hospedeiros. Em um novo teste, quinze indivíduos adultos de *A. bethaniae* (sendo 8 fêmeas e 7 machos) coletados previamente em campo foram inseridos, individualmente, em quinze colônias de *P. nidificator*. Os mesmos foram observados durante 96 horas, sendo 10 minutos de observação a cada três horas. O número de pseudoescorpiões mortos foi contabilizado a cada 24h. Detalhes do tamanho corporal das espécies de pseudoescorpiões podem ser observados na Figura 3.

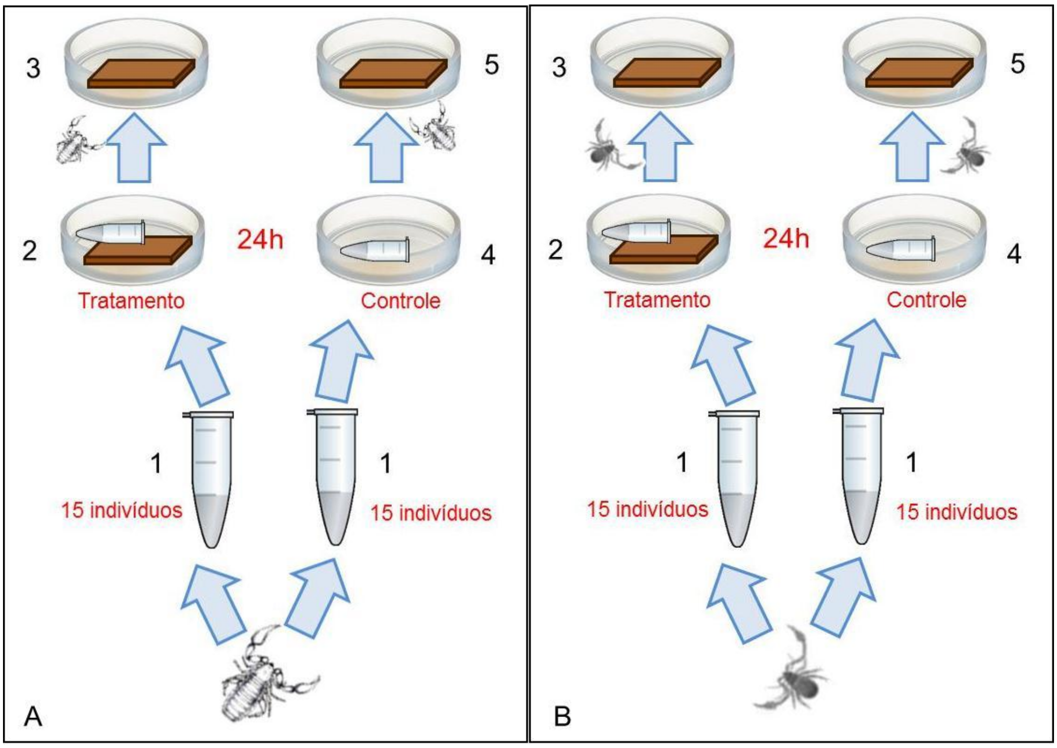


Figura 2. Diagrama do experimento de impregnação por odor, sendo (A) a sequência de *Paratemnoides nidificator* e (B) de *Parachernes melanopygus* no experimento. Cada animal foi removido de sua colônia de origem e (1) introduzido em um eppendorf esterilizado, cuja tampa fora removida e substituída por uma malha de nylon; (2) em seguida o tubo foi introduzido em uma placa de Petri contendo uma nova colônia de *P. nidificator*, onde permaneceu por 24h; (3) após o tempo de exposição, o indivíduo foi removido do tubo e introduzido na colônia em que foi exposto. (4) no grupo controle (sem exposição aos odores da colônia), os animais foram colados no tubo e introduzidos em uma placa de Petri vazia e esterilizada, onde permaneceram por 24h; (5) depois, cada animal foi removido de seu tubo e introduzido em uma colônia de *P. nidificator.* Na segunda parte do experimento, toda a sequência descrita acima foi repetida, porém os animais foram expostos, ou não, aos odores da colônia por 48h.

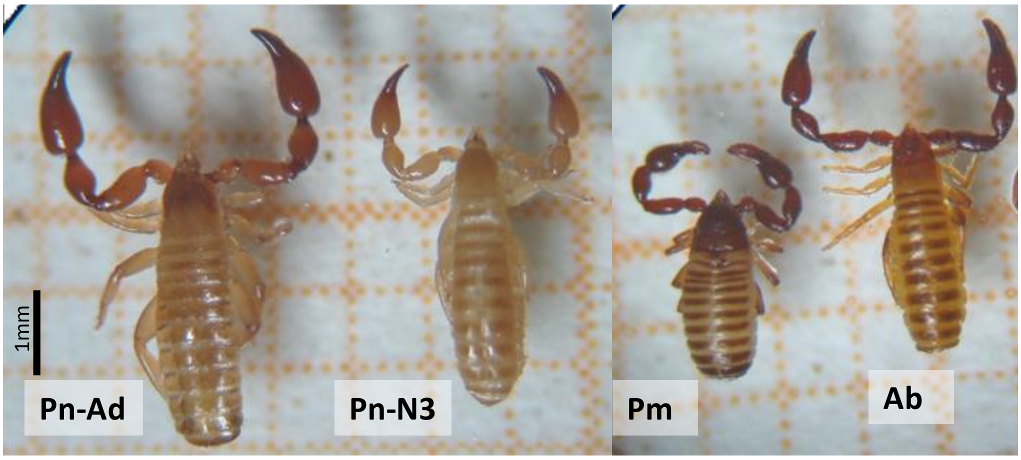


Figura 3. Imagem ilustrativa das diferenças de tamanho dos pseudoescorpiões utilizados neste estudo. As siglas **Pn-Ad** e **Pn-N3** indicam respectivamente adulto e tritoninfa (ninfa de terceiro estádio) de *Paratemnoides nidificator* (Atemnidae) (espécie hospedeira). As siglas **Pm** e **Pw** indicam as espécies parasitas, respectivamente, uma fêmea adulta de *Parachernes melanopygus* (Chernetidae) (parasita social obrigatório); e **Ab** indica uma fêmea adulta de *Americhernes bethainae* (Chernetidae) (especie em sobreposição de hábitat).

RESULTADOS

Caracterização das colônias

Ao longo do desenvolvimento deste estudo foram amostradas 290 colônias nas cinco cidades de amostragem e *P. melanopygus* foi detectado apenas em 16% destas, equivalendo a 47 colônias. Colônias constituídas apenas por *P. melanopygus*, ou indivíduos solitários, não foram encontrados durante os anos de amostragem deste estudo.

Efeito da interação das espécies

Os resultados do experimento de sobrevivência demonstram que as espécies reagiram de modos diferentes nos tratamentos uniespecíficos e mistos. A espécie *P. nidificator* obteve maior taxa média de sobrevivência quando isolada (85%) do que na presença de *P. melanopygus* (53%). O chernetídeo mostrou valores opostos obtendo maior sobrevivência média na presença de *P. nidificator* (80%) ao invés de quando mantido isolado (22%). Houve interação significativa entre as variáveis modo de vida e a espécie de pseudoescorpião e sobrevivência média ($F_{(1,48)}=384.924$; $p<0.0001$; Tabela 2, Figura 4).

Os resultados também mostraram que o chernetídeo foi incapaz de capturar suas próprias presas, os cupins *Armithermes* sp. ou larvas de besouros *P. dermestoides* oferecidas. Durante as observações *P. melanopygus* não exibiu nenhum comportamento de captura da presa ou algum tipo de interação. Na verdade, a espécie evitou as presas vivas sempre que oferecidas. Também não foi observado o consumo de presas mortas ou comportamentos de exploração e manipulação de carcaça. De fato, *P. melanopygus* mostrou-se dependente das habilidades de captura da espécie hospedeira. Além disso, registrou-se o consumo de jovens da espécie hospedeira por parte dos jovens e adultos do parasita (consumo médio de 30% das ninfas da colônia; 4±2 indivíduos; média±DP; n=12 colônias). Fêmeas não-reprodutivas de *P. nidificator* e machos adultos foram responsáveis pela caça e oferta de presas aos jovens. Ninfas parasitas trapacearam os adultos hospedeiros solicitando alimento aos mesmos. Para se reproduzir, os parasitas utilizaram as câmaras de seda do hospedeiro eventualmente matando e eliminando as ninfas hospedeiras que se abrigavam nessas estruturas.

Tabela 1. Detalhamento das 290 colônias coletadas durante os anos de estudo contendo as duas espécies de pseudoescorpiões em agregação (*Paratemnoides nidificato*r e *Parachernes melanopygus*). A tabela apresenta o número máximo, mínimo, médio e desvio padrão dos indivíduos pertencentes a cada fase de desenvolvimento das duas espécies do estudo, para as estações chuvosa e seca. Os códigos M, F, T, D, P representam respectivamente o número de Machos, Fêmeas, Tritoninfas, Deutoninfas e Protoninfas quantificadas em cada colônia amostrada.

	Parachernes melanopygus						*Paratemnoides nidificator*					
	Estação Chuvosa											
Colônias	M	F	T	D	P	Total	M	F	T	D	P	Total
Max.	2	5	5	4	6	18	6	8	14	12	19	52
Min.	0	0	0	0	0	1	0	2	1	0	0	5
Média	0,7	1,6	1,7	1,7	1,1	7,4	2,9	4,1	5,7	4,8	2,7	20,3
DP	0,8	1,4	1,5	1,3	1,4	4,6	1,7	1,8	3,4	3,3	4,3	11,8
	Estação Seca											
Colônias	M	F	T	D	P	Total	M	F	T	D	P	Total
Max.	4	3	5	4	4	13	5	8	14	11	5	35
Min.	0	0	0	0	0	1	0	2	1	0	0	7
Média	1	1,4	2	1,6	0,7	6,7	2,4	4,4	5,5	4,3	2	18,5
DP	1,2	1	1,6	1,2	1,3	3,8	1,4	1,9	4,2	2,7	1,9	8,8

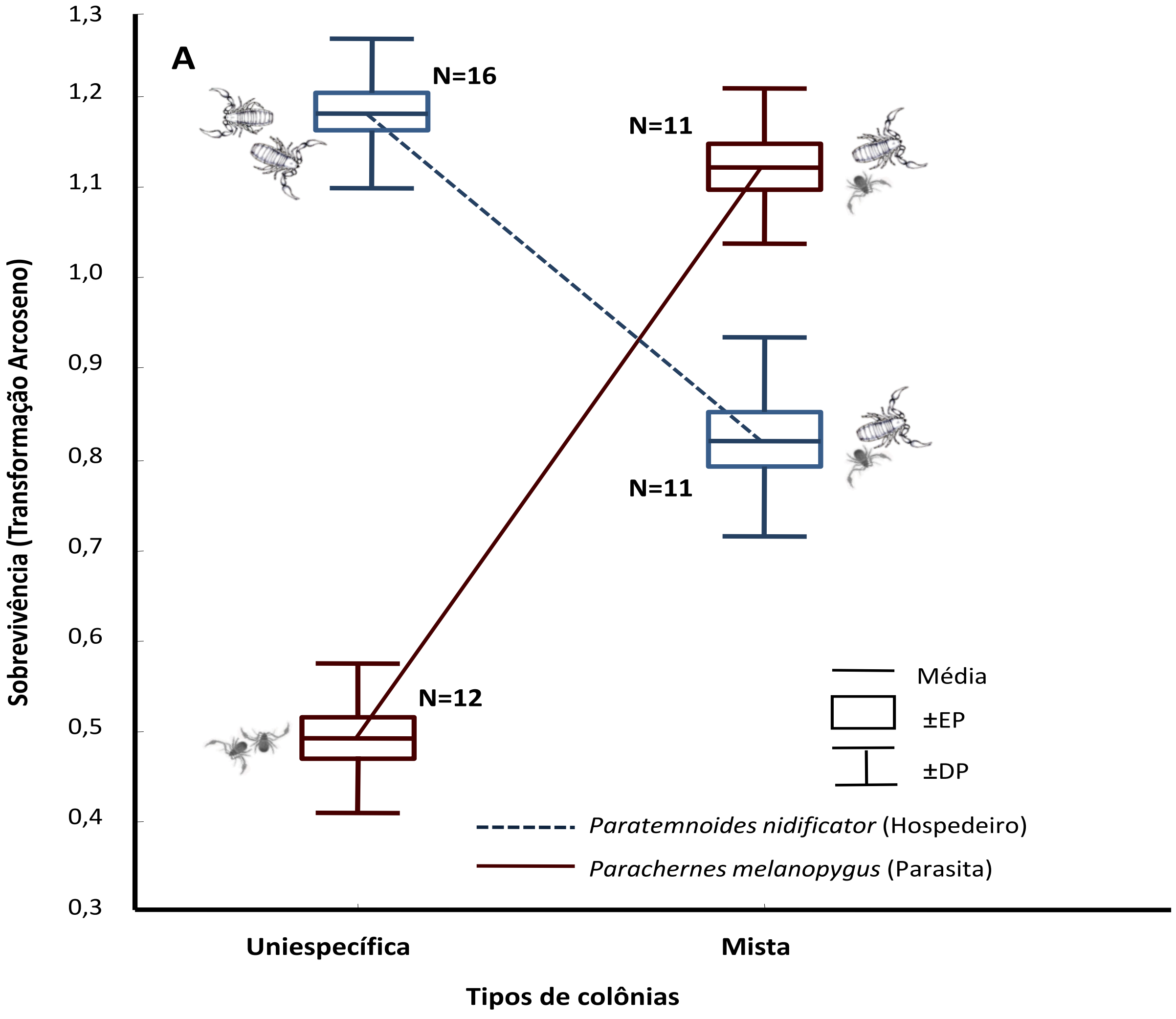
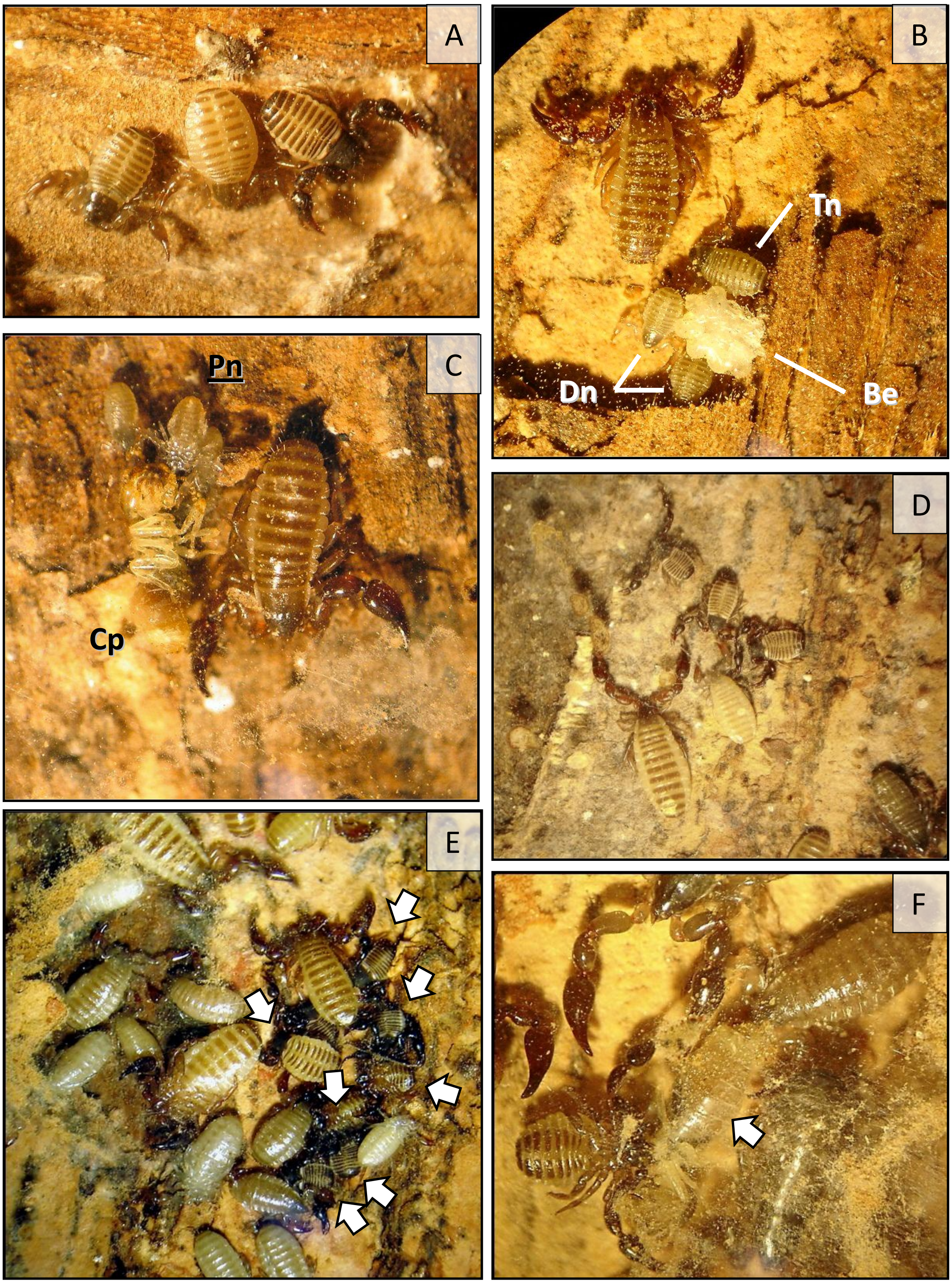


Figura 4. Efeito da interação entre o tipo de agregação (uniespecífica ou mista) e das espécies envolvidas na interação em relação à sobrevivência (média e desvio padrão) de *Paratemnoides nidificator* e *Parachernes melanopygus*.

Tabela 2. Resultados do teste de ANOVA para dois fatores avaliando a interação entre a sobrevivência de cada espécie de pseudoescorpião nos tratamentos desenvolvidos e o tipo de agregação (uniespecífica ou mista). As análises foram realizadas com os dados de sobrevivência transformados em Arcoseno da √X+0,5.

Variáveis	Soma dos quadrados	GL	Quadrado da média	F=	p=
Espécie	0,489	1	0,489	58,906	<0,0001
Tipo de colônia	0,238	1	0,238	28,649	<0,0001
Interação entre espécie e tipo de agregação	3,194	1	3,194	384,924	<0,0001
Erro	0,407	49	0,008		



Prancha 4. Relação parasitária entre *Parachernes melanopygus* (Chernetidae) e *Paratemnoides nidificator* (Atemnidae). (A) Imagem do pseudoescorpião parasita social *Parachernes melanopygus.* À esquerda estão duas tritoninfas e a direita um adulto; (B) Fêmea jovem de *P. nidificator* guardando três ninfas (duas deutoninfas [Dn] e uma tritoninfa [Tn]) e uma bolsa incubadora [Be] do pseudoescorpião parasita; (C) Fêmea não-reprodutiva de *P. nidificator* cuidando das protoninfas [Pn] parasitas. A fêmea capturou um cupim [Cp], o ofereceu para os parasitas e permanece em posição de guarda enquanto se alimentam; (D) Adultos do pseudoescorpião parasita sinalizam para os hospedeiros, enquanto estes respondem e executam o comportamento defensivo de agregação; (E) Detalhes de uma colônia de *P. nidificator* parasitada por *P. melanopygus*. As setas apontam dos indivíduos parasitas. (F) Indivíduos de *P. nidificator* compartilhando a presa (um operário de *Armithermes*) com um pseudoescorpião parasita.

Diferenças no desenvolvimento das espécies

O desenvolvimento das duas espécies deste estudo foi muito discrepante. Os resultados de colônias mantidas em laboratório comprovaram que os pseudoescorpiões *P. nidificator* podem sobreviver aproximadamente quatro anos, sendo cerca de um ano de desenvolvimento pós-embrionário e até três anos de vida adulta (observação pessoal). Entretanto, a expectativa de vida, aqui não quantificada, deve ser fortemente reduzida na presença do parasita. Para a maioria das colônias parasitadas, poucos indivíduos adultos de *P. nidificator* sobreviveram por mais de oito meses de vida adulta. Já os indivíduos de *P. melanopygus* sobreviveram até um ano e meio, sendo aproximadamente seis meses de desenvolvimento pós-embrionário e um ano de vida adulta. O tempo de desenvolvimento embrionário e pós-embrionário das duas espécies foi diferente (dados resumidos na Tabela 3).

Tabela 3. Comparação entre o número de filhotes, tempo de desenvolvimento embrionário e pós-embrionário dos pseudoescorpiões *Paratemnoides nidificator* e *Parachernes melanopygus* em colônias mistas.

	Número de Embriões por bolsa incubadora		Desenvolvimento embrionário 1º estágio		Desenvolvimento embrionário 2º estágio		Desenvolvimento pós-embrionário	
	Mediana (indiv.)	DP	Mediana (dias)	DP	Mediana (dias)	DP	Mediana (meses)	DP
Paratemnoides nidificator	12,50 (*n*=10)	±2,79	14,00 (*n*=10)	±1,16	14,50 (*n*=10)	±1,35	8,00 (*n*=20)	±0,92
Parachernes melanopygus	7,00 (*n*=8)	±1,81	11,00 (*n*=8)	±1,04	10,50 (*n*=8)	±1,06	6,00 (*n*=16)	±0,89
Teste de Mann-Whitney	U=3,02; p=0,0013	-	U=3,55; p=0,002	-	U=3,46; p=0,003	-	U=3,61; p=0,0002	-

Ciclo de vida de *Parachernes melanopygus*

As colônias mantidas em laboratório para experimentação ou observação permitiram descrever o ciclo de vida de *P. melanopygus* (Figura 5) As fêmeas de *P. melanopygus* se reproduzem no interior das colônias de *P. nidificator*, a bolsa embrionária permanece aderida à abertura genital da fêmea, e esta pode ou não construir uma semi-câmara de seda (incompleta; em forma de domo). A fêmea permanece com sua bolsa por até dois dias após a mudança dos embriões para a segunda fase de desenvolvimento. Então, a fêmea de *P. melanopygus* localiza ativamente uma fêmea de *P. nidificator* que não esteja se reproduzindo ou cuidando diretamente de seus filhotes (que não esteja portando bolsa embrionária ou guardando suas protoninfas). O *P. melanopygus* deposita sua bolsa embrionária junto a esta nova fêmea que acaba por adotar os embriões. Esta fêmea de *P. nidificator* se torna, então, a responsável pelos cuidados dos filhotes. As ninfas se desenvolvem no interior da colônia se misturando aos filhotes da espécie hospedeira e compartilhando os seus alimentos, ou recebendo presas da mãe hospedeira ou de outros adultos. Além disso, os parasitas podem se alimentar dos filhotes de *P. nidificator*, que apesar de serem maiores, são vulneráveis durante o período de torpor pré-ecdise. Vários filhotes e adultos de *P. melanopygus* podem compartilhar as ninfas de *P. nidificator* durante a alimentação. Raramente as ninfas de *P. melanopygus* construíram suas câmaras de ecdise, na forma de pequenos domos, diferentes das câmaras de *P. nidificator*. A fase de torpor e ecdise geralmente ocorre nas câmaras construídas pelos jovens de *P. nidificator*. A dispersão de *P. melanopygus* parece ser muito restrita, não sendo evidenciada evasão individual ativa. Os adultos também não participam dos eventos de captura de presas, porém compartilham o alimento com os adultos de *P. nidificator* ou podem roubar as presas dos filhotes hospedeiros. A reprodução, caracterizada por pareamento, dança e transferência de espermatóforo, ocorreu dentro das câmaras de seda do hospedeiro.

Mecanismos de dispersão

Em laboratório, dois mecanismos de dispersão foram observados em *P. melanopygus*. Sendo duas tentativas de forésia durante a oferta de presas. Uma tentativa ocorreu com uma operária de *Camponotus* sp., e a segunda tentativa com um pentatomídeo. Os pseudoescorpiões envolvidos na tentativa de forésia eram dois machos adultos.

O segundo mecanismo de dispersão está relacionado à estratégia de dispersão do hospedeiro, a fissão da colônia (veja Tizo-Pedroso & Del-Claro, 2007). No laboratório, três eventos de fissão de colônias parasitadas foram observados e durante a segregação do novo grupo, notou-se que os parasitas acompanharam uma ou ambas as novas colônias hospedeiras (Tabela 4).

Identificação interespecífica

O experimento para avaliar a identificação intra e interespecífica, baseado em troca de indivíduos revelou que tanto indivíduos de *P. nidificator* como de *P. melanopygus*, oriundos de colônias diferentes, são identificados em maior frequência do que os indivíduos controle (da sua colônia de origem) (*P. nidificator*, teste binomial, Z=2,927; p=0,003; *P. melanopygus*, teste binomial, Z=2,867; p=0,004) (Figura 6). Indivíduos de *P. nidificator* no grupo tratamento sofreram agregação por parte dos indivíduos residentes em maior proporção do que indivíduos aparentados (73,3% dos indivíduos). Em todos os casos em que a identificação foi bem sucedida,

a agressão culminou na morte do indivíduo introduzido. Algo muito semelhante foi registrado durante a introdução de *P. melanopygus*. A maior proporção dos indivíduos do grupo tratamento foi reconhecida e atacada (81,2% dos indivíduos) de modo similar à agressão sofrida por *P. nidificator* nos grupos tratamento. Para ambas as espécies nos grupos controle, apenas 20% dos indivíduos sofreram agressão e foram mortos.

Estratégias de invasão das colônias hospedeiras

Os indivíduos dos grupos experimentais, que permaneceram 24h dentro da colônia, sem contato direto (tratamento), e os grupos que permaneceram isolados sofreram comportamentos de agressão em frequências muito semelhante. Para ambas as espécies, a proporção de indivíduos reconhecidos e eliminados não diferiu significativamente dos seus controles (*P. nidificator*, teste binomial, Z=-0,37; p=0,71; *P. melanopygus*, teste binomial, Z=0,73; p=0,46). A proporção de indivíduos identificados e mortos no grupo tratamento foi de 33,33% para *P. nidificator* e de 58,33% para *P. melanopygus* (Figura 7).

Na segunda etapa do experimento, os pseudoescorpiões nos grupos tratamento e controle permaneceram nos tubos por 48h, antes de serem inseridos em novas colônias. Para *P. nidificator*, a proporção de indivíduos aceitos nas colônias não-aparentadas não diferiu significativamente entre os grupos experimentais (teste binomial, Z=0,745; p=0,446). Os indivíduos de *P. melanopygus* no grupo controle sofreram agressão por parte dos indivíduos hospedeiros residentes em maior proporção do que os indivíduos no grupo controle (teste binomial, Z=2,236; p=0,0253, Figura 8). Os pseudoescorpiões parasitos expostos aos odores da colônia foram mais bem sucedidos na aproximação e invasão das colônias. Nestes casos, os indivíduos hospedeiros residentes falharam com maior frequência na identificação e exclusão destes parasitos.

As observações dos *A. bethaniae* em colônias de *P. nidificator* comprovaram que este pequeno pseudoescorpião é suficientemente ágil para evitar os ataques dos *P. nidificator*. Notou-se que estes pseudoescorpiões se comportaram diferente de *P. melanopygus*, evitando o contato direto com *P. nidificator*, na maior parte do tempo de observação. Apesar disto, os *A. bethaniae* foram identificados e mortos pelos pseudoescorpiões residentes em algum momento. Os indivíduos de *A. bethaniae* foram consumidos pelos membros das colônias, o que não aconteceu nos testes de identificação com *P. melanopygus* ou *P. nidificator* descritos nos itens anteriores. A Figura 9 mostra a progressão da identificação dos indivíduos inseridos nas colônias.

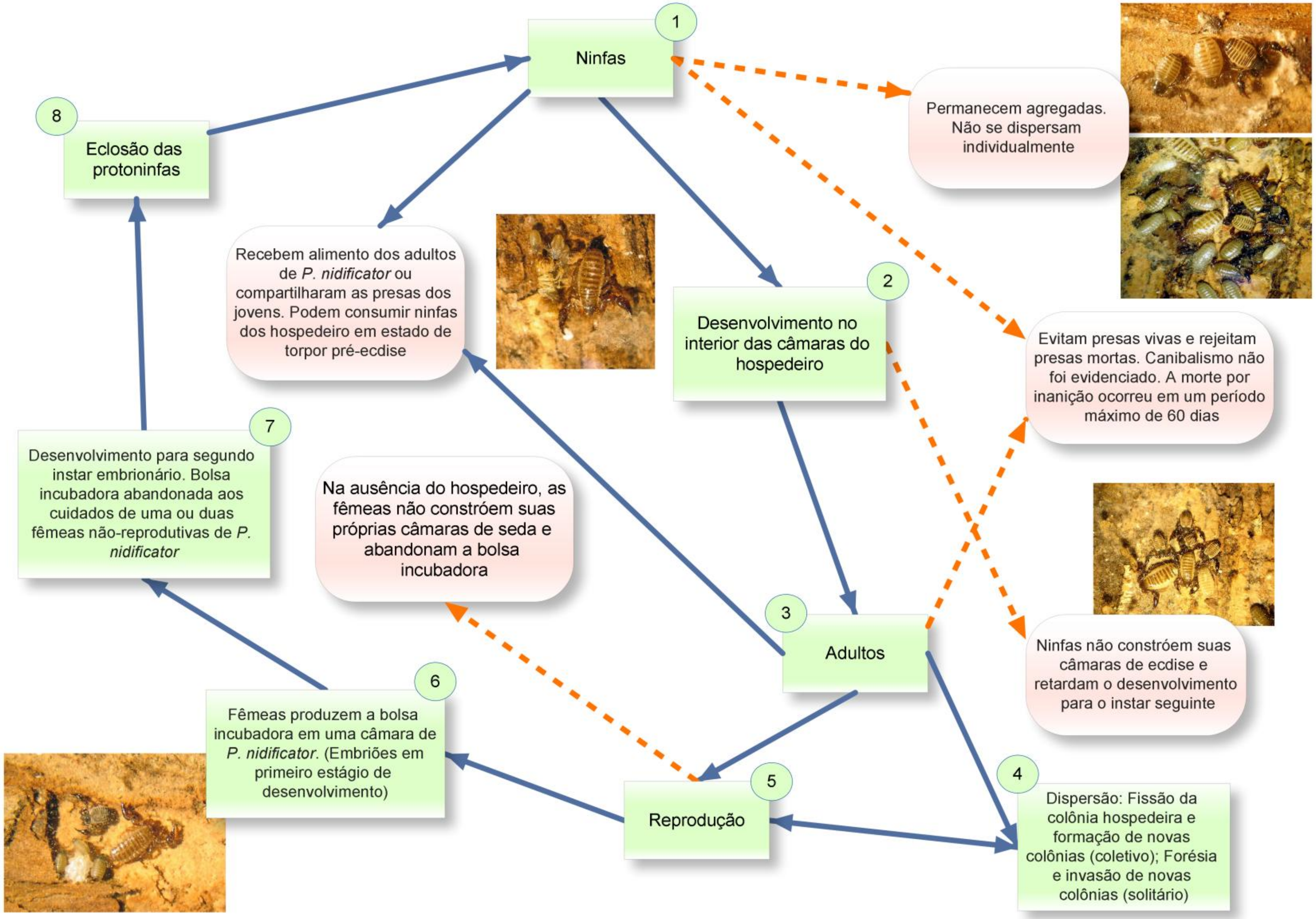


Figura 5. Ciclo de vida do pseudoescorpião parasita social *Parachernes melanopygus*. As linhas contínuas indicam etapas normais do ciclo na presença dos hospedeiros, enquanto as linhas pontilhadas indicam efeitos negativos ao parasita na ausência dos hospedeiros.

Tabela 4. Composição das colônias mistas de *Paratemnoides nidificator* e *Parachernes melanopygus* após o comportamento de fissão das colônias maternas em laboratório. As siglas Pn e Pm indicam, respectivamente, as espécies do estudo, enquanto as siglas M, F, T, D, P, indicam os sexos e fases de desenvolvimento (respectivamente Machos, Fêmeas, Tritoninfas, Deutoninfas e Protoninfas).

Colônias parasitadas	Composição antes da fissão	Composição após fissão	
	Colônia materna	Colônia filha 1	Colônia filha 2
Colônia 1	15Pn; 4Pm	Pn: 2M; 4F; 2T; 2D Pm: 1M; 1F; 1T	Pn: 2M; 2F; 1T Pm: 1F
Colônia 2	28Pn; 11Pm	Pn: 3M; 2F; 7T; 5D; 2P Pm: 1M; 3F; 3T; 2D	Pn: 2M; 4F; 3T Pm: 1F; 1T
Colônia 3	22Pn; 8Pm	Pn: 2M; 1F; 6T; 6D; 2P Pm: 2F; 2T; 1D	Pn: 2F; 2T; 1D Pm: 1M; 1F; 1T

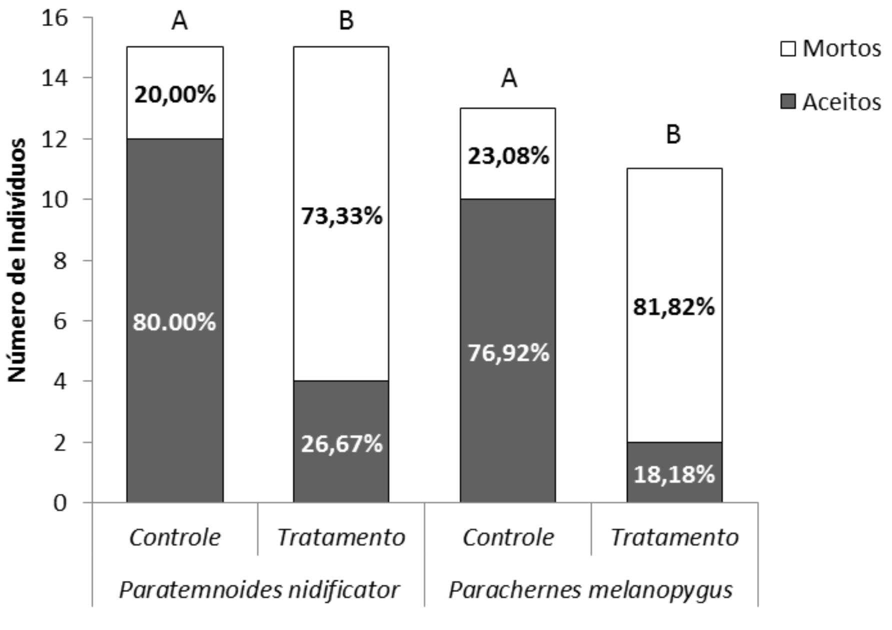


Figura 6. Sucesso na identificação e eliminação de indivíduos coespecíficos em colônias de *Paratemnoides nidificator* não aparentados (tratamento) e originados da mesma colônia materna (controle) e sucesso na identificação e eliminação dos pseudoescorpiões parasitas sociais *Parachernes melanopygus*, oriundos de colônias não aparentadas (tratamento) e de mesma colônia materna (controle). As letras indicam diferenças estatísticas calculadas pelo teste binomial. Os testes foram realizados apenas para investigar diferenças nas respostas controle e tratamento da mesma espécie.

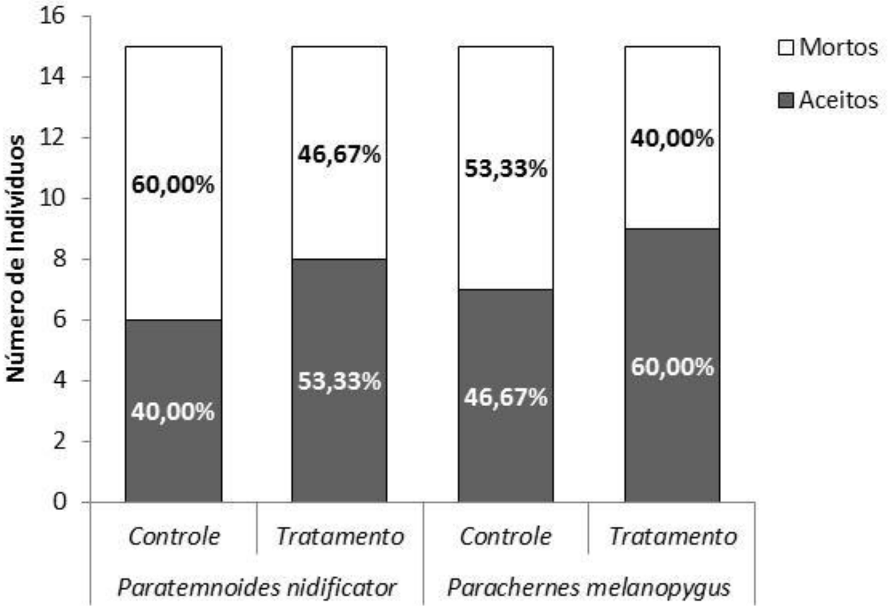


Figura 7. Sucesso na identificação e eliminação de indivíduos coespecíficos em colônias de *Paratemnoides nidificator* e de parasitas sociais *Parachernes melanopygus*, após 24h de permissão (tratamento) ou impedimento (controle) da impregnação de odores da colônia. Valores dos testes estatísticos não significativos.

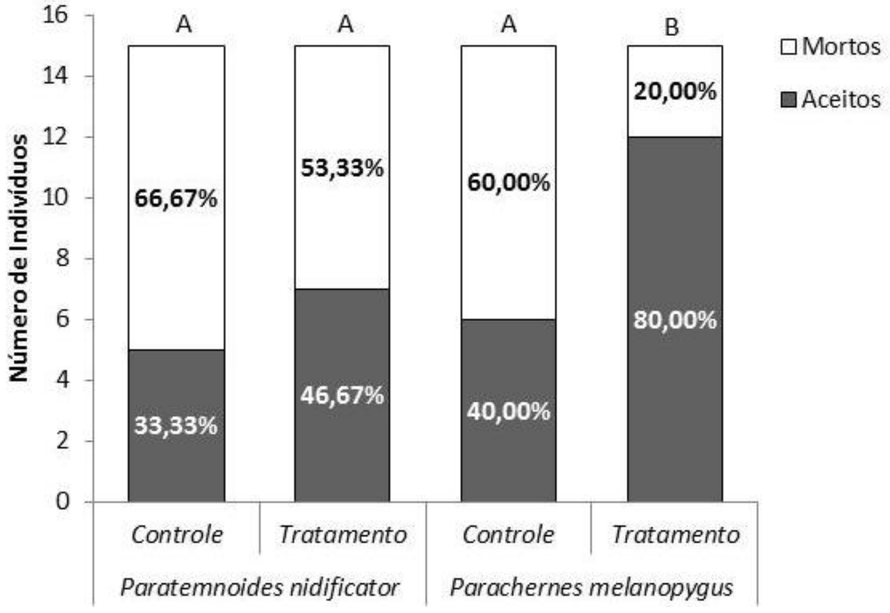


Figura 8. Sucesso na identificação e eliminação de indivíduos coespecíficos em colônias de *Paratemnoides nidificator* e de parasitas sociais *Parachernes melanopygus*, após 48h de permissão (tratamento) ou impedimento (controle) da impregnação de odores da colônia. As letras indicam diferenças significativas.

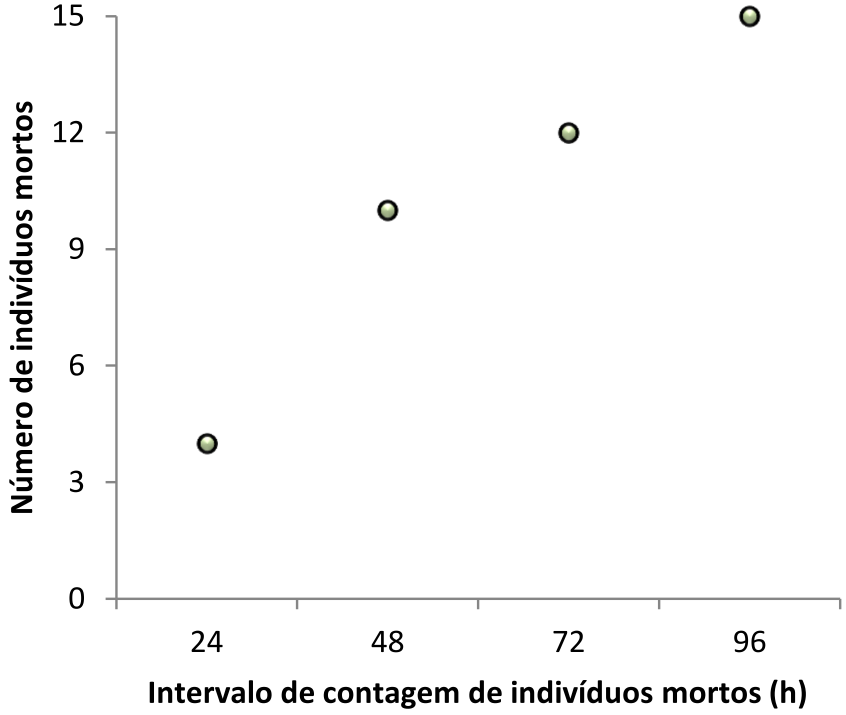


Figura 9. Tempo de permanência nas colônias e exposição aos indivíduos de *Paratemnoides nidificator* e número acumulado de pseudoescorpiões *Americhernes bethainae* identificados, mortos e consumidos pelos aminais residentes.

DISCUSSÃO

Os resultados nos permitem classificar o pseudoescorpião *P. melanopygus* como parasita verdadeiro, de acordo com o modelo ecológico clássico de parasitismo. O parasita subsiste pela exploração dos recursos, filhotes e comportamentos do seu hospedeiro. Além disso, ao longo dos anos de estudo, nenhum indivíduo solitário de *P. melanopygus* foi encontrado em campo, tampouco colônias constituídas unicamente por esta espécie, sendo um indício a favor da hipótese de parasitismo. Adicionalmente, as adaptações, aqui demonstradas, para a invasão bem sucedida das colônias hospedeiras e a exploração dos comportamentos sociais e parentais do hospedeiro, indicam uma corrida evolutiva antagônica. Estas evidências suportam a conclusão de que *P. melanopygus* é um parasita social obrigatório.

Dispersão, localização e invasão da colônia hospedeira

As relações estabelecidas no parasitismo social e parasitismo de ninhada são mediadas por características adaptativas e contra-adaptativas. Nestes modelos de corrida evolutiva antagônica, as estratégias para enganar o hospedeiro e invadir a colônia, ou ninho, são fundamentais para o sucesso do modo de vida parasitária (Stuart, 2002 e suas referências). Estratégias baseadas em adaptações fisiológicas, morfológicas, comportamentais e principalmente químicas, buscam impedir os mecanismos de identificação do hospedeiro. Sistemas de identificação são fundamentais para a manutenção das sociedades dos insetos (Howard & Blomquist, 2005). Assim, os mecanismos de identificação inter e intraespecífico também atuam como estratégias para evitar o parasitismo (Dettner & Liepert, 1994; Lenoir et al., 2001). Quando não é possível evitar, outras estratégias podem ser empregadas para minimizar o impacto (Achenbach & Foitzik, 2009)

Burlar o sistema de identificação do hospedeiro é a etapa primordial para o sucesso do parasita. As duas principais estratégias para isto são: o mimetismo químico e a camuflagem química (Akino, 2002). De acordo com Strohm et al. (2008), a camuflagem química deve ocorrer com maior frequência entre as vespas sociais, uma vez que os parasitas podem sequestrar diversos componentes de uma série de substâncias presentes nos ninhos, além daquelas produzidas pelos indivíduos que compõem a colônia. Assim, a camuflagem química deve ser mais comum entre os parasitas de ninhada. Parasitas que exploram hospedeiros solitários não conseguem se expor a tantos vestígios químicos. De fato, a camuflagem química pode ser tanto evidenciada em casos em que o parasita social pertence a um grupo taxonômico diferente do seu hospedeiro (Akino et al., 1999; Akino, 2002; Nash et al., 2008) ou ao mesmo grupo taxonômico (Bagnères et al., 1996; Lenoir et al., 1997; Sledge et al., 2001; Lorenzi et al., 2004; Brandt et al.,

2005b), ou mesmo a combinação das duas estratégias químicas (veja revisões de Dettner & Liepert, 1994; Lenoir et al., 2001).

No pseudoescorpião *P. nidificator*, um mecanismo de identificação também baseado em sinais químicos mantém a coesão do grupo e permite a identificação de outros coespecíficos oriundos de outras colônias. Estes pseudoescorpiões reagem agressivamente matando coespecíficos invasores (Tizo-Pedroso, dados não publicados). Os resultados do presente estudo demonstram que *P. melanopygus* é capaz de burlar este mecanismo de identificação. O aumento na aceitação dos pseudoescorpiões parasitas em relação ao tempo de sua exposição ao hospedeiro, demonstrado nos experimentos, sugerem que pode estar ocorrendo camuflagem química. Este fato contrapõe o predomínio de mimetismo químico na maioria dos parasitas sociais.

A aproximação de uma colônia hospedeira é um momento crucial para que a invasão do parasita seja bem sucedida. Uma tentativa de invasão direta certamente causaria a identificação e eliminação do pseudoescorpião parasita. Então, o indivíduo permanece nas áreas periféricas da colônia por alguns dias aumentando suas chances de sucesso. É possível que existam estruturas morfológicas facilitadoras da camuflagem química. Na aproximação, o parasita pode estar capturando, passivamente, odores do hospedeiro pelo contato com o substrato, com dejetos da colônia ou com os ninhos, como ocorre em outros parasitas que utilizam camuflagem química (Dettner & Liepert, 1994; Lenoir et al., 2001).

Os resultados demonstraram que *P. melanopygus* explora o sistema de identificação do seu hospedeiro. Fato corroborado pelo sucesso de *P. nidificator* na identificação dos indivíduos de *A. bethaniae* durante os experimentos adicionais. Observou-se que o aumento no tempo de exposição de *A. bethaniae* não foi acompanhado pelo aumento do sucesso de invasão. Isto indica que o parasita está simulando os odores e o mecanismo de identificação do seu hospedeiro. A identificação e remoção do parasita, nos experimentos de troca de indivíduos entre diferentes colônias aparentadas, confirmam a necessidade do parasita de se ajustar em relação ao odor próprio de cada colônia. Este fato tem grande implicação nas estratégias de dispersão do parasita. Um indivíduo em processo de dispersão deve encontrar outra colônia, adquirir odores e se ajustar, sofrendo o risco de ser detectado e morto.

Assim sendo, a estratégia de dispersão baseada na fissão da colônia oferece uma alternativa muito mais segura ao parasita: menor risco de predação e garantia de continuar explorando seu hospedeiro. Entretanto, a redução do tamanho da colônia hospedeira pela ação do parasita também afetada a disponibilidade de recursos para o próprio parasita e o tempo que este permanecerá na colônia. Regulando assim, a necessidade de buscar novos hospedeiros.

Características adaptativas: tamanho corporal e ciclo de vida

O ciclo de vidas das espécies de pseudoescorpiões deste estudo (parasito e hospedeiro) mostrou diferenças. Parte destas diferenças pode ser o resultado da discrepância dos tamanhos corporais de parasitos e hospedeiros. *Parachernes melanopygus* é consideravelmente menor (1,5mm a 2mm) do que seu hospedeiro (3mm a 7mm). Entretanto, esta é uma condição sinapomórfica, pois todas as espécies de *Parachernes* são relativamente pequenas, sugerindo que esta característica pode não representar uma condição adaptativa. Apesar disso, o tamanho reduzido dos pseudoescorpiões parasitas deve aumentar a chance de erro do hospedeiro na discriminação entre seus próprios filhotes e indivíduos parasitas.

Uma característica peculiar das formigas inquilinas é o tamanho corporal geralmente menor do que o tamanho das espécies hospedeiras. Esta condição pode indicar uma característica adaptativa do parasita conferindo-o desenvolvimento prematuro em relação ao desenvolvimento do próprio hospedeiro, reduzindo sua necessidade nutricional (Bourke & Franks, 1991; Nonacs & Tobin, 1992; Aron et al., 1999). Esta característica também se expressa de modo similar nas aranhas cleptoparasitas obrigatórias do gênero *Argyrodes* (Theridiidae). Estas aranhas geralmente são menores do que as espécies congenéricas capazes de estabelecer relações parasitárias oportunítiscas (Elgar, 1993).

É conhecido que o tamanho corporal reduzido está relacionado ao ciclo de vida mais rápido. De fato, *P. melanopygus* se desenvolve mais rapidamente que *P. nidificator*. Esta diferença não deve indicar o resultado de uma pressão seletiva para o desenvolvimento acelerado, mas apenas uma condição natural. Apesar disto, as diferenças naturais do desenvolvimento destas espécies parecem simular o desenvolvimento das formigas inquilinas (Aron et al., 1999). Assim, embora o tamanho reduzido do parasita e curto ciclo de vida não indiquem características adaptativas, possivelmente tenham seu papel como fatores precursores para o surgimento da vida parasitária em pseudoescorpiões.

O modelo parasitário de *Parachernes melanopygus*

Formas complexas de parasitismo são bem conhecidas em várias famílias de aranhas, sendo que algumas espécies cleptorapasitas estabelecem notáveis relações com aranhas sociais (e.g. *Argyrodes*) (Whitehouse et al., 2002). As aranhas, em especial do gênero *Argyrodes*, perderam parte dos seus atributos de caçadoras ativas e de mães cuidadoras, direcionando assim os custos destes comportamentos às espécies hospedeiras (Agnarsson, 2002).

De modo geral, as aranhas cleptoparasitas exploram as presas de suas aranhas hospedeiras. Os parasitas do gênero *Anelosimus* (Theridiidae) sociais compartilham a mesma origem filogenética, também relacionada ao cuidado maternal. O comportamento parental é suprimido e os filhotes parasitas usurpam presas de outras espécies de aranhas desde as fases iniciais de suas vidas (Agnarsson, 2002, 2004). Whitehouse e Lubin (2005) reconheceram o parasitismo por *Argyrodes* como constituinte de uma função de forrageamento, uma vez que os custos de captura de presas, associados ao cuidado maternal, são atribuídos aos hospedeiros.

O modelo parasitário de *Parachernes*, aparentemente, também evoluiu como uma alternativa para reduzir os custos do cuidado maternal. Esta interação pode ter uma origem na usurpação das presas de *P. nidificator* por um ancestral de *P. melanopygus*, como alternativa comportamental para reduzir os custos de captura. As colônias de *P. nidificator* exploram uma grande variedade de presas (Tizo-Pedroso & Del-Claro, 2007) e poderiam representar uma oportunidade de acesso constante ao alimento. Assim, indivíduos adultos de um ancestral de *P. melanopygus* provavelmente se favoreceram das presas capturadas de *P. nidificator*. Em longo prazo, esta relação oportunística favoreceu a evolução da estratégia cleptoparasita mais complexa, envolvendo atribuição dos custos do cuidado maternal ao hospedeiro.

Por compartilharem o mesmo microhabitat, um ambiente relativamente durável e homogêneo, a sobreposição das áreas de vida destas espécies pode ter sido um pressão favorável para a evolução do parasitismo social. Ocorrendo a falha na sua identificação, o parasita estaria livre para explorar todos os complexos comportamentos parentais do hospedeiro (Tizo-Pedroso & Del-Claro, 2005; 2008), recebendo também abrigo e proteção constante. Apesar da origem filogenética distante das espécies, a relação entre o cuidado maternal e o aumento da tolerância também parece ser a base para a manutenção da relação parasitária, tal como fora hipotetizado para os *Argyrodes* cleptorapasitas (Agnarsson, 2002).

Raridade do parasita e virulência

O termo virulência é muito abrangente e possui definições específicas para as diferentes áreas de estudo (Schall, 2002). Porém, como um consenso, entende-se que a infecção por um parasita afeta de modos diferentes vários atributos do hospedeiro, podendo causar perda em um ou mais componentes de aptidão, enquanto outro componente pode ser direta ou indiretamente incrementado (veja Schall, 2002).

Parachernes melanopygus causou perdas significativas em vários componentes da aptidão do hospedeiro, como redução dos recursos alimentares, exploração de atributos comportamentais e remoção de filhotes. Aparentemente nenhum atributo associado à aptidão dos hospedeiros é incrementado na associação com o parasito. Segundo Schall (2002), as informações mais difíceis de se obter sobre a virulência do parasita se referem aos seus efeitos na redução da expectativa de vida do hospedeiro. Os experimentos sobre mortalidade do hospedeiro, do presente estudo, demonstram claramente o impacto direto do parasitismo na sobrevivência dos hospedeiros. De fato, o parasita não causa apenas a severa redução no número de indivíduos adultos da colônia, mas elimina grande parte da prole do hospedeiro. A expectativa de vida do hospedeiro não pôde ser medida, porém é possível afirmar que *P. nidificator* teve maior probabilidade de morte; seja pela ação direta (ataque e morte pelo parasita), ou indireta do parasita (diminuição da expectativa de vida pela redução do acesso aos recursos). Deste modo, *P. melanopygus* pode ser considerado um parasita altamente virulento, pois reduz o tamanho da colônia hospedeira, causando sua mortalidade em médio prazo.

A extensão dos danos causados por um parasita pode ser consequência da sua raridade, ou seja, de sua distribuição espacial restrita a pequenas parcelas das populações hospedeiras. A frequência e a evolução de mecanismos de defesa contra a invasão estão relacionadas com a prevalência do hospedeiro (Schmid-Hempel, 1998). Esta condição reduz diretamente a chance de evolução de alelos que possam conferir características defensivas na população como um todo, gerando consequentemente maior virulência (veja Kilner, 2005). Um modelo alternativo e muito específico prediz que a severa redução da aptidão do hospedeiro deve gerar grande incremento à sobrevivência do parasita. O efeito da virulência pode, então, não estar relacionado à raridade do parasita, mas indicar uma estratégia evolutivamente estável. Os cucos e 'honeyguides' reduzem a competição pelos recursos causando a morte da prole do hospedeiro (revisado por Kilner, 2005). O fenômeno de virulência nos pseudoescorpiões é similar aos impactos causados pelas aves parasitas de ninhada. Os cucos causam redução da prole do hospedeiro para obter incremento em sua própria reprodução (Kilner, 2005). Além disso, a fecundidade do parasita tende a ser maior quando a virulência é alta, apesar de reduzir seu tempo com o hospedeiro (Day, 2003). Neste ponto de vista, a virulência de *P. melanopygus* pode estabelecer um equilíbrio com a raridade e a densidade do parasita e o impacto na aptidão das duas espécies na associação. No caso dos pseudoescorpiões, os parasitas (jovens e adultos) exploram os hospedeiros requerendo recursos enquanto se passam por filhotes do hospedeiro, o que gera uma condição excepcional em relação aos parasitas de ninhada (aves ou insetos) e aos parasitas sociais.

Relações filogenéticas e evolução do parasitismo social

A extensa discussão sobre o modo de vida inquilinista em insetos aponta diferentes perspectivas para a evolução desta relação parasitária. Na maioria dos himenópteros, o parasita social obrigatório geralmente explora uma única espécie hospedeira. Além disso, o parasita é, em geral, muito próximo (filogeneticamente) do seu hospedeiro, quando não pertencente a um grupo irmão (Stuart, 2002; Huang & Dornhaus, 2008). Formas parasitárias intermediárias e facultativas geralmente exploraram dois ou mais hospedeiros, não necessariamente filogeneticamente próximos (Stuart, 2002; Huang & Dornhaus, 2008). Assim, a regra de Emery prediz que a espécie parasita evoluiu em simpatria com seu hospedeiro, sendo esta a causa da relação parasitária obrigatória e espécie-específica. O modelo alternativo se baseia na evolução alopátrica das espécies (discussões sobre as hipóteses em Bourke & Franks, 1991; Berlocher, 2003; Savolainen &

Vepsalainen, 2003; Sumner et al., 2004; Hora et al., 2005; Smith et al., 2007; Huang & Dornhaus, 2008).

Embora estas hipóteses expliquem satisfatoriamente o surgimento dos inquilinos em insetos, não são aplicáveis ao contexto do parasitismo social nos pseudoescorpiões. Apesar de as duas espécies pertencerem à mesma superfamília (Cheliferoidea), elas se encontram em clados filogeneticamente distantes (veja Harvey, 1992 para análises dos grupos; Proctor, 1993). Um modelo de parasitismo social em formigas que não se enquadra na regra de Emery foi estudado por Maschwitz e colaboradores (2000). Segundo os autores, espécies que não se enquadram no modelo simpátrico devem ter experimentado um processo adaptativo diferente, provavelmente a partir de um ancestral parasita menos complexo, que sofreu ajuste de vários atributos, tais como sistema de comunicação, nicho e outras características, para explorar seu hospedeiro de modo mais eficiente.

Observações de campo e registros de coletas indicam que *P. nidificator* e *P. melanopygus* possuem ampla distribuição geográfica, ocorrendo em diferentes ambientes. Este fato indica que diferentes populações podem existir sob diferentes pressões ambientais, possivelmente com baixo fluxo gênico entre elas, o que poderia moldar variações na relação parasito-hospedeiro nos diferentes ambientes, devido a diferentes respostas de cada espécie no processo de coevolução (Thompson, 2005; Jackson, 2008; Nash et al., 2008). Os resultados aqui apresentados nos permitem construir um cenário promissor para entender as diferentes pressões seletivas e rotas alternativas para a evolução do parasitismo social obrigatório, possivelmente um processo evolutivo similar ao ocorrido nos himenópteros sociais, agregando atributos e estratégias particulares. O parasitismo social obrigatório de *P. melanopygus* sugere uma longa história de interações e adaptações para explorar seu hospedeiro, indicando uma relação evolutivamente antiga. Este fenômeno proporciona uma nova perspectiva para os estudos de corrida coevolutiva antagônica.

AGRADECIMENTOS

Agradeço a MSc. Renata Pacheco por ceder exemplares de *P. melanopygus* para análise deste estudo, e ao Dr. Heraldo Vasconcelos por sugestões nas análises da primeira etapa do estudo. Agradeço ao CNPq pelo apoio financeiro concedido como bolsa para curso de mestrado para a realização do estudo entre os anos 2005 a 2007. Agradeço a FAPEMIG pelo apoio financeiro como bolsa de doutoramento desde 2007.

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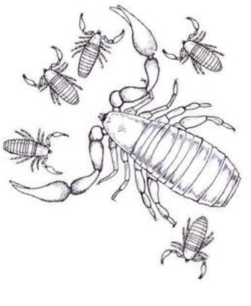
CAPÍTULO 4

ECOLOGICAL AND EVOLUTIONARY PATHWAYS OF SOCIAL BEHAVIOR IN PSEUDOSCORPIONS (ARACHNIDA: PSEUDOSCORPIONES)

(Acta Ethologica, 2009)



acta ethol (2009) 12:13–22
DOI 10.1007/s10211-009-0052-y

REVIEW

Ecological and evolutionary pathways of social behavior in Pseudoscorpions (Arachnida: Pseudoscorpiones)

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Received: 25 September 2008 / Revised: 5 February 2009 / Accepted: 26 February 2009 /

Abstract Despite the great biodiversity in the Arachnida, some taxa are still now poorly known, mainly in terms of biology, ecology, and behavior. Pseudoscorpions are small arachnids (2–8 mm) that live in cryptic environments, being in general solitary predators of other invertebrates. The most studied Pseudoscorpion species are those from temperate areas, which revealed that Pseudoscorpiones present some level of sociality based on maternal care. Most developed sociality is seen in tropical species. Here, we reviewed this issue, presented examples of social behavior, and suggested the steps involved in the evolution of permanent sociality in the Neotropical Atemnidae genus, *Paratemnoides*. We discussed that the extended parental care, division of labor, cooperative breeding and feeding, and the tolerance among members dividing the same share could be considered enough to characterize a true social life, same in invertebrates.

Keywords Arachnida · Cooperation · Evolution · Bark Fauna · Neotropics · Cerrado

Communicated by R. F. Oliveira

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Introduction

For centuries, social behavior has caused fascination among researchers of natural sciences. It occurs specially due to its rarity in the major part of taxonomic groups and peculiar selective and evolutionary process. Nowadays, there is an enormous quantity of papers related to general aspects of social life, which includes classification models, origins, and evolution (e.g., Wilson 1971). Considering invertebrates, the major part of known social life is restricted to insects, mainly Hymenoptera. It is not common in Arachnida, where spiders, in particular, compound a group recognized as solitary, intolerant, and sometimes territorial and cannibalistic animals (D´Andrea 1987; Gonzaga 2007; Lubin and Bilde 2007). However, one can be surprised with notable examples of huge spider colonies able to produce permanent aggregations maintained by a cooperation system (D´Andrea 1987; Gonzaga 2007; Lubin and Bilde 2007). Nevertheless, the differences among insects and spiders (e.g., Wilson 1971; Darchen and Delage-Darchen 1986; Avilés 1997; Plateaux-Quénu 1997; Choe and Crespi 1997; Costa 2006) are obvious and well discussed. In Arachnida, the most complex models of cooperative societies occur in Araneae, for example *Anelosimus eximius* and *Stegodyphus dumicola*, among others (Avilés 1997; Gonzaga 2007; Lubin and Bilde 2007). In Arachnida, only Pseudoscorpions can present social life as developed as spiders (Tizo-Pedroso and Del-Claro 2007).

Recently, a well-done analysis revealed important similarities among insects' and spiders' social life (Choe and Crespi 1997; Costa 2006), but the universality of social stages classification is also a matter of question (Wilson 1971; Darchen and Delage-Darchen 1986; Avilés 1997; Plateaux-Quénu et al. 1997; Wcislo 1997; Costa 2006). Indeed, the three basic attributes for a species to be considered eusocial (Table 1), based on insects (Michener 1974), are not totally applied to other invertebrates. Depending on the ecological factors, non-insect species can fill up the attributes of eusociality in a specific moment but not in other circumstances (Costa 2006). In the existent systems, it is difficult to point out where Pseudoscorpions could be placed. Thus, we will use the model proposed to social spiders by Kullmann (1972) to classify the known Pseudoscorpions species and discuss the main characteristics and evolutionary process related to Pseudoscorpions social behavior.

The Pseudoscorpiones order

Pseudoscorpions are small arachnids (2–8 mm) that live in cryptic environments such as leaf litter, rock crevices, under stones and barks of live trees, and or rotten trunks, among others (Weygoldt 1969; Harvey1986). In Europe and North America, there is a species very common inside old and missed books, *Chelifer cancroides* (Linnaeus 1758; Cheliferidae), which has scared through time several librarians, being popularly known as book scorpions (Levi 1953). These animals, also named false scorpions, resemble scorpions in morphological aspects like shape and presence of chelated pedipalps, but differ strongly in size, being smaller and by the absence of the elongated metasoma with the sting in distal portion (Weygoldt 1969; Harvey 1986). Pseudoscorpions occur in almost all terrestrial environments, including islands, where they arrive through phoresy associated to birds for example, wherein an exception are polar regions (Harvey 1986 and references therein).

Pseudoscorpiones is a diversified order that represents more than 3% of all known arachnids, the fourth most diverse group in this class. They are distributed in 25 families, 470 genera, and around 3,400 described species (see Harvey 2002, 2007 for recent statement of systematic). If we consider the small number of taxonomists in this peculiar group, the cryptic habit of the major part of known species, and lack of precise information about tropical invertebrate diversity, we can speculate that these numbers could be, in fact, bigger. Fossil proofs demonstrated that these animals have walk about on Earth since early Devonian, 380 millions of years, and present very few morphological modifications in relation to the extant species (Shear et al. 1989). These ancestors, related to Chthonioidea, already had pedipalps, chelicerae, galea (structure used to produce silk), and trichobothria to perceive vibrations. Due to its similarities, in size, morphological aspects, and suggested habitats by fossil records, some researchers believe that the biological and behavioral features could have been maintained (Shear et al. 1989; Poinar et al. 1998).

Life history

Microhabitat

Pseudoscorpions, in the Old and the New World, are predominantly solitary animals that can live in the ground substratum, in the vegetation, or in both; they use one or other ways to find a better ecological resource. In spite that the most common species lives in the leaf litter, rock crevices, or bark trees, there are also species that inhabit unexpected places like rosettes of Bromeliaceae (Weygoldt 1969; Aguiar and Bührnheim 2003) and other vegetation in coast (Gabbutt 1970), bat guano (Andrade and Gnaspini 2002), ant and bee nests (Cole et al. 1995; Gonzalez et al. 2007), and the body of birds and mammals (Francke and Villegas-Guzman 2006). Regardless that the lifetime of adults is poorly known (Levi 1948, 1953), literature data suggest that their lifetime is too variable just as their habitat preferences. *C. cancroides* (Cheliferidae) for example, can live several years, including three post-embryonic stages that can delay 1 or 2 years. To other species, Weygoldt (1969) pointed out that the post-embryonic development can delay more than 1 year, but also without present reliable information about adult lifetime. We have been studying a Neotropical species, *Paratemnoides nidificator* (Atemnidae), and our data regarded in laboratory conditions showed that the whole lifetime of this species is around 4 years in laboratory ($X \pm SD = 46 \pm 14$ months; $N = 34$ individuals, 17 males and 17 females).

Table 1 The basic features of eusocial Hymenoptera (adapted from Wilson 1971) applied to cooperative spiders and Pseudoscorpions

Social features	Eusocial insects	Cooperative spiders	Cooperative Pseudoscorpions
Cooperative breeding[a]	+	+	+
Overlapping generations[a]	+	+	+
Reproductive caste[a]	+	–	–
Cooperative forage	+	+	+
Haploidiploid system	+	–	–

[a] Attributes most commonly used by most authors to consider a species as eusocial

Diet

Springtails, book lice, beetles, and other insect larvae, mites, and other small invertebrates constitute the food items of these active predators (e.g., Gilbert 1951; Weygoldt 1969; Harvey 1986). Both adults and juveniles are able to hunt, and in general, juveniles feed with higher frequency (Levi 1948; Weygoldt 1969). In the hunting behavior, the pedipalps are important weapons for prey capture (Schlegel and Bauer 1994). There is a poison gland associated to one or both pedipalps' fingers (or can be absent in some families) to subdue and paralyze the prey (Harvey 1992). In fact, the toxin is inoculated through a more developed tooth present in the distal portion of the chelae that is also used to grasp the prey's body to its pedipalps (Gilbert 1951; Schlegel and Bauer 1994). In Epiocheirata, there is no poison gland, which is an important taxonomic aspect (Harvey 1992). Solitary species present some prey specificity, for example, *C. cancroides* is a predator of book lice and other small insects (Levi 1948, 1953); in caves of South America, *Maxchernes iporangae* (Mahnert and Andrade 1998; Chernetidae) feeds on small invertebrates that lives on bat feces (Andrade and Gnaspini 2002). On the other hand, recent studies have showed that social species can be generalist and that it is probably related to the major needs of food supply to satisfy an entire colony. Tizo-Pedroso and Del-Claro (2007) studied the forage ecology and social life of *P. nidificator* (Atemnidae) in the Brazilian savannas and documented the use of more than 60 distinct prey items (15 taxonomic groups), which included dangerous preys like ants and spiders (Fig. 1). Pseudoscorpions can also present cannibalism, a characteristic of solitary species that also can occur among individuals of different colonies in the social species (Weygoldt 1969; Tizo-Pedroso and Del-Claro 2007).

Dispersal behaviors

Due to its small size, Pseudoscorpions present restrictions to disperse or to migrate to other environments. The most common way to explore a new site is, indeed, to walk from one place to another. It enables Pseudoscorpions to occupy a new piece of a bark tree a few meters distant from the original position in the same tree or in a neighbor tree, for example. However, Pseudoscorpions can present an unexpected way of dispersion. They can be phoretic, attaching itself to the body parts of a larger flyer insect as a vehicle or they can ride the vector (Poinar et al. 1998; Zeh and Zeh 1992a, b). Phoresy is a common way of dispersion also observed in other arachnids like mites and also insects that use the body of birds and mammals. To Pseudoscorpions, it is barely discussed and has already been evidenced in 11 of the 25 families (Poinar et al. 1998). Some authors believe that it can represent an important way to the foundation of new colonies in social species (Fig. 2; Tizo-Pedroso and Del-Claro 2007). This field work is promising because there are some incredible cases of phoresy in Pseudoscorpions, like that of *Cordylochernes scorpioides* (Linnaeus 1758; Chernetidae, Zeh and Zeh 1992c, d). This animal uses the body of Harlequin giant beetles (*Acrocinus longimanus*, Cerambicidae) as a vehicle, and males dispute the vector. Additionally, the copulation and sperm transfer in this species can occur on the beetle's dorsum (Zeh and Zeh 1997).

Fig. 1 Invertebrate taxonomic groups used as food item by *P. nidificator* in Brazilian Cerrado. *Numbers above columns* represent the total of morph species in the groups (adapted from Tizo-Pedroso and Del-Claro 2008)

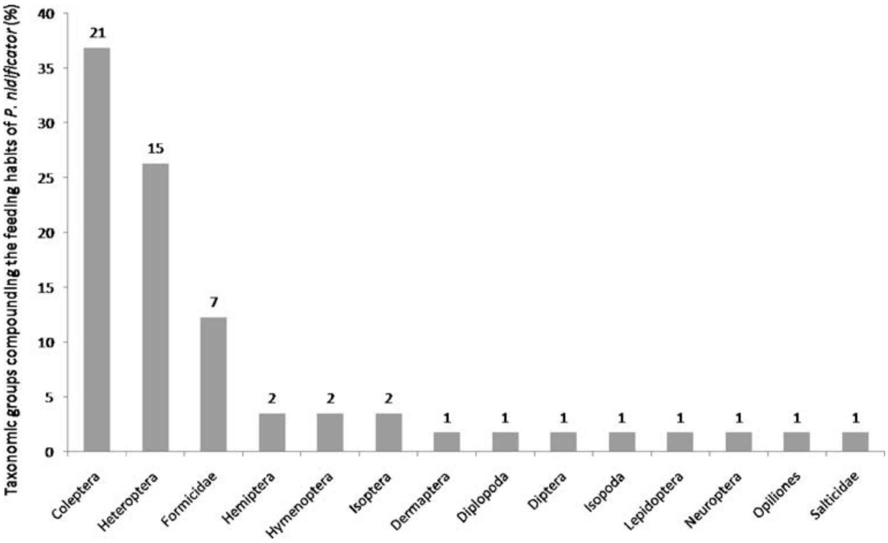

Fig. 2 Multiple phoresy behavior. Several individuals of *P. nidificator* attach themselves on the vector appendices (in this case a hemypteran predator) to disperse to new environments

Reproduction

The reproductive behavior of Pseudoscorpions is known only in 13 of the 25 families (Zeh and Zeh 1997). They are dioic animals, with internal fecundation and indirect sperm transfer, through a spermatophore. This structure, the spermatophore, a package full of sperm, is deposited on the ground in the courtship ("pairing behavior"), or this "bag" is simply abandoned in a common way to be found by the females (Weygoldt 1969). When there is pairing behavior, the spermatophore is more complex in its structure, and it presents some triggers that enable attachment to the female's genital opening (Weygoldt 1969). These animals, in general, reproduce once a year, but it can be different in social species, which might present successive reproduction events through the year, mainly in summer and spring (Tizo-Pedroso and Del-Claro 2007). Unfortunately, there are few data about the reproductive system such as information about ecology, natural history, and behavior of these animals. In fact, in some cases, there is no direct contact between male and females, thus so, there is no pairing behavior (Zeh and Zeh 1997).

The social life of Pseudoscorpions

As previously mentioned, Pseudoscorpions are primarily solitary animals. However, these solitary species present parental care, a common characteristic expected in all known species (e.g., Weygoldt 1969). In Chthonioidea, a classical example, the female produces a brood pouch that is maintained and attached to its genital opening. It is similar to a sac full of fluids and embryos inside. The mother sometimes can build a silk chamber, but it depends on the species. When the female does not produce the silk chamber, it remains with the pouch until the nymphs hatch, and in 1 or 2 days, the dispersion occurs. When the chamber is produced, the female stays inside the chamber until the protonymphs hatch. Also, 1 or 2 days later, the dispersion occurs (e.g., Weygoldt 1969). To all known species, females produce a nutritive fluid that feeds embryos and nymphs in development.

The major part of Cheliferoidea is solitary but its embryonic sac is different, which is a membranous and well-defined structure that results in a clear separation of each embryo. In this case, the structure is named brood sac (Fig. 3). This superfamily is divided into Chernetidae, Atemnidae, Cheliferidae, and Withiidae. The existence of some degree of sociality in members of the Cheliferidae, Chernetidae, Atemnidae, and also in Neobisiidae was identified. These families could represent the first steps in the development way of social behavior in this animal group: gregarity. Levi (1948, 1953) reported the founded aggregations of *C. cancroides* (Cheliferidae), a species recognized to be solitary and sometimes territorial (Levi 1953; Weygoldt 1969). Gregarity was evidenced through simple observation of groups of individuals together in the soil at the basis of plants. In Neobisiidae were evidenced cases of aggregations in one species from the litoranean zone, *Neobisium maritimum* (Leach 1817). This European species lives insides crevices of rocks, and two or three reproductive females can build reproductive chambers side by side (Gabbutt 1966; 1970). However, it is only an anecdotal observation since there are no data about any cooperation, only a suggestion. Weygoldt (1969) in his extensive studies in Pseudoscorpion biology described females of *Neobisium muscorum* (Leach 1817) that build cooperatively their reproductive silk chamber. Another extraordinary example was presented by Orghidan and

Fig. 3 Female of *Americhernes bethaneae* (Mahnert 1978) in its reproductive silk chamber. The embryos develop in the brood sac attached in the mother's genital opening

Dumitrescu (1964), that reported aggregations of dozens of adults and their silk chambers in the Cheliferidae *Hysterochelifer meridianus* (Linnaeus 1758) and in the Cheridiidae *Apocheiridium ferum* (Simon 1879). Turk (1953) described a small Chernetidae from Argentina, *Sphenochernes schulzi* (Turk 1953), that appears to have some degree of cooperation like capture of large prey (ants) or collective dispersion. Another form of sociality occurs in Atemnidae, in this case based on more elaborated maternal care. In this case, females of *Atemnus politus* (Simon 1878) are able to provide maternal care up to the brood dispersion. The more elaborated cases of sociality in Pseudoscorpions are seen in *Paratemnoides* genus (Table 2).

The *Paratemnoides* case

The *Paratemnoides* genus (Harvey 1992) encloses an important number of species known in Atemnidae (Chamberlin 1931). Nowadays, 33 species are recognized and widely distributed through Americas, Africa, and Asia (Harvey 2008). In contrast to the great richness of this genus, the literature provides very few data about its natural history, ecology, or behavior. The few information available report two social species in the Americas: *P. nidificator* (Balzan 1888) and *Paratemnus elongatus* (Banks 1895). Recently, *Paratemnus minor* (Balzan 1892) was recognized as a synonym of *P. nidificator*. For a review in statement of *Paratemnoides*, see Klausen (2005). Brach (1978) was the first to call attention to aspects of the cooperative life in Pseudoscorpions. The author observed colonies of *P. elongatus* in the bark of *Pinus elliotti* at Florida, and he reported a series of communal behaviors like the group life, multiple phoresy, and the existence of silk chambers, built side by side inside the colonies. The forage behavior of this species was investigated in more details by Zeh and Zeh (1990) that observed groups of *P. elongatus* capturing preys up to 30 times heavier than an individual hunter. After that, natural history aspects, with details of group life and post-embryonic development, were reported also to *P. minor* in Brazil (Hahn and Matthiesen 1993a, b). However, the extreme sociality in Pseudoscorpions was revealed only in recent days in a series of papers by Tizo-Pedroso and Del-Claro (2005, 2007, 2008) with *P. nidificator*.

Table 2 Available knowledge about social behavior in Pseudoscorpions

Species	Family	Distribution[a]	Social level	Classification[b]	Author(s) and publication year
Paratemnoides nidificator	Atemnidae	Central and South America	Permanent and cooperative life form	Non-territorial permanent social	Hahn and Matthiesen (1993a, b); Tizo-Pedroso and Del-Claro (2005, 2007, 2008)
Paratemnoides elongatus	Atemnidae	Central and South America and south of North America	Permanent and cooperative life form	Non-territorial permanent social	Brach (1978); Zeh and Zeh (1990)
Atemnus politus	Atemnidae	Europe and north of Africa	Extended maternal care	Subsocial	Weygoldt (1969)
Apocheiridium ferum	Cheiridiidae	Europe	Large aggregations of adults and silk chamber	Temporary social	Orghidan and Dumitrescu (1964)
Chelifer cancroides	Cheliferidae	Cosmopolitan	Facultative aggregations	Temporary social	Levi (1948, 1953)
Hysterochelifer meridianus	Cheliferidae	Europe and north of Africa	Large aggregations of adults and silk chamber	Temporary social	Orghidan and Dumitrescu (1964)
Sphenochernes schulzi	Chernetidae	South America: Argentina	Some level of cooperation and group dispersion	No sufficient information for classify	Turk (1953)
Neobisium maritimum	Neobisiidae	France, Ireland; Portugal; United Kingdom	Two or three females can build silk reproductive chambers side-by-side in rock crevices	Non-territorial temporary social	Gabbutt (1962, 1966)
Neobisiuim muscorum	Neobisiidae	Europe	Facultative cooperation in brood silk chamber by females in laboratory	Non-territorial temporary social	Weygoldt (1969)

[a] Additional information was obtained in Harvey's online catalog of Pseudoscorpiones (Harvey 2008)

[b] Based on Kullmann (1972)

P. nidificator is a common species that lives in communal nests under barks of Cerrado (the Brazilian tropical savanna) trees. Nests are composed of adults (sex ratio 2:3, males and females, respectively) and nymphs, sometimes more than 200 individuals (Tizo-Pedroso and Del-Claro 2007). Inside each nest, we can find several molt (minimum of three to up to 40 units) and brood chambers (less than seven units). The differences between the two types of chambers help us to understand the development of social life in this species. The silk molt chambers (Fig. 4a) are built exclusively by nymphs, in cooperation, and are used in the process of ecdysis. These chambers also act as a shelter against climatic disturbance, protection against natural enemies, and a place where nymphs and adults can interact. Brach (1978) suggested that when inside of the chambers, adults can termorregulate, which could maintain warm during the coldest hours. In the Cerrado, which is very dry and hot during the day but the temperature falls ten or more Celsius degrees at the night, we speculate that chambers can also help in the maintenance of humidity. Experimental manipulation revealed that the development of *P. nidificator* nymphs without the molt chamber can be interrupted by the attack of fungus, which kills them. Additionally, nymphs alone are unable to finish the chamber until the torpor phases of ecdysis needing help of their colony mates (unpublished data). The brood chamber is also built with the silk (Fig. 4b), this time produced by a reproductive female, which does the entire job alone. The female remains inside the chamber until the nymphs arise and pull off the brood sac. Then, the mother and the nymphs will leave the chamber only to feed on preys captured by other adults. So, males and other non-reproductive females allow the young individuals to feed freely on the prey they captured. Thus, this species exhibit not only nest cohabitation and food share but cooperation levels reaches cooperative parental care. Maternal care in this species shows another distinct feature. If a mother, for instance, is alone in the bark of a tree without help of coespecifics to get a prey and time is passing, it and its brood will be hungry. Tizo-Pedroso and Del-Claro (2005) showed that reproductive females of *P. nidificator* can offer themselves as food to brood in a process known as matriphagy. These authors suggested that in this case, by reducing the chances of cannibalism and increasing the individual tolerance, matriphagy should be considered an important step in the evolution of permanent sociality in this particular species.

Whitehouse and Lubin (2005), based on the functions of spiders society, proposed a new way to evaluate how social behavior evolved in Araneae. These authors suggested that colonies can have a protective, reproductive, or forage function. To the cooperative spiders, the authors suggest that the main function is to improve reproduction. Whitehouse and Lubin (2005) do not discard the possibility of overlap between functions. Social structure among Pseudoscorpions and cooperative spiders is similar, which suggest that the main function of sociality in Pseudoscorpions could also be reproductive. In social spiders, hunt cooperation is suggested to be more of a consequence than cause of group life (Whitehouse and Lubin 2005). In Pseudoscorpions, it is different. Although the reproductive function of group life be present and strong in *P. nidificator* (Tizo-Pedroso and Del-Claro 2007), the cooperative hunting is also fundamental. In colonies without hunt cooperation, the individuals disperse or die. Thus, we suggest that in social Pseudoscorpions, the positive result of a combination of distinct functions (reproduction, forage, and defense) could have favored the group life.

Non-territorial permanent sociality (sensu Avilés 1997) is considered the highest level of social organization in arachnids. To be a permanent social, the species has to present: group life, overlapping generations, common nest,

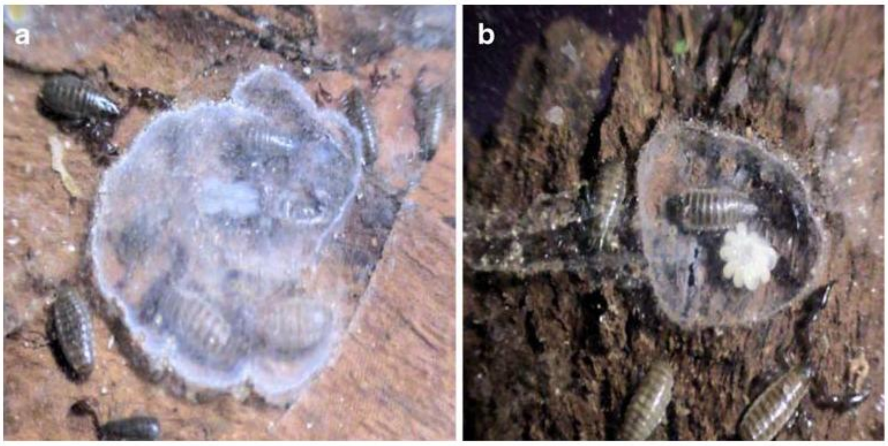

Fig. 4 Silk chambers in *P. nidificator*. **a** Molt silk chambers; **b** reproductive silk chamber

and cooperative behavior. In the case of *P. nidificator*, we suggest that this species goes beyond this classification. In fact, the nymph activities (mainly built of molt chambers that can be used by adults, see above) differ strongly from non-reproductive adult activities (hunt and defense) and from the reproductive female. Thus so, could it be considered division of labor, resembling social hymenopterans? Could this species be classified as *quasisocial* like several hymenopterans wasps? To us, extensive parental care, division of labor, cooperative breeding and feeding, and the tolerance among members that shares the same nest sounds enough to characterize a true social life seen in other invertebrates.

Sociality and Pseudoscorpiones phylogeny

The phylogenetic relationships between species that present some level of sociality could provide a better understanding of how social behavior evolved in Pseudoscorpions. Still, nowadays, available information is not enough to map and analyze phylogenetically the social strategies in this group. Murienne et al. (2008) proposed a general phylogeny to Pseudoscorpions based on molecular data, and their results do not corroborate the previous ones of Harvey (1992) that used traditional morphological analysis. The main difference is that to Murienne et al. (2008), superfamilies Neobisioidea, Garypoidea, and Cheliferoidea are not monophyletic groups. Here, we pointed and discussed the position of social species in the group (Fig. 5) based on Harvey (1992).

The Cheliferoidea superfamily groups six of nine known social species of Pseudoscorpions (Fig. 5) that are distributed in three families: Chernetidae (one species), Cheliferidae (two species), and Atemnidae (three species). These three families can be considered sister groups; however, according to Harvey (1992), they are not a monophyletic clade (but see also Proctor 1993). The other social species are in Neobisiidae and Cheiridiidae, groups that are very distant (Fig. 5).

Behavioral characteristics reveal that in Neobisiidae, the two social species, in fact, are gregarious with a very simple cooperation system. The Cheiridiidae species also present a very simple social behavior and huge aggregations without any cooperation. The major problem to understand social behavior in a phylogenetic perspective in Cheliferoidea is that the species present so different levels and mechanisms of sociality that it is difficult to suggest a common origin to this subgroup. For example, could it be that Cheliferidae followed a parasocial rote (sensu Wilson 1971) while Atemnidae followed a subsocial rote (sensu Wilson 1971)? The data about Chernetidae are so few that we can affirm nothing about it.

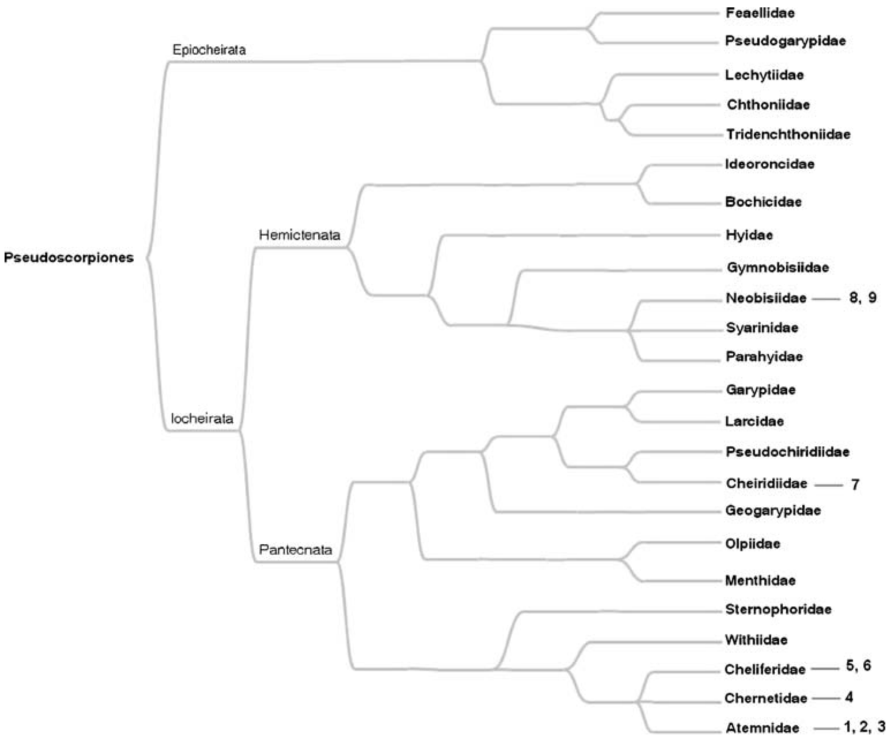

Fig. 5 The Pseudoscorpions phylogeny (adapted from Harvey, 1992), with the social species. *1 P. nidificator*; *2 P. elongatus*; *3 A. politus*; *4 S. schulzi*; *5 H. meridianus*; *6 C. cancroides*; *7 A. ferum*; *8 N. maritimum*; *9 N. muscorum*

Steps in evolution of social behavior in *Paratemnoides*

To establish and discuss similarities between social Pseudoscorpions and other social Arthropods is difficult, mainly due to the fact that they belong to groups phylogenetically distant, as for example Apidae (Hymenoptera), Theiridiidae (Araneae), and Atemnidae (Pseudoscorpiones). Despite this fact, Pseudoscorpiones are still now poorly known in all aspects compared with other arthropods. There are few details in the major part of papers that describes social behavior and also lack known cases that could be considered intermediate steps in the evolution of sociality in this group. Any proposal about the evolutionary steps that conducted Pseudoscorpions to sociality is only a speculation. In the specific case of *P. nidificator*, the extreme parental care, matriphagy (Tizo-Pedroso and Del-Claro 2005), is very suggestive. Matriphagy can reduce chance of cannibalism and increases tolerance among nymphs. Thus, individual tolerance in *P. nidificator* possibly resulted of matriphagy (Tizo-Pedroso and Del-Claro 2005) and could have also increased the chances of cooperative breeding and hunting among individuals, which progressively resulted in a more elaborate strategy of social life (Fig. 6). In cooperative spiders, the individual tolerance is also indicated as an initial step (Avilés 1997), followed by the life in a common nest (Lubin and Bilde 2007), cooperative hunting, and breeding (Lubin and Bilde 2007). Despite the fact that Pseudoscorpions and spiders have several biological differences, the similarities in social attributes suggest a convergent evolution. However, up to this moment, there is no enough information in the literature to support a linear hypothesis as proposed in the pioneer evolutionary studies of spider sociality (Kullmann 1972; D'Andrea 1987; Plateaux-Quénu et al. 1997).

Indeed, social life is rare among arachnids, and social *Paratemnoides* genus is a peculiar and unique example of permanent sociality (sensu Avilés 1997) in Pseudoscorpions. These animals call our attention to other relevant questions related to the evolution of the ecological scenery that allowed its derivation, like: Are we underestimating the occurrence of social behavior in this group? Is there any other social species in the Brazilian savannas and, also, in the almost unknown invertebrate fauna of the Amazonian forest? Could we find more examples in other similar tropical systems? Where are the intermediate Pseudoscorpion species that represents the step between the simple parental care present in all of them and the complex sociality observed in *Paratemnoides*? There is a lot of work to be done.

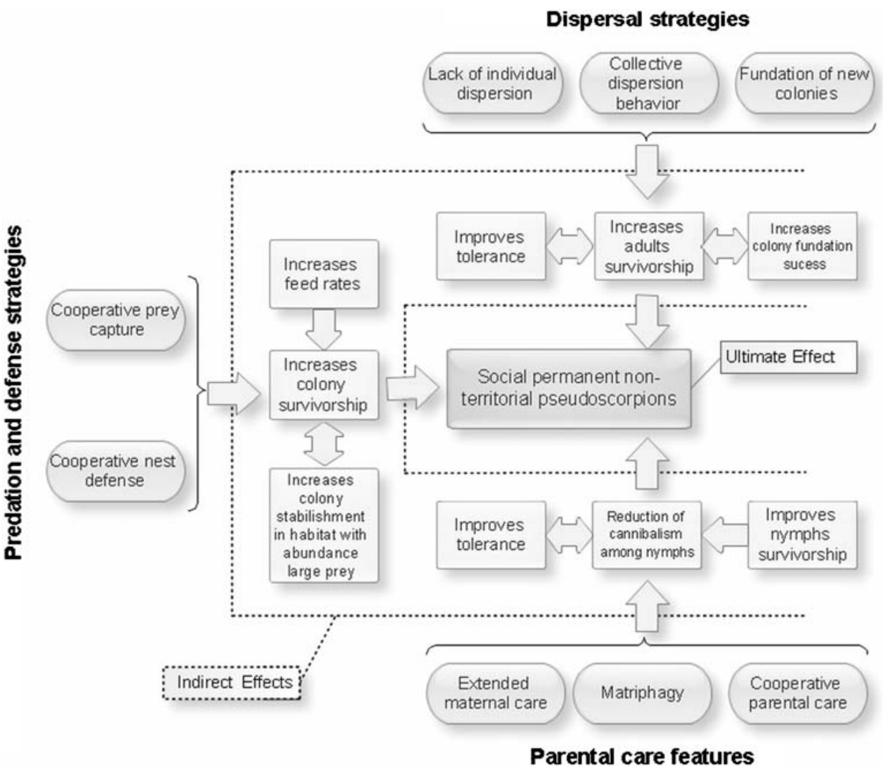

Fig. 6 Suggestive steps that conduced to the evolution of social behavior in *P. nidificator* (Pseudoscorpiones: Atemnidae). All Pseudoscorpions present parental care (basic feature). Matriphagy could increment it, reducing chances of cannibalism and enlarging tolerance and cooperative behaviors related to feeding, defense, and dispersal. Possibly, the sum of different adaptative features more probably resulted in a social permanent non-territorial species (sensu Avilés 1997) than a strong isolated aspect

Acknowledgments We thank Dr. Rui Oliveira for inviting us to write this review, Marina F. Mineo and Pietro K. M. Mendonça and two anonymous referees for suggestions and English review, and to Plamen Mitov for sending us copy of old papers about Pseudoscorpions. K. Del-Claro thanks the financial support from the CNPq (PQ) and the Fapemig. E. Tizo-Pedroso is supported by the Fapemig.

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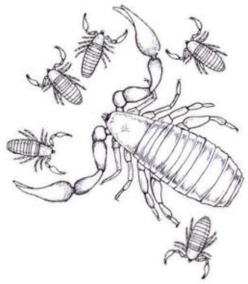
CONSIDERAÇÕES FINAIS

NOVAS PERSPECTIVAS NOS ESTUDOS COM PSEUDOESCORPIÕES SOCIAIS



O presente estudo trouxe novas inferências para a ecologia e a evolução do comportamento social em pseudoescorpiões. Em especial, contribuiu para traçar atributos do comportamento social e compreender etapas no processo de evolução: (1) os pseudoescorpiões sociais apresentam comportamentos muito plásticos, sendo capazes de se ajustar a condições ambientais muito variáveis e manter a vida gregária. (2) Este estudo mostrou que a reprodução de *Paratemnoides nidificator* está sincronizada com o período de maior abundância de presas e que a escassez de alimento não causa a segregação do grupo, mas favorece os comportamentos de divisão das colônias. (3) Os pseudoescorpiões sociais mostram condições adequadas para a evolução da divisão de tarefas, o que maximiza a organização das colônias, incrementa o papel de cada animal na manutenção do grupo, e por fim, acelera o desenvolvimento das colônias. (4) O complexo sistema social dos pseudoescorpiões pode ser uma porta (por meio da seleção natural) para que o comportamento social também apareça em outros pseudoescorpiões. (5) Estes fatores, somados aos complexos comportamentos parentais de *P. nidificator*, têm atuado na seleção do comportamento social.

Novas perspectivas no estudo do comportamento social dos pseudoescorpiões ainda deverão abordar um grande leque de variáveis, em especial os custos e benefícios da vida social. Nossos estudos estão constituindo apenas a etapa inicial para começarmos a entender como a socialidade complexa foi (e ainda está) sendo selecionada em um grupo tão pequeno de pseudoescorpiões. Espera-se que os resultados deste trabalho possam subsidiar testes de novas hipóteses. Atualmente, novos projetos estão sendo desenvolvidos, alguns ainda em fase inicial, outros, porém já em conclusão. Enumerar os projetos em fase mais avançada me parece uma medida importante para destacar os novos rumos para as próximas etapas.

Este pequeno aracnídeo tem experimentado um processo evolutivo quase único entre os pseudoescorpiões, mas que em suas pequenas partes mostra uma história convergente a outros organismos sociais. Assim, os pseudoescorpiões podem contribuir para compreensão da evolução do comportamento social em aracnídeos por meio de outra perspectiva, o surgimento de uma sociedade sob as cascas de árvores.