OXFORD

Article

Can morphological and behavioral traits predict the foraging and feeding dynamics of social arachnids?

Renan F. Moura[a],*, Everton Tizo-Pedroso[b] and Kleber Del-Claro[a]

[a]Laboratório de Ecologia Comportamental e de Interações, Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, 38402-020, Brazil; [b]Centro de Ensino e Aprendizado em Rede, Universidade Estadual de Goiás, Anápolis, GO, 75123-315, Brazil

*Address correspondence to Renan F. Moura. E-mail: renanfmoura@gmail.com
Handling editor: Ximena Nelson

Abstract

Complex social insect species exhibit task specialization mediated by morphological and behavioral traits. However, evidence of such traits is scarce for other social arthropods. We investigated whether the social pseudoscorpion *Paratemnoides nidificator* exhibits morphologically and behaviorally specialized individuals in prey capture. We measured body and chela sizes of adult pseudoscorpions and analyzed predation processes. Larger individuals spent more time moving through the colony and foraging than smaller pseudoscorpions. Individuals that captured prey had increased body and absolute chelae sizes. Although larger individuals had relatively small chelae size, they showed a higher probability of prey capture. Larger individuals manipulated prey often, although they fed less than smaller pseudoscorpions. Individuals that initiated captures fed more frequently and for more time than the others. Natural selection might be favoring individuals specialized in foraging and colony protection, allowing smaller and less efficient adults to avoid contact with dangerous prey. To our knowledge, there is incipient information regarding specialized individuals in arachnids, and our results might indicate the emergence of a morphologically specialized group in this species.

Key words: altruistic species, behavioral ecology, cooperative species, morphological specialization, Pseudoscorpiones, social arachnids

All over the world, many species, from human beings to honey bees, have built complex societies that allowed them to thrive. By working together, social species can repel natural enemies (Sridhar et al. 2009; Grüter et al. 2012; Sorato et al. 2012) and collect food (Sullivan 1984; Wilson 2000; Griesser et al. 2006), nourishing the young and even the weak (Lubin and Bilde 2007; Carter and Wilkinson 2015; Silk and House 2016). Nonetheless, despite having great advantages, the functioning of such intricate societies cannot work without an efficient process of task specialization (Gordon 2016).

Advanced societies have specialized individuals that increase both the individual and colony performance by efficiently executing specific tasks. For instance, some social species have individuals that perform better as soldiers when protecting their colonies from natural enemies (Powell 2008; Shackleton et al. 2015; Grüter et al. 2017), whereas others may be occupied in the colony's maintenance or obtaining food (Svanbäck and Eklöv 2003; Johnson 2008). Task specialization typically occurs among individuals of distinct developmental stages or ages: old termites of *Coptotermes formosanus*, for instance, are the main individuals responsible for grooming the queen (Du et al. 2016); in *Apis mellifera* bees, older adults spend more time foraging than the younger ones that perform safer tasks inside the colony (Jeanne 1986; Tofilski 2002; Tofilski 2006). In particular cases,

specialized individuals present specific morphometric traits that allow them to perform tasks with high efficiency. To exemplify, the bee *Tetragonisca angustula* has specialized individuals in colony protection: in comparison with foragers, they are 30% heavier and have a pair of long legs that are used to immobilize predators (Grüter et al. 2012).

Species with complex social structures are prominent among insects (Wilson 1971; Hamilton 1972; Wilson 2008; Wong et al. 2013), but when it comes to other arthropods, there are not many similar examples (Wilson 2000; Lubin and Bilde 2007). Although social spiders do not form such complex societies, they represent, perhaps, the most studied arthropods beyond insects and crustaceans (see Settepani et al. 2013; Junghanns et al. 2017; Chak et al. 2020). To exemplify, colonies of the social spider *Anelosimus studiosus* exhibit task specialization and have high variation in individual traits, where bold (aggressive) individuals are considered more efficient and participative in prey capture events than the shy ones (docile) (Chang et al. 2016; Parthasarathy et al. 2019).

In arachnids, there is evidence of social nonspider species such as the pseudoscorpion *Paratemnoides nidificator* (synonym of *P. elongatus*; Judson 2016). This small and gregarious species (adults exhibit 3–7 mm length, including pedipalps) lives under tree barks of the Brazilian Cerrado (Tizo-Pedroso and Del-Claro 2014) and is one of the few known social species among the pseudoscorpions (Weygoldt 1969). Its social organization fits the highest degree of the subsocial spectrum (Wilson 2000): they exhibit generation overlap and cooperative brood care, although there is no queen and all individuals can reproduce (Tizo-Pedroso and Del-Claro 2007). Colonies of *P. nidificator* have a few to hundreds of related individuals (Tizo-Pedroso and Del-Claro 2007; Del-Claro and Tizo-Pedroso 2009), and in previous studies, Tizo-Pedroso and Del-Claro identified altruistic and social traits in its colonies. For instance, in extreme conditions of food scarcity, the nymphs feed on their mothers' bodies, a behavior known as matriphagy (Tizo-Pedroso and Del-Claro 2005). They also exhibit division of labor mediated by age: nymphs spend more time building silk chambers—which are used to house nymphs, eggs, and pregnant females—than adults, which often perform tasks such as foraging and colony guarding (Tizo-Pedroso and Del-Claro 2011). These pseudoscorpions are sit-and-wait predators and exhibit a preference for large prey items (Tizo-Pedroso and Del-Claro 2007; Moura et al. 2018). By performing cooperative hunting, they can capture prey up to 4 times larger (length) than themselves, including several arthropods such as aggressive ants and spiders (Tizo-Pedroso and Del-Claro 2007; Moura et al. 2018; Ribeiro et al. 2018). The predation process of *P. nidificator* initiates with one attacking pseudoscorpion: this individual grabs either an antenna or one of the prey's legs and drags it under the tree bark, where other pseudoscorpions can join the attack (Moura et al. 2018). A recent study suggests that *P. nidificator* colonies have a well-structured hierarchy of feeding behavior: when a prey item is captured, adults allow nymphs to feed first whereas most of them remain nearby, protecting the feeding individuals (Tizo-Pedroso and Del-Claro 2018). Previous observations indicate that certain adult individuals within *P. nidificator* colonies perform foraging behaviors more often, and perhaps more effectively than others.

Here we aim to expand on our current knowledge of *P. nidificator* by verifying whether its colonies present individuals with differential foraging performances. The complex social traits exhibited by *P. nidificator* (Tizo-Pedroso and Del-Claro 2005; Tizo-Pedroso and Del-Claro 2007; Tizo-Pedroso and Del-Claro 2018), aligned with their ability to cooperatively capture large prey (Tizo-Pedroso and Del-Claro 2007; Moura et al. 2018), led us to investigate whether *P. nidificator* colonies have specialized adult individuals that perform foraging behaviors more often and efficiently than others. If that is confirmed, we predict that specialized individuals exhibit distinct morphological traits.

Materials and Methods

Experimental procedures

In the laboratory, we studied a total of 78 individuals of *P. nidificator* (3–15 individuals per colony) raised in 10 colonies for 2 years (see the complete dataset). During this period, they were fed with a combination of ants *Camponotus mus* and termites (*Coptotermes* sp.). We housed each colony using a piece of tree bark that was fixed into a covered a Petri dish (15 cm in diameter), which allowed us to observe the individuals through the glass (see details in Tizo-Pedroso and Del-Claro 2005; Tizo-Pedroso and Del-Claro 2007; Supplementary Figure S1). We tracked all adults (males and females) by marking their opisthosoma with different color combinations of nail polishes (see Tizo-Pedroso and Del-Claro 2018). All the other pseudoscorpions were left unmarked (protonymphs, deutonymphs, and tritonymphs). After 2 days of acclimation, we vertically positioned each Petri dish containing a single colony into a polystyrene holder. Then, we placed a ruler beside each dish and took pictures of it (Nikon D5000 18-55 mm VR KIT). We repeated this process for each colony. We then used the digitalized pictures to calculate the morphometric measures applied in statistical procedures (see the subsections "Data management" and "Statistical analysis"). The ruler allowed us to calibrate all measurements regardless of possible differences in the angles and distances of the pictures.

After the acclimation period, we positioned a light bulb with a faint white light to provide better visualization of the colony and waited for 3 min to mitigate the stress caused to the animals due to the handling process. Then, we offered 1 *C. mus* (0.5–0.8 cm body length) as prey to each colony. We chose this species as *P. nidificator* is commonly observed feeding on several *C.* ants in natural conditions (Moura et al. 2018). The ant was released over the piece of tree bark, being able to move freely around the Petri dish. At this point, we video-recorded all individuals within the colony (Canon VIXIA HF R600). When the ant was finally captured, we noted the single individual that started the predation process (which was considered the individual that successfully captured the prey), and we pointed the camera to the prey (with a footage area of ~3 cm of height and 4 cm of width) and continued recording for 1 more hour. Previous tests showed us that 1 h was enough for most pseudoscorpions to feed, simultaneously, on such prey. Ant trials were performed daily, but when a colony successfully captured a prey item, we waited for 48 h before repeating the trial with the same colony. This period ensured that each colony would be motivated to forage during the next trial. Trials were repeated 3–5 times with each colony: 6 colonies were observed 5 times, 3 colonies were observed 4 times, and 1 colony was observed 3 times. Our initial intent was to perform 5 trials per colony; however, we had to reduce the number of trials for certain colonies as some marked individuals died or lost their markings during the experimental period. Afterward, by observing these recordings, we qualified the behavioral repertoire of *P. nidificator* into 7 distinct behaviors (Table 1).

Table 1. Description of the behavioral repertoire exhibited by *P. nidificator* individuals during the study

Behavior	Description
Grooming	Chela cleaning by using the chelicerae
Immobile	No perceived activity
Movement	Active movement throughout the colony
Prey chase	Active prey hunting throughout the colony
Sit-and-wait	An immobile individual puts its chelae out of the colony's edge and waits for a prey to approach.
Holding prey	Prey immobilization using the chelae
Feeding	An individual attaches its chelicerae on dead or weakened prey

Data management

For further analyses, we divided the footage sessions into 2 segments: until prey capture and after prey capture. In the first segment, we analyzed the behavior of all marked individuals over the first 15 min of footage prior to prey capture. In cases where the predation process took longer, we analyzed the last 15 min of footage. During the second segment, we recorded the predation events for 1 h within the 3 × 4 cm shooting area and observed the behavior of the single individual that started the capture process and all other adults that joined it or remained in the footage area. All observations followed the focal-animal sampling: 1 at a time, each marked individual was observed until the end of the footage (Altmann 1974).

For each marked individual, we calculated the proportion of each observed behavior by dividing its duration period by the total period of observation. We did this to remove the effect of recording time, as it occasionally varied among individuals. For instance, if an individual was visible for 80% of the recorded time, we calculated all its behavioral proportions based on this percentage and ignored the time it was missing. These variations occurred when the individual left the recording area, went to the opposite side of the tree bark, or kept itself hidden in the bark recesses. From camera recordings until prey capture, we calculated the proportion of time of each behavior performed by marked pseudoscorpions and created a variable that included foraging and nonforaging behaviors.

Foraging behavior is a variable that included all acts related to movement, prey chase, and sit-and-wait posture, whereas nonforaging behavior included immobile time and grooming behaviors. We opted to gather variables since foraging is a complex process that involves multiple senses and behaviors (Raine and Chittka 2009). For instance, although *P. nidificator* usually rely on sit-and-wait tactics, they may also actively search and even chase prey when they are nearby (R.F.M., personal observation). Thus, combining behaviors may provide a more comprehensive view of how individuals forage (Remsen and Robinson 1990).

For recordings after prey capture, we were particularly interested to understand how *P. nidificator* organizes to feed. Given this, we separately evaluated only 2 behaviors: the time spent holding prey and feeding.

For statistical procedures, we used the proportion of the average time of these variables, dividing the behavioral proportion's sum by the number of videos in which a correspondent individual appeared (3–5 videos). We used this approach for recordings before and after prey capture. For example, if an individual appeared in 5 videos and spent, in each video, 25%, 5%, 0%, 10%, and 10% of its time performing the foraging behavior, by summing the proportion of these values and dividing the result by the number of videos, in this case,

$0.5/5 = 0.10$ (10%), we obtain the mean proportion of this behavior for that specific pseudoscorpion.

We calculated morphometric measurements using ImageJ software (Rasband 2016) on digitalized pictures (calibrated according to the positioned ruler near each colony). We calculated the following measures from marked pseudoscorpions: body length, chela area, and relative chela size. We estimated the body length by measuring each individual from its chelicerae margins to the opisthosoma end; pedipalps were excluded (Supplementary Figure S2). We opted to measure body length (millimeter) rather than width or area to disentangle the effect of body condition (i.e., how well-fed would a pseudoscorpion be during the measurement period) from body size. We approached chela size by measuring the outline (square millimeter) of these structures, including the articulated claw (1 chela per individual; Supplementary Figure S3). We determined the relative chela size by calculating the ratio between chela area and body length; this variable provides a measure of chela size proportionally to the pseudoscorpion body length, so we could test, for instance, whether larger pseudoscorpions have disproportionally large chelae (i.e., allometry).

It is important to clarify that although males and females of *P. nidificator* exhibit certain behavioral distinctions (e.g., females perform parental care; Tizo-Pedroso and Del-Claro 2005; Tizo-Pedroso and Del-Claro 2011), there is no evidence of differences concerning either their hunting behavior or their hierarchical feeding pattern: both males and females forage and feed on prey similarly (Tizo-Pedroso and Del-Claro 2011; Tizo-Pedroso and Del-Claro 2018). There is also no apparent morphological divergence between the sexes. In fact, we can only distinguish males from females by observing their genital openings: males have a "Y-shaped" opening whereas females exhibit a simple "dot-shaped" opening (personal observation). Thus, we conducted all analyses based on the assumptions that both males and females have no evident morphological distinction and that both perform foraging behaviors with equal frequency and proficiency.

Statistical analysis

First, we evaluated associations between body length and chela area variables using linear regressions. For recordings until prey capture, we tested whether body length was linearly associated with the foraging behavior variable. We used logistic regressions and Spearman's correlations to associate chela area, relative chela size, and body length variables with the occurrence of prey capture (whether a pseudoscorpion captured or not at least 1 prey until the end of the study), and the total number of captured prey per pseudoscorpion, respectively. We carried out 3 separate generalized linear mixed models (GLMMs) to verify relations between chela area, body length, and relative chela size (independent variables) and the occurrence of prey capture, using the colony identity ($n = 10$) as a random factor (Bates et al. 2014).

For recordings after prey capture, we applied linear regressions testing chela area, body length, and relative chela size (independent variables) specifically against the time holding prey and feeding behaviors described (see Table 1). We applied a GLMM testing for body length differences between those pseudoscorpions that were observed feeding at least once and those that were not observed feeding, using once again colony identity as a random factor. Finally, we applied a chi-square test to compare groups of individuals—captured or not prey—with the frequency of feeding behavior, and a Mann–Whitney test to assess differences between these 2 groups regarding the time spent feeding per individual.
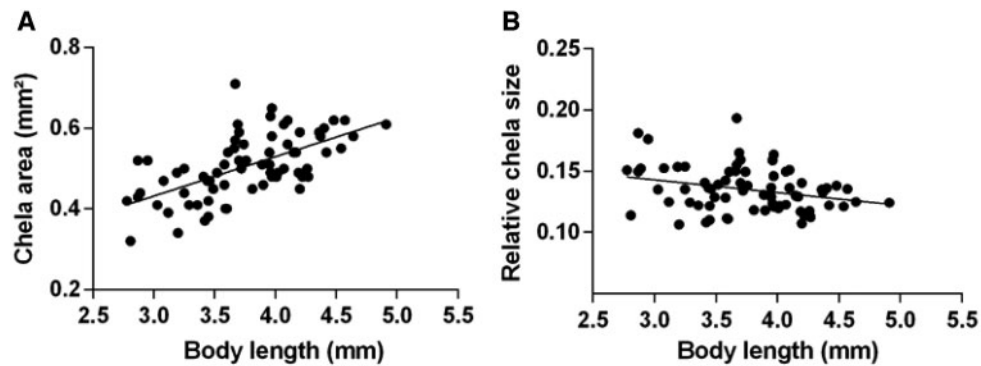
Figure 1. Linear regressions comparing *P. nidificator* body length with chela area (**A**) and relative chela size (**B**) (see "Materials and Methods" section for detailed descriptions of the applied variables). Larger pseudoscorpions had also larger chelae (a). Larger pseudoscorpions had relatively small chelae in comparison with their body length, although the effect size was very low (see "Results" section for details). All results are significant, according to $\alpha = 0.05$.
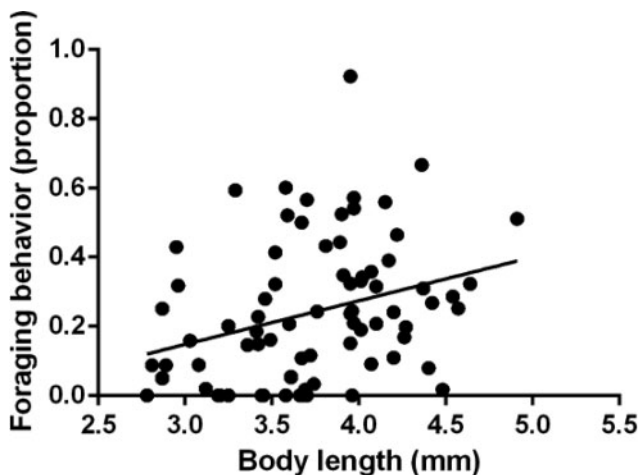

Figure 2. Linear regression between pseudoscorpion's body length and the proportion of foraging time spent, relative to the total time of observation per individual (15 min). Larger individuals spent more time performing foraging behaviors than smaller ones. We calculated the foraging behavior variable for each individual by using the mean of all its foraging behaviors combined (movement, prey chase, and sit-and-wait behavior; see "Results" and Table 1 for detailed descriptions of the applied variables). The result is significant, according to $\alpha = 0.05$.

We assessed statistical assumptions according to Zuur et al. (2010) and evaluated data normality by using boxplots, histograms, and Lilliefors normality tests. All tests were performed in the R statistical software. The variance homogeneity was assessed by using the function "var. test" from the "stats" package. We opted for non-parametric approaches (e.g., Spearman's correlation) when our data did not show variance homogeneity and normal distribution. We also used the "InfluencePlot" function from the "car" package (Fox and Weisberg 2018) and the "chisq.out.test" function from the "outliers" package (Dixon 1950) to identify, analyze, and remove possible outliers.

Results

We studied 3–15 marked adults per colony ($\overline{x} = 7.80 \pm 4.02$ SD; $n = 78$). Seventy individuals were used for morphometric measurements (e.g., body length), and 63 were observed in recordings after

Table 2. Logistic regression (left) and Spearman's correlation tests (right) comparing the occurrence of prey capture and the number of captures per pseudoscorpion to 3 predictive morphometric and behavioral variables

Occurrence of capture				Number of captures			
	Odds ratio	*Z*	*P*-value	*N*	*R*	*S*	*P*-value
Chela area	293.76	1.68	0.084	70	0.14	48945	0.24
Body length	4.97	2.72	**0.003**	78	0.29	56252	**0.010**
Relative chela size	0.00	−0.56	0.57	70	−0.06	60379	0.64

Both occurrence of capture and the number of captures were positively correlated with body length (see "Materials and Methods" section and Table 1 for detailed descriptions of the applied variables). Bold values indicate significant results according to $\alpha = 0.05$.

the prey capture. Eight individuals could not be used in morphometric measures as they were absent or not well framed in the pictures to be measured with precision. We found considerable differences regarding the body length of adult pseudoscorpions (2.78 to 4.91 mm; $\overline{x} = 3.75 \pm 0.05$ SE; $n = 78$) and chela (0.32 to 0.71 mm² of area; $\overline{x} = 0.50 \pm 0.01$ SE; $n = 70$). There was a positive relationship between body length and chela area ($F_{1,68} = 39.84$, $R^2 = 0.37$, $P < 0.001$; Figure 1A). We also observed that larger individuals had a slightly reduced relative chela size in comparison with smaller individuals ($F_{1,68} = 5.87$, $R^2 = 0.08$, $P = 0.018$; Figure 1B).

Recordings before prey capture

We observed that larger individuals spent slightly more time performing foraging behaviors (movement, prey chase, sit-and-wait behaviors combined) than the smaller ones ($F_{1,76} = 7.58$, $R^2 = 0.09$, $P = 0.007$; Figure 2; see Supplementary Table S1 for analysis considering each behavior separately), but neither chela size and relative chela size were associated with foraging behavior (chela size: $F_{1,68} = 2.81$, $R^2 = 0.04$, $P = 0.099$; relative chela size: $F_{1,68} = 0.42$, $R^2 = 0.006$, $P = 0.52$). We also found that body length was the most relevant variable to predict the chance of a pseudoscorpion in capturing prey: for each increase of 1 mm in body length, the chance increased almost 5 times (odds ratio = 4.97; Table 2). Furthermore, body
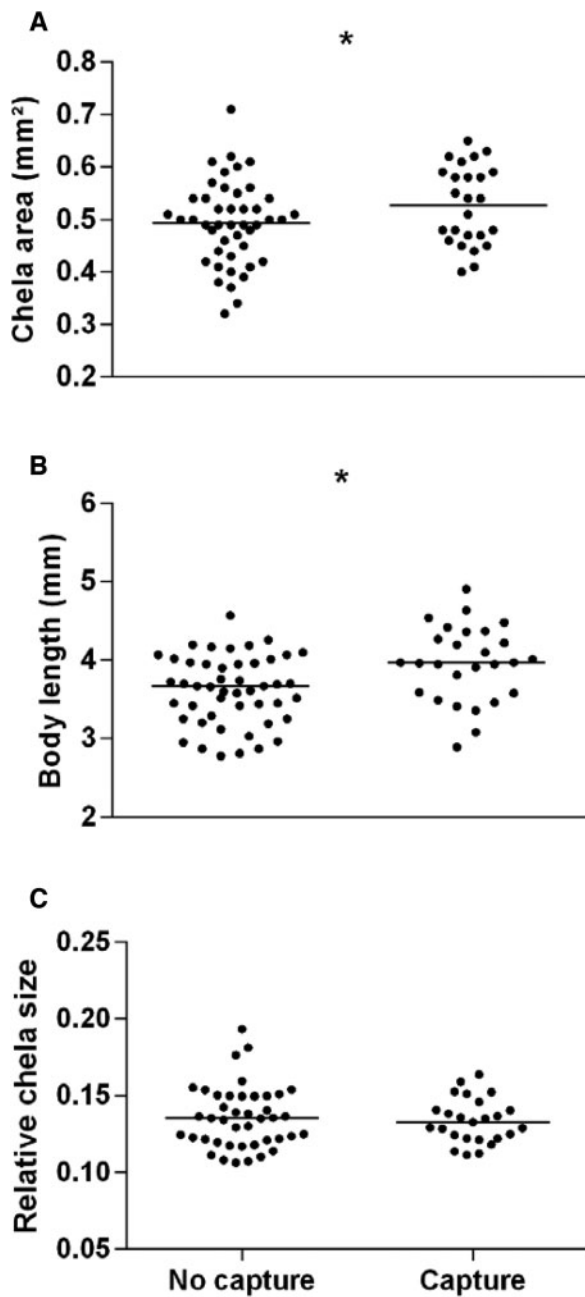
Figure 3. Results of GLMM comparisons between individuals that did not perform prey capture and those that did, regarding chela area, body length, and relative chela size. Individuals captured at least 1 prey had increased values of chela area (**A**) and body length (**B**), but there were no differences considering relative chela size (**C**) (see "Materials and Methods" and Table 1 for detailed descriptions of the applied variables). Asterisks indicate significant comparisons, according to $\alpha = 0.05$. Horizontal bars indicate the median values.

length was positively associated with the number of prey captured (maximum of 3 captures by the same individual); this means that larger pseudoscorpions tend to capture prey more often than smaller pseudoscorpions. However, we observed no effects of both chela area and relative chela size on the occurrence and number of captures (Table 2).

GLMMs revealed that individuals that captured at least 1 prey had larger chela area ($\bar{x} = 0.53 \pm 0.02$ SE) than those that did not ($\bar{x} = 0.49 \pm 0.01$ SE; $F = 4.43$, $P = 0.039$; $n = 70$; Figure 3A). They also had larger body length ($\bar{x} = 3.96 \pm 0.09$ SE) than pseudoscorpions that did not capture any prey ($\bar{x} = 3.64 \pm 0.06$ SE; $F = 10.72$, $P = 0.002$; $n = 78$; Figure 3B). Regarding relative chela size, there were no differences between individuals that captured prey ($\bar{x} = 1.34 \pm 0.003$ SE) and those that did not ($\bar{x} = 1.36 \pm 0.003$ SE; $F = 0.33$, $P = 0.57$; $n = 70$; Figure 3C).

Recordings after prey capture

We observed that larger individuals spent more time holding prey during feeding behaviors than the smaller ones ($F_{1,61} = 7.25$, $R^2 = 0.11$, $P = 0.009$; Figure 4A), although larger individuals spent less time feeding ($F_{1,61} = 4.77$, $R^2 = 0.07$, $P = 0.033$; Figure 4B). Surprisingly, we found that individuals that fed at least once had smaller body length than those that did not feed ($\bar{x} = 3.68 \pm 0.08$ SE; $\bar{x} = 3.88 \pm 0.09$ SE; $F = 4.57$, $P = 0.037$; $n = 63$; Figure 4C). Furthermore, individuals with increased relative chela size held prey for shorter periods ($F_{1,52} = 9.67$, $R^2 = 0.16$, $P = 0.003$; Figure 4D), but there was no effect of this variable on their feeding behavior ($F_{1,50} = 0.04$, $R^2 = 0.001$, $P = 0.85$). There were no effects of chela area, body length, and relative chela size on any other behavioral variable (Supplementary Table S2). About 57% of individuals that captured at least 1 prey were observed feeding, whereas <33% of those that did not capture any prey were observed feeding ($\chi^2 = 4.49$, $P = 0.034$; $n = 80$; Figure 5A). Furthermore, individuals that captured at least 1 prey spent more time feeding than those that did not ($U = 550.5$, $P = 0.046$; Figure 5B).

Discussion

We suggest that *P. nidificator* colonies have morphologically and behaviorally specialized individuals in predation processes. We observed a weak allometric association between body length and chela size, where larger individuals had a reduced chela size. Although this variable had no association with most behavioral performances of *P. nidificator*, we demonstrated that larger pseudoscorpions and those with increased chela size captured prey more often as they spent more time foraging. Larger individuals also spent more time handling and subduing prey, although they spent less time feeding than the smaller ones. Furthermore, pseudoscorpions that fed at least once had a shorter body length than those not observed feeding. These 2 last results strengthen our argument that body size is not a simple product of food intake. Finally, we observed that individuals that initiated prey capture fed more frequently and for longer periods, irrespective of their size.

Larger pseudoscorpions were more aggressive and spent more time foraging, indicating that colonies have individuals with distinct behavioral traits; however, we emphasize that this result should be taken with caution as the effect size was very low. Tizo-Pedroso and Del-Claro (2018) also found behavioral differences among *P. nidificator*: some individuals do not participate in predation processes and they are the last individuals to feed. In social spiders, larger individuals are more aggressive and effective in prey capture (Brown et al. 2007), although this can be a transitory effect caused by hunger levels experienced by each individual. In some social spiders, however, individuals exhibit consistent behavioral variation, which is depicted by differences in individual traits or developmental stage (Settepani et al. 2013; Parthasarathy et al. 2019). Even considering that smaller and shy *P. nidificator* had increased periods of apparent
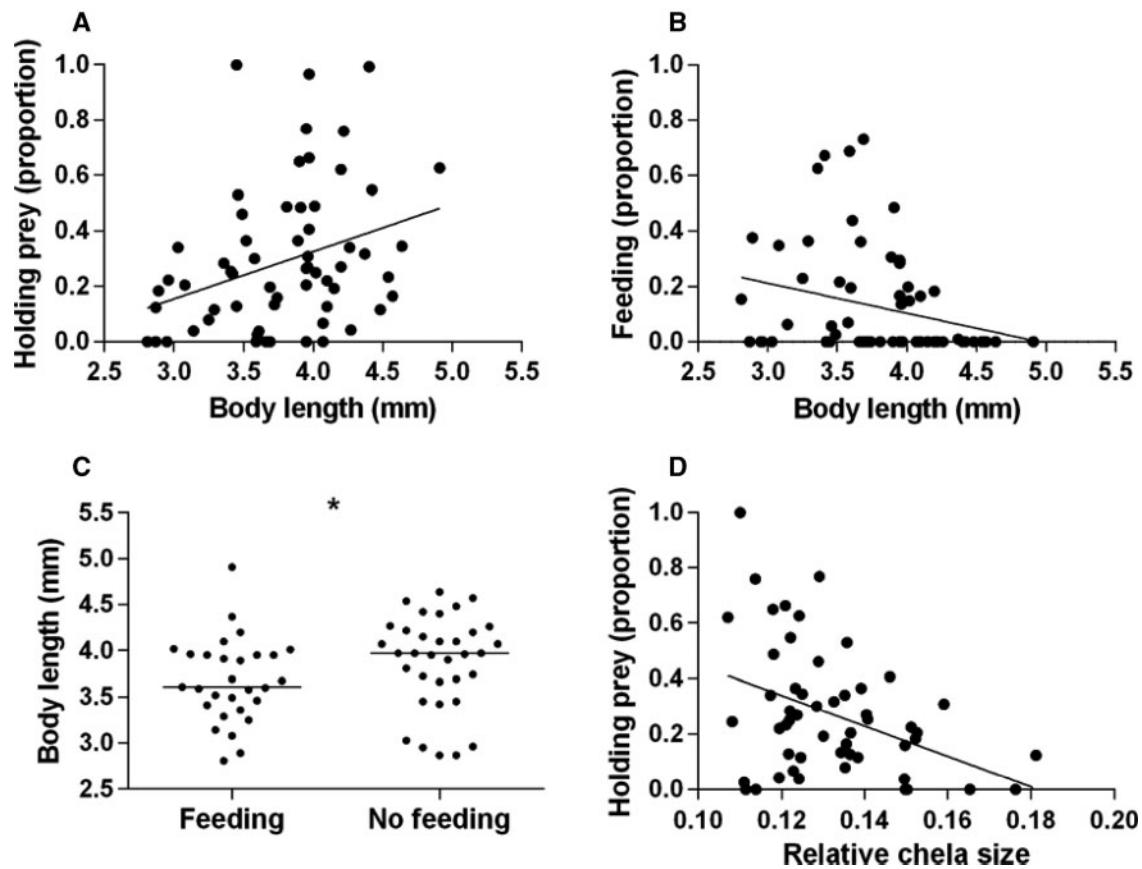
Figure 4. Linear regressions (**A**, **B**, and **D**) and a GLMM (**C**) testing the relationship between several variables of *P. nidificator* after the capture of an offered prey (1 h of observation). Larger pseudoscorpions held prey for long periods (**A**), but they spent less time feeding than smaller individuals (**B**). Pseudoscorpions observed feeding at least once had a smaller body length, in average, than those not observed feeding (**C**). Individuals with increased relative chela size held prey for shorter periods (**D**). All comparisons were significant, according to $\alpha = 0.05$. Horizontal bars in (**C**) indicate the medians.

inactivity, we speculate that they might be more proficient in other tasks, such as parental care and colony maintenance, which may explain such behavioral variation. This characteristic is often observed in social ants and bees, where some individuals rarely forage, being specialized in tasks such as colony maintaining and brood care (Wilson 2000).

We observed that larger individuals with larger chelae captured more prey than the smaller ones, although they had relatively smaller chelae in comparison with smaller individuals. Morphological specializations are factors related to foraging efficiency, colony protection, and the social behavior of many social species, as they may allow the capture of high-quality prey (Svanbäck and Eklöv 2003; Grüter et al. 2012; Grüter et al. 2017). However, for *P. nidificator*, we suggest that chela size plays a minor role in predation, as most of its effect sizes were small and because individuals with increased relative chela size tended to held captured prey for shorter periods. Body length, on the other hand, seems to be more relevant for captures especially if we consider that *P. nidificator* typically needs to force and trap large prey under the tree barks (see Moura et al. 2018). Hence, individuals with larger bodies should control and hold prey for longer periods, easing the predation process.

The occurrence of larger pseudoscorpions, nonetheless, could be a consequence of prey capture rather than an effect, since we

observed an association between body length and a set of predatory behaviors. This result could mean that aggressive individuals feed on prey more often, resulting in individuals of large sizes. Nonetheless, although larger pseudoscorpions spent more time manipulating prey, they spent slightly less time feeding. Also, individuals that did not feed had larger body sizes than those that fed at least once. Given that we failed to demonstrate that both feeding time (Figure 4B) and occurrence (Figure 4C) were positively associated with body length, we cannot argue that larger body sizes are a simple product of increased food intake. Furthermore, we showed that larger individuals spent more time foraging and handling prey, and such activities clearly demand energy. For *P. nidificator*, foraging activities should be particularly costly given their preference for large and often dangerous prey (Moura et al. 2018). Thus, we suggest there is a group of naturally large and aggressive individuals with higher predation potential in *P. nidificator* colonies.

The observed feeding pattern partially supports Tizo-Pedroso and Del-Claro's (2018) claims, where they observed a hierarchical pattern of prey sharing in *P. nidificator* feeding behavior: it starts with nymphs and the few adults that performed the prey capture, and then the rest of the individuals may feed on the carcass. Nonetheless, our results suggest that the larger attacking pseudoscorpions allow not only nymphs to feed first, as described by Tizo-Pedroso and Del-Claro (2018), but also smaller adults.
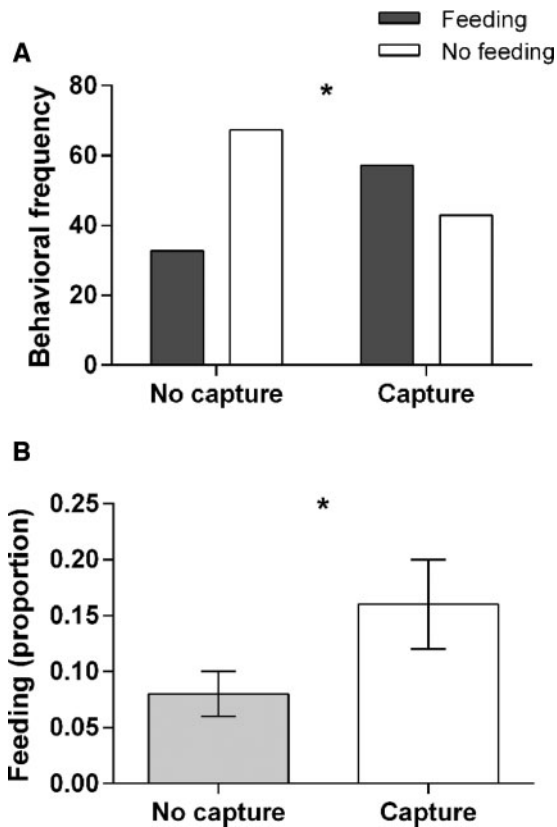
Figure 5. Results of chi-square (**A**) and Mann–Whitney (**B**) tests on the feeding behavior of pseudoscorpions that did not perform any prey capture and those that did. The single individual that started the prey capture fed more frequently than those that did not capture any prey (**A**). The single individual that started the prey capture fed for longer periods than those that did not capture any prey (**B**). All comparisons were significant, according to $\alpha = 0.05$. Error bars indicate the standard error of the mean.

Smaller adults benefit from prey sharing processes as they have a reduced potential in prey capture, which is critical for their survival since *P. nidificator* consistently forages on large and dangerous prey (Tizo-Pedroso and Del-Claro 2007; Moura et al. 2018). Larger pseudoscorpions also benefited the smaller ones by allowing them to spend more time feeding. However, we observed that the feeding behavior changed according to predation timing: the single pseudoscorpion that started the predation process was rewarded by feeding more frequently and for longer periods than the others. This exception might explain the risk taken by aggressive individuals (Willey and Jackson 1993; Mukherjee and Heithaus 2013), revealing that the benefits experienced by smaller pseudoscorpions are not pervasive.

In conclusion, we speculate that selection might be favoring larger, more aggressive, and presumably more effective pseudoscorpions to attack prey often, whereas the smaller individuals—less exposed to the risks of foraging activities—are still able to occur as they feed on prey captured by larger pseudoscorpions. This foraging behavior is also described in social spiders, where juveniles feed on prey captured by adults, as they are not fully developed to forage on their own (Lubin and Bilde 2007).

Here, we demonstrated that *P. nidificator* individuals exhibit significant differences regarding their behavior and morphology, and although some of our findings were subtle, we believe they indicate the presence of behaviorally and morphologically specialized

individuals in this species. Regardless, we still need to understand whether less proficient individuals in prey capture stand out in other tasks within colonies and how the presence and frequency of large prey might have shaped its social behavior—not to mention the completely unknown paths regarding the genetic aspects of this species. As far as we know, there is insipient evidence of task specialization, especially among nonspider species, and no evidence of specialized morphological subcastes among arachnids (Lubin and Bilde 2007). Hence, the social singularity of *P. nidificator* makes it a good model for studies that aim to clarify the ecology and evolution of social arthropods.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Altmann J, 1974. Observational study of behavior: sampling methods. *Behaviour* **49**:227–266.

Bates D, Mächler M, Bolker B, Walker S, 2014. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**:1–48.

Brown C, Jones F, Braithwaite VA, 2007. Correlation between boldness and body mass in natural populations of the poeciliid Brachyrhaphis episcopi. *J Fish Biol* **71**:1590–1601.

Carter GG, Wilkinson GS, 2015. Social benefits of non-kin food sharing by female vampire bats. *Proc Biol Sci* **282**:20152524.

Chak STC, Barden P, Baeza JA, 2020. The complete mitochondrial genome of the eusocial sponge-dwelling snapping shrimp *Synalpheus microneptunus*. *Sci Rep* **10**:7744.

Chang CC, Ng PJ, Li D, 2016. Aggressive jumping spiders make quicker decisions for preferred prey but not at the cost of accuracy. *Behav Ecol* **28**:479–484.

Del-Claro K, Tizo-Pedroso E, 2009. Ecological and evolutionary pathways of social behavior in Pseudoscorpions (Arachnida: Pseudoscorpiones). *Acta Ethol* **12**:13–22.

Dixon WJ, 1950. Analysis of extreme values. *Ann Math Stat* **21**:488–506.

Du H, Chouvenc T, Osbrink WLA, Su NY, 2016. Social interactions in the central nest of *Coptotermes formosanus* juvenile colonies. *Insectes Soc* **63**:279–290.

Fox J, Weisberg S, 2018. *An R Companion to Applied Regression*. Sage Publications, Thousand Oaks.

Gordon DM, 2016. From division of labor to the collective behavior of social insects. *Behav Ecol Sociobiol* **70**:1101–1108.

Griesser M, Nystrand M, Ekman J, 2006. Reduced mortality selects for family cohesion in a social species. *Proc Biol Sci* **273**:1881–1886.

Grüter C, Menezes C, Imperatriz-Fonseca VL, Ratnieks FLW, 2012. A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. *Proc Natl Acad Sci USA* **109**:1182–1186.

Grüter C, Segers FHI, Santos LLG, Hammel B, Zimmermann U et al., 2017. Enemy recognition is linked to soldier size in a polymorphic stingless bee. *Biol Lett* **13**:20170511.

Hamilton WD, 1972. Altruism and related phenomena, mainly in social insects. *Annu Rev Ecol Syst* **3**:193–232.

Jeanne RL, 1986. The evolution of the organization of work in social insects. *Monit Zool Ital J Zool* **20**:119–133.

Johnson BR, 2008. Within-nest temporal polyethism in the honey bee. *Behav Ecol Sociobiol* **62**:777–784.

Judson MLI, 2016. Pseudoscorpions (Arachnida, Chelonethi) in Mexican amber, with a list of extant species associated with mangrove and *Hymenaea* trees in Chiapas. *B Soc Geol Mex* **68**:57–79.

Junghanns A, Holm C, Schou MF, Sørensen AB, Uhl G et al., 2017. Extreme allomaternal care and unequal task participation by unmated females in a cooperatively breeding spider. *Anim Behav* **132**:101–107.

Lubin Y, Bilde T, 2007. The evolution of sociality in spiders. *Adv Study Behav* **37**:83–145.

Moura RF, Tizo-Pedroso E, Del-Claro K, 2018. Colony size, habitat structure, and prey size shape the predation ecology of a social pseudoscorpion from a tropical savanna. *Behav Ecol Sociobiol* **72**:1–9.

Mukherjee S, Heithaus MR, 2013. Dangerous prey and daring predators: a review. *Biol Rev* **88**:550–563.

Parthasarathy B, Joshi CH, Kalyadan SS, Somanathan H, 2019. Early ontogenic emergence of personality and its long-term persistence in a social spider. *Behav Ecol Sociobiol* **73**:1–12.

Powell S, 2008. Ecological specialization and the evolution of a specialized caste in *Cephalotes* ants. *Funct Ecol* **22**:902–911.

Raine NE, Chittka L, 2009. Measuring the adaptiveness of social insect foraging strategies: an empirical approach. In: Jarau S, Hrncir M, editors. *Food Exploitation by Social Insects: Ecological, Behavioral, and Theoretical Approaches*. Boca Raton (FL): CRC Press. 9–28.

Rasband WS, 2016. *ImageJ*. Bethesda (MD): US National Institutes Heal. Available from: http://imagej.nih.gov/ij/.

Remsen JV Jr, Robinson SK, 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud Avian Biol* **13**:144–160.

Ribeiro RF, Gomes FC, Tizo AFS, Tizo-Pedroso E, Del-Claro K, 2018. Cooperative foraging in neotropical pseudoscorpions: effects of prey changes on behavioral adjustments of colonies. *Acta Ethol* **21**:153–161.

Settepani V, Grinsted L, Granfeldt J, Jensen JL, Bilde T, 2013. Task specialization in two social spiders *Stegodyphus sarasinorum* (E residae) and A nelosimus eximius (T heridiidae). *J Evol Biol* **26**:51–62.

Shackleton K, Al Toufailia H, Balfour NJ, Nascimento FS, Alves DA et al., 2015. Appetite for self-destruction: suicidal biting as a nest defense strategy in Trigona stingless bees. *Behav Ecol Sociobiol* **69**:273–281.

Silk JB, House BR, 2016. The evolution of altruistic social preferences in human groups. *Philos Trans R Soc B Biol Sci* **371**:20150097.

Sorato E, Gullett PR, Griffith SC, Russell AF, 2012. Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Anim Behav* **84**:823–834.

Sridhar H, Beauchamp G, Shanker K, 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim Behav* **78**:337–347.

Sullivan KA, 1984. The advantages of social foraging in downy woodpeckers. *Anim Behav* **32**:16–22.

Svanbäck R, Eklöv P, 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization?. *Oikos* **102**:273–284.

Tizo-Pedroso E, Del-Claro K, 2005. Matriphagy in the neotropical pseudoscorpion *Paratemnoides nidificator* (Balzan 1888)(Atemnidae). *J Arachnol* **33**:873–877.

Tizo-Pedroso E, Del-Claro K, 2007. Cooperation in the neotropical pseudoscorpion, *Paratemnoides nidificator* (Balzan, 1888): feeding and dispersal behavior. *Insectes Soc* **54**:124–131.

Tizo-Pedroso E, Del-Claro K, 2011. Is there division of labor in cooperative pseudoscorpions? An analysis of the behavioral repertoire of a tropical species. *Ethology* **117**:498–507.

Tizo-Pedroso E, Del-Claro K, 2014. Social parasitism: emergence of the cuckoo strategy between pseudoscorpions. *Behav Ecol* **25**:335–343.

Tizo-Pedroso E, Del-Claro K, 2018. Capture of large prey and feeding priority in the cooperative pseudoscorpion *Paratemnoides nidificator*. *Acta Ethol* **21**:109–117.

Tofilski A, 2002. Influence of age polyethism on longevity of workers in social insects. *Behav Ecol Sociobiol* **51**:234–237.

Tofilski A, 2006. Influence of caste polyethism on longevity of workers in social insect colonies. *J Theor Biol* **238**:527–531.

Weygoldt P, 1969. *The Biology of Pseudoscorpions*. Cambridge: Harvard University Press.

Willey MB, Jackson RR, 1993. Predatory behavior of a social spider *tegodyphus sarasinorum* (Araneae: eresidae): why attack first?. *Can J Zool* **71**:2220–2223.

Wilson EO, 1971. *The Insect Societies*. Harvard University Press, Cambridge, Massachusetts.

Wilson EO, 2000. *Sociobiology*. Harvard University Press, Cambridge, Massachusetts.

Wilson EO, 2008. One giant leap: how insects achieved altruism and colonial life. *Bioscience* **58**:17–25.

Wong JWY, Meunier J, Kölliker M, 2013. The evolution of parental care in insects: the roles of ecology, life history and the social environment. *Ecol Entomol* **38**:123–137.

Zuur AF, Ieno EN, Elphick CS, 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* **1**:3–14.