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To cite this article: Vinícius L. de Miranda, Elmo B.A. Koch, Jacques H.C. Delabie, Laís S. Bomfim, Jéssica F. Padre & Cléa S.F. Mariano (01 May 2026): Relationship between polymorphism and division of labor in colonies of *Azteca chartifex spiriti* Forel, 1912 (Hymenoptera: Formicidae: Dolichoderinae), *Annales de la Société entomologique de France* (N.S.), DOI: [10.1080/00379271.2026.2651383](https://doi.org/10.1080/00379271.2026.2651383)

To link to this article: <https://doi.org/10.1080/00379271.2026.2651383>



Published online: 01 May 2026.



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Relationship between polymorphism and division of labor in colonies of *Azteca chartifex spiriti* Forel, 1912 (Hymenoptera: Formicidae: Dolichoderinae)

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(Accepté le 21 mars 2026)

Summary. *Azteca chartifex spiriti* Forel, 1912 is a Neotropical ant that exhibits noticeable polymorphism within its worker caste. The aim of this study was to analyze the division of labor among workers based on this polymorphism. We evaluated four key behaviors: colony defense, foraging, nest reconstruction, and the tending of honeydew-producing insects across three polydomous colonies. Head width was measured in workers performing these predefined tasks. Statistical analyses (Chi-square tests) revealed that while nest defense was consistently performed by major workers (87%), other behaviors exhibited significant plasticity. Task allocation for nest reconstruction and Hemiptera tending varied significantly between colonies, suggesting an influence of colony-specific factors, such as ontogeny rather than a strict relationship between shape and task. This balance between specialized defense and flexible task allocation is crucial for understanding the ecological dominance and colony functioning of *A. chartifex spiriti*.

Résumé. Relation entre le polymorphisme et la division du travail dans les colonies d'*Azteca chartifex spiriti* Forel, 1912 (Hymenoptera : Formicidae : Dolichoderinae). *Azteca chartifex spiriti* Forel, 1912 est une fourmi néotropicale présentant un polymorphisme notable au sein de sa caste ouvrière. Cette étude visait à analyser la division du travail entre les ouvrières en fonction de ce polymorphisme. Nous avons évalué quatre comportements clés : la défense de la colonie, la recherche de nourriture, la reconstruction du nid et le soin aux hémiptères trophobiontes, au sein de trois colonies polydomiques. Des mesures morphométriques de la largeur de la tête ont été effectuées sur des ouvrières réalisant ces tâches prédéfinies. Les analyses statistiques (tests du χ^2) ont révélé que si la défense du nid était systématiquement assurée par les ouvrières major (87%), les autres comportements présentaient une plasticité significative. La répartition des tâches pour la reconstruction du nid et le soin aux hémiptères variait significativement d'une colonie à l'autre, suggérant l'influence de facteurs spécifiques à chaque colonie, tels que l'ontogenèse, plutôt qu'un déterminisme morphologique rigide. Cet équilibre entre défense spécialisée et répartition flexible des tâches est crucial pour comprendre la dominance écologique et le fonctionnement des colonies d'*A. chartifex spiriti*.

Keywords: behavior; arboreal ants; polydomous structure; defense

Division of labor is considered a primary factor responsible for the ecological success and dominance of social insects (Hölldobler & Wilson 1990). The theory of caste ergonomics predicts that colony efficiency is optimized by producing morphologically specialized workers for specific tasks, thereby minimizing energetic costs and maximizing performance (Oster & Wilson 1978). In polymorphic species, this specialization often results in a tight correlation between body size (or shape) and the behavioral repertoire, where smaller workers tend to perform

internal tasks while larger workers or soldiers specialize in defense (Powell 2008).

However, recent studies have challenged the view that morphology strictly dictates task allocation. Behavioral plasticity allows workers to respond to immediate colony demands regardless of their size, suggesting that morphological specialization may not be the sole determinant of individual efficiency (Dornhaus 2008; Mertl & Traniello 2009). Understanding the balance between size-based roles and behavioral plasticity is crucial for explaining

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social organization in arboreal ants, which face complex foraging and territorial defense challenges.

Worker polymorphism is a hallmark of many social insect societies, where morphological differentiation often underlies specialized behavioral roles (Hölldobler & Wilson 1990). In the genus *Azteca* Forel, 1878 (Formicidae: Dolichoderinae), this polymorphism is frequently expressed through a bimodal distribution of head sizes, allowing for a functional distinction between ‘minor’ workers (smaller individuals typically involved in brood care and nest maintenance) and ‘major’ workers (larger individuals often associated with defense) (Wheeler 1986; Longino 2007). Understanding how these morphological subcastes divide labor among specific behavioral categories such as foraging, nest reconstruction, and colony defense is essential for testing hypotheses regarding ergonomic efficiency and colony-level fitness in arboreal environments (Oster & Wilson 1978).

Azteca is a Neotropical genus composed of 84 arboreal species that dominate in the habitats they occupy (Bolton 2025). The arboreal nature of these species promotes a range of biotic associations with both plants and other insects. For example, plants of the genus *Cecropia* provide nesting sites for the ants (Carneiro et al. 2018), and correspondingly, the ants protect the plants against potential herbivores (Adams 1994; Ayala et al. 1996; Johnson et al. 2001).

In addition to their associations with plants, ants of the genus *Azteca* are also found in mutualistic relationships with social wasps, such as *A. chartifex* Forel, 1896 and *Polybia rejepta* (Fabricius, 1798) (Souza et al. 2013; Virgínio et al. 2015; Somavilla & Fernandes 2020). This association benefits both partners, as the ants provide protection against the wasps’ natural predators, and the wasps reciprocate with similar defensive actions (Herre et al. 1986). Another notable interaction occurs between *Azteca* and sap-sucking Hemiptera of the suborder Sternorrhyncha of the superfamily Coccoidea. In these associations, the hemipterans excrete honeydew, which is collected by the ants and used as an important food resource. However, the ants’ diet is not limited to honeydew, as they are also proficient predators with generalized feeding habits (Delabie et al. 1991; Johnson et al. 2001; Davidson et al. 2003; Longino 2007).

The worker caste of ants can specialize in performing various tasks within a colony. This specialization in executing distinct activities is known as the division of labor. Morphological and age-related variations among workers, along with their social interactions, can influence the division of labor, thereby contributing significantly to the ecological success of social insects (Ravary et al. 2007). Worker polymorphism in ants has been previously investigated by Wilson (1953), using species such as *Camponotus castaneus* (Latreille, 1802), *Atta texana* (Buckley, 1860), and *Oecophylla smaragdina* (Fabricius, 1775) as

model organisms. Polymorphism can be examined by exploring the relationships among morphological variables; the analysis of body size measures may indicate either allometric growth of individuals within a unimodal distribution or the segregation of polymorphic groups into a bimodal distribution (Oster & Wilson 1978). In *Azteca*, the worker caste is polymorphic (Wheeler 1986, 1991) and is subdivided into two distinct groups: major workers and minor workers.

The aim of this study was to investigate the organization of work within the worker caste of the Neotropical ant *Azteca chartifex spiriti* Forel, 1912, and to correlate the functions performed by workers with the subcastes present in the colonies. Specifically, we tested whether size variation dictates specialization in four key behaviors: colony defense, foraging, nest reconstruction, and hemipteran tending. By examining the relationships between worker morphology, task allocation, and colony structure, we aimed to achieve a broader understanding of the division of labor in these arboreal ants.

Materials and methods

Study area

The study was conducted in two experimental cocoa fields of the Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC) (14°45’19”S, 39°13’53”W) and the Universidade Estadual de Santa Cruz (UESC) (14°47’52”S, 39°10’20”W), both located in the municipality of Ilhéus, Bahia, Brazil (Figure 1). These two sites are approximately 7.2 km apart in a straight line. Both are situated within the Brazilian Atlantic Forest, one of the most biodiverse and threatened biomes in the world (GIZ 2022). The dominant vegetation in the region is dense ombrophilous forest, characterized by trees with a closed canopy and a complex vertical structure (SBSAF 2021). The primary agricultural activity is cacao (*Theobroma cacao* L., Malvaceae) cultivation, mainly in agroforestry systems known as “cabruca,” where cacao trees are planted under the shade of remnant native vegetation (Schroth et al. 2011; IIS 2021). This system plays an important role in biodiversity conservation, providing suitable habitats for various organisms, including arboreal ants (Delabie et al. 2007).

The regional climate is equatorial (Af), according to Köppen’s (1936) classification, characterized by high humidity and temperature, with no well-defined dry season (Climate-Data.org 2023). The mean annual temperature is approximately 23.9°C, with minimal seasonal variation (Rodrigues & Costa 2021). Average annual rainfall is around 1325 mm, relatively evenly distributed throughout the year, with peak precipitation occurring between March and July (GIZ 2022). Relative humidity remains consistently high, typically above 80% year-round (Climate-Data.org 2023). These environmental conditions favor the development of diverse ant communities, particularly species of the genus *Azteca*.

Study organism

The arboreal ant *Azteca chartifex spiriti* is commonly found in the cocoa plantations of Bahia, regionally known as “caçarema” ants and used traditionally for biological control purposes (Majer et al.



Figure 1. Geographic location and environmental context of the study area. **A**, Position of Brazil within South America, highlighting the State of Bahia. **B**, Regional view of the State of Bahia and neighboring states, showing the location of the municipality of Ilhéus (red point). **C**, High-resolution satellite imagery showing the land cover of the study sites at CEPLAC and UESC along the Jorge Amado Highway (BR-415). Yellow diamonds represent the sampled colonies of *Azteca chartifex spiriti*.

1994; Delabie et al. 2024). It is a territorial ant with a characteristic nest exhibiting a polydomous nesting structure, meaning that the colony is divided into at least two structures (Delabie et al. 1991; Debout et al. 2007; Miranda et al. 2021). The colony consists of a central larger structure, which we call the main or central nest, and smaller nests, referred to as satellite nests (Delabie et al. 1991; Miranda et al. 2021). This nesting strategy increases colony resilience, facilitates resource allocation, optimizes foraging efficiency, and reduces predation risk (McGlynn 2012). Previous studies of *A. chartifex spiriti* have shown that the spatial structure of the nest is highly organized, with interconnected chambers and pathways that support efficient worker movement and resource allocation (Miranda et al. 2021). The species lives in arboreal environments, where it can take advantage of available resources while maintaining proximity to trophobionts such as sap-sucking hemipterans (Bondar 1939; Miranda et al. 2021).

Description of the experiments

The colonies of these ants are very conspicuous and were located through active visual search in the cacao canopy. These ants are well documented in the region since the beginning of the twentieth century and are the subject of regular publications for their importance in agroforestry (see Delabie et al. 2024). Their morphology, as well as their nest structure, are well known and their identification only requires comparison with the laboratory reference collection.

To quantify the division of labor, we established four predefined behavioral categories: (1) colony defense (response to nest disturbance), (2) foraging (collection of solid resources or predation), (3) nest reconstruction (repair of carton structures), and (4) mutualistic tending (interaction with honeydew-producing hemipterans). The experiments took place in June 2018 and involved three colonies of *Azteca chartifex spiriti* of similar size and nest volume, two located at UESC and one at CEPLAC.

To observe defensive behavior, three sampling points were defined within each colony’s structure: (1) the primary and larger nest, where the queen, brood, and workers reside; (2) adjacent satellite nests (intermediate defense zones), typically used for rearing the brood and also inhabited by many workers; and (3) peripheral satellite nests, situated across the colony’s territory and sheltering scale insects (Coccoidea). At each of the nine sampling points (three per colony), the tip of a machete was inserted into pre-defined locations to simulate disturbance. Following this stimulus, 50 individuals displaying defensive behavior were randomly collected at each point, totaling 450 specimens.

To assess foraging behavior, two contexts were tested. (1) Bait foraging – oil-preserved sardines were offered as bait at the colony-bearing trees for 5 min. After this period, 50 foragers that engaged with the bait were collected. (2) Predatory foraging – foraging trails were identified on the trees at approximately 2 m from the nearest nest. Along these trails, *Nasutitermes* sp. termite nymphs were offered. Fifty ant workers displaying predatory behavior towards the termites were then collected.

To identify workers involved in mutualistic tending, 50 individuals were sampled directly from peripheral satellite nests where scale insects were present: the first series included an unidentified Pseudococcidae, and the second series included the Coccidae *Ceroplastodes melzeri* Bondar, 1925. For the nest reconstruction experiment, the primary nest structure was partially damaged with a machete. After a 15-minute response interval, 50 workers actively engaged in rebuilding activities were collected. All collected ants were mounted on entomological pins. The cephalic capsule width, a robust and minimally damage-prone

morphological trait, was measured using an Olympus® SZ stereomicroscope (Olympus Corp., Tokyo, Japan) and Image Pro Discovery software (Media Cybernetics, Rockville, MD, USA). Based on these measurements and following the characteristic bimodal distribution of head widths in this species (Wheeler 1986), workers were categorized into minor and major subcastes to evaluate the relationship between morphology and task performance.

Data analysis

For each colony, the distribution of head width measurements was assessed across the observed behavioral categories. To test for differences in head width among individuals engaged in defensive behavior at varying distances, a non-parametric Kruskal–Wallis test was performed, followed by a post hoc Dunn’s test with Bonferroni correction ($p < 0.05$). Additionally, to statistically evaluate if the proportion of major and minor workers varied significantly across the different tasks (defense, foraging, tending, reconstruction), chi-square tests (χ^2) were performed, comparing the observed counts against an expected equal distribution or between tasks. All statistical analyses were performed in R version 4.4.1 (R Core Team 2025).

Results

Head width in *Azteca chartifex spiriti* workers varied across behavioral categories and colonies, with the

highest mean value recorded for individuals involved in nest defense (0.5768 ± 0.03 mm) and the lowest for those engaged in predatory foraging (0.4572 ± 0.08 mm), both occurring in colony C3 (Table 1). A total of 1200 workers were measured; the mean head width was 0.557 ± 0.08 mm for colony 1, 0.528 ± 0.077 mm for colony 2, and 0.548 ± 0.069 mm for colony 3 (mean \pm SD).

Regarding defensive behavior, the majority of workers performing this function belonged to the major worker subcaste (Figure 2). Overall, no significant difference was found in the head width of workers performing defensive behavior across the observed distances ($H = 4.176$; $n = 450$; $p = 0.124$). This lack of significance was consistent in separate analyses of colonies C1 ($H = 1.756$; $p = 0.415$) and C2 ($H = 3.041$; $p = 0.218$). In Colony C3, however, a significant difference was recorded ($H = 7.385$; $p = 0.024$), with smaller workers observed at the periphery compared to the primary nest (Figure 3).

Regarding bait foraging (Figure 4A), χ^2 analysis indicated that both worker subcastes engaged in this behavior in balanced proportions in Colony C1 ($\chi^2 = 0.00$, $p = 1.00$), whereas in colonies C2 and C3 the behavior was exhibited significantly more frequently by major workers ($\chi^2 = 25.92$, $p < 0.001$; C3: $\chi^2 = 13.52$, $p < 0.001$). In predatory

Table 1. Mean values and standard deviations of head width measurements across observed behavioral categories across the three evaluated colonies of *Azteca chartifex spiriti*.

Behavior	Type	Colony	Mean \pm Standard deviation (mm)
Defense	NP defense	C1	0.5876 ± 0.06
		C2	0.5628 ± 0.07
		C3	0.5768 ± 0.03
	Intermediate defense	C1	0.5892 ± 0.07
		C2	0.5862 ± 0.04
		C3	0.5686 ± 0.05
	Peripheral defense	C1	0.5822 ± 0.07
		C2	0.5678 ± 0.06
		C3	0.5308 ± 0.08
Foraging	Bait	C1	0.5312 ± 0.08
		C2	0.5678 ± 0.05
		C3	0.5484 ± 0.07
	Predation	C1	0.5112 ± 0.08
		C2	0.4872 ± 0.08
		C3	0.5162 ± 0.08
Rearing of Hemiptera	Pseudococcidae	C1	0.5300 ± 0.08
		C2	0.4964 ± 0.07
		C3	0.4776 ± 0.06
	Coccidae	C1	0.5352 ± 0.08
		C2	0.4694 ± 0.05
		C3	0.5798 ± 0.06
Reconstruction	Reconstruction	C1	0.5938 ± 0.06
		C2	0.4866 ± 0.08
		C3	0.5908 ± 0.04

Note: NP = Principal nest

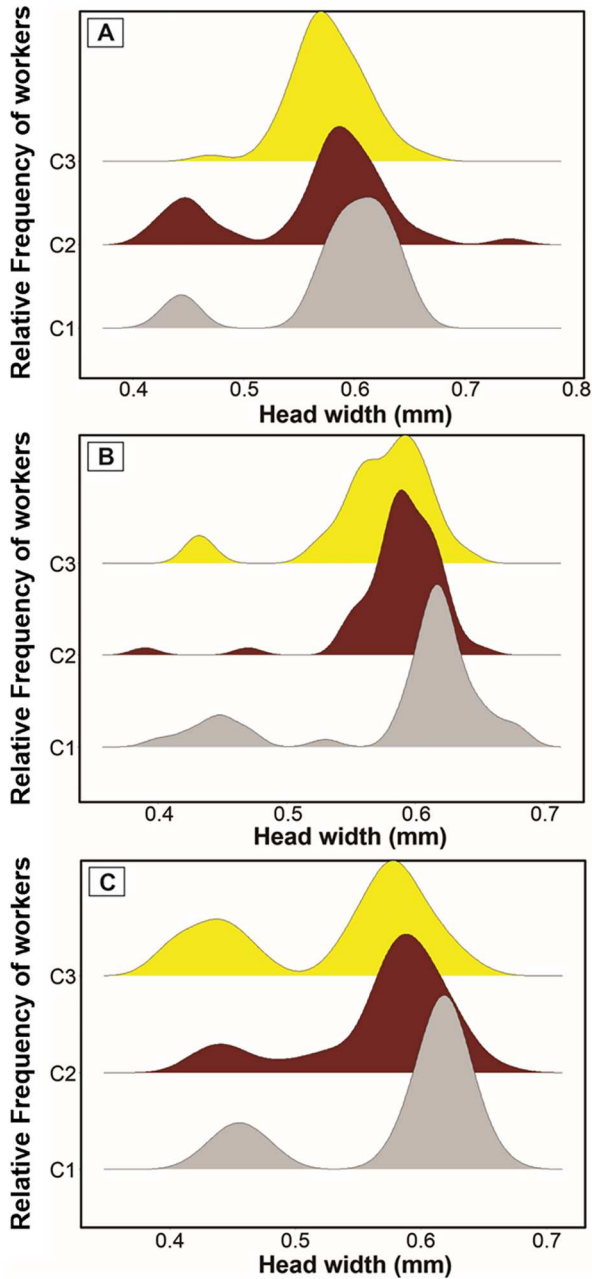


Figure 2. Frequency of *Azteca chartifex spiriti* workers observed performing defensive behavior following a disturbance to the nests. **A**, Defense at the primary nest. **B**, Defense at the intermediate nest. **C**, Defense at the peripheral nest.

behavior, the distribution of major and minor workers was balanced in colonies C1 and C3 ($p > 0.05$), while Colony C2 showed a significant bias towards minor workers ($\chi^2 = 5.12, p = 0.02$) (Figure 4B).

The allocation of workers for tending scale insects varied significantly among colonies ($\chi^2 = 40.33, df = 2, p < 0.001$). Minor workers were predominant in Colony C2 (80%), whereas Colony C1 showed a higher proportion of majors (61%) and Colony C3 exhibited a more balanced

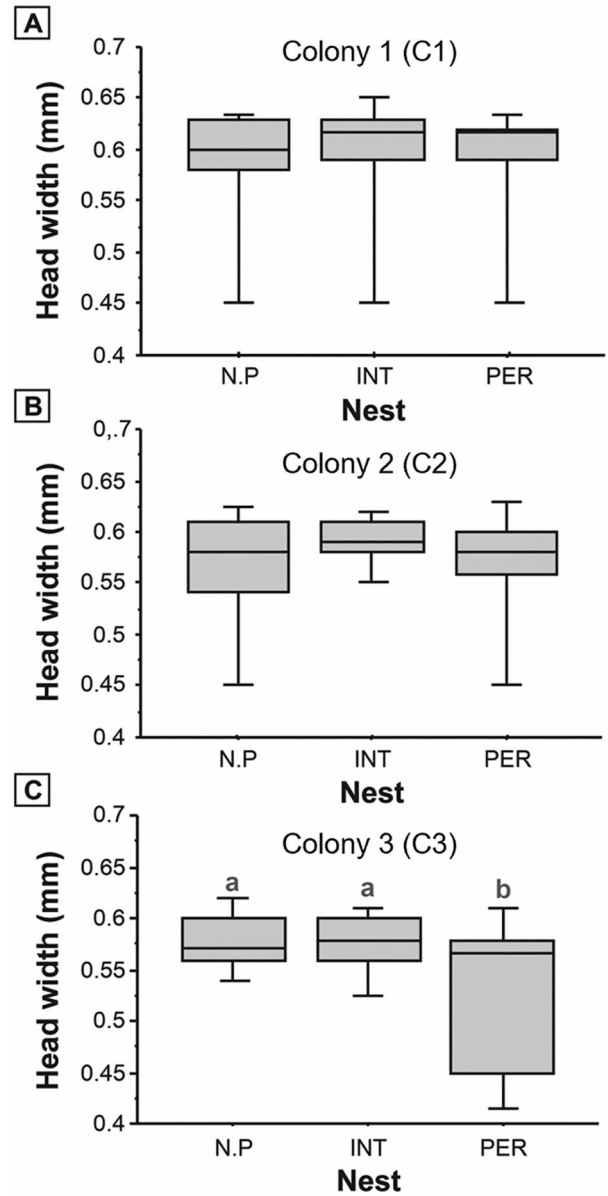


Figure 3. Relationship between the mean head width of *Azteca chartifex spiriti* and the location where defensive behavior was observed in the three studied colonies. **A**, Colony 1. **B**, Colony 2. **C**, Colony 3. Abbreviations: NP, primary nest; INT, intermediate distance; PER, peripheral distance.

distribution with a slight bias towards majors (56%) (Figure 5). Consequently, the tending of Hemiptera (Figure 5A, B) did not follow a consistent morphometric pattern across the three colonies.

Nest reconstruction behavior was primarily performed by major workers in colonies C1 (86%) and C3 (96%), whereas in Colony C2, minor workers were more often involved (66%) (Figure 6). Statistical analysis confirmed significant variation in caste allocation for reconstruction dependent on the colony ($\chi^2 = 54.96, df = 2, p < 0.001$).

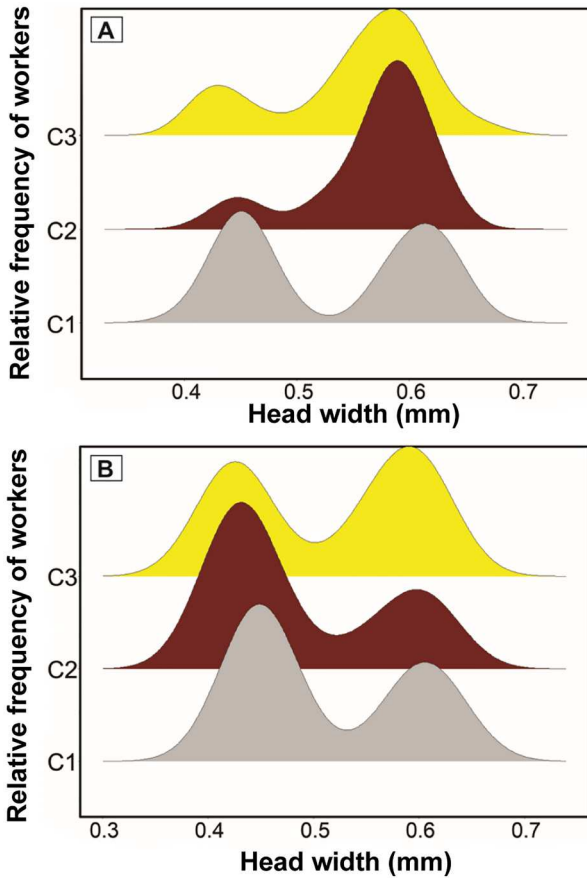


Figure 4. Frequency of *Azteca chartifex spiriti* workers. **A**, Observed performing foraging activities with an offered bait (sardine in edible oil). **B**, Observed performing predation on termite nymphs.

The percentages and head widths of the workers exhibiting all behaviors per colony are presented in Table 2.

Discussion

In this study, *Azteca chartifex spiriti* colonies exhibit a clear division of labor only in nest defense, where major workers predominated. This result aligns with the findings of Wheeler (1986), who reported that over 80% of major workers in the closely related *A. chartifex laticeps* (now *A. chartifex*) were engaged in nest defense following disturbances. Our data, showing an average of 87% participation by major workers across three colonies, suggest that defense is a primary and stable role for this subcaste.

However, task allocation for other behaviors lacked a consistent pattern across the studied colonies. For instance, while defense was generally stable, significant variation in worker size was detected in the peripheral defense of

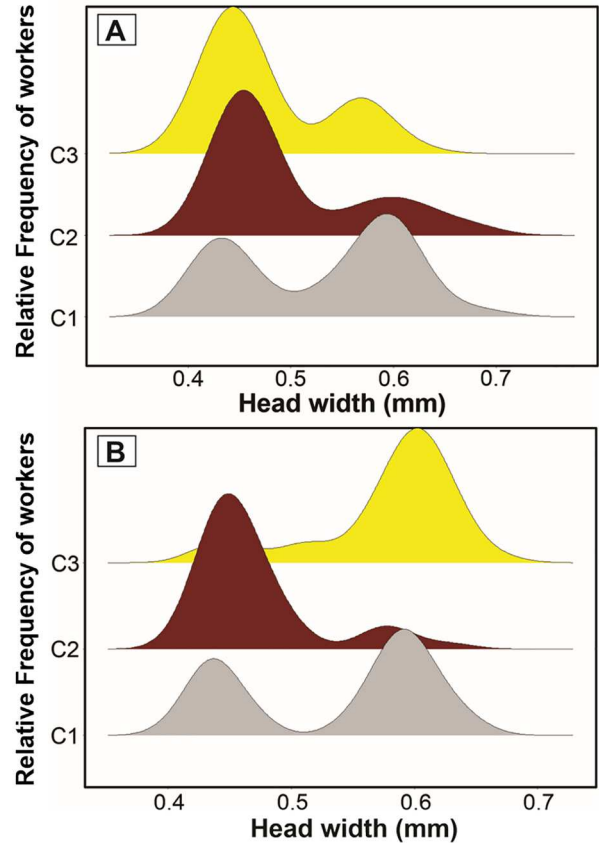


Figure 5. Frequency of *Azteca chartifex spiriti* workers observed caring for and rearing sap-sucking hemipterans of the superfamily Coccoidea. **A**, Unidentified Pseudococcidae. **B**, *Ceroplastodes melzeri* Bondar, 1925 (Coccidae).

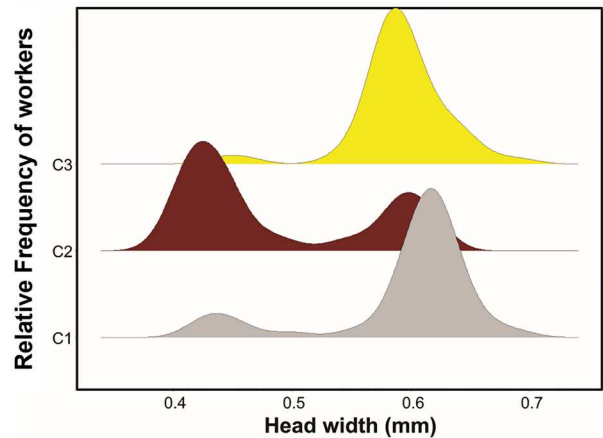


Figure 6. Frequency of *Azteca chartifex spiriti* workers observed performing nest reconstruction following an experimentally induced damage.

Colony 3 (C3) and in the nest reconstruction tasks of Colony C2. These differences suggest that colony-specific factors, such as ontogeny or population size, may influence

Table 2. Percentage and size of individuals observed performing behaviors across the three evaluated colonies of *Azteca chartifex spiriti*.

Colony	Behavior	Level	% of major workers	MaW size (mm)	% of minor workers	MiW size (mm)	
C1	Defense	NP defense	88%	0.56–0.65	12%	0.43–0.45	
		Intermediate defense	80%	0.59–0.68	20%	0.4–0.53	
		Peripheral defense	78%	0.58–0.66	22%	0.43–0.48	
	Foraging	Bait	50%	0.57–0.65	50%	0.41–0.49	
		Predation	38%	0.58–0.64	62%	0.41–0.55	
	Rearing of Hemiptera	Pseudococcidae	60%	0.53–0.69	40%	0.41–0.5	
		Coccidae	62%	0.55–0.64	38%	0.41–0.47	
	Reconstruction	Reconstruction	82%	0.57–0.69	18%	0.42–0.55	
	C2	Defense	NP defense	76%	0.54–0.74	24%	0.42–0.49
			Intermediate defense	96%	0.52–0.64	4%	0.39–0.47
Peripheral defense			86%	0.5–0.66	14%	0.42–0.48	
Foraging		Bait	88%	0.51–0.63	12%	0.43–0.46	
		Predation	34%	0.54–0.62	66%	0.4–0.49	
Rearing of Hemiptera		Pseudococcidae	28%	0.54–0.68	72%	0.42–0.5	
		Coccidae	12%	0.57–0.63	88%	0.41–0.51	
Reconstruction		Reconstruction	30%	0.57–0.69	70%	0.44–0.55	
C3		Defense	NP defense	96%	0.53–0.66	4%	0.47–0.52
			Intermediate defense	92%	0.52–0.64	8%	0.43–0.44
	Peripheral defense		34%	0.54–0.64	66%	0.40–0.47	
	Foraging	Bait	76%	0.52–0.67	24%	0.42–0.5	
		Predation	56%	0.53–0.62	44%	0.40–0.52	
	Rearing of Hemiptera	Pseudococcidae	16%	0.56–0.62	84%	0.41–0.5	
		Coccidae	100%	0.43–0.67	0%		
	Reconstruction	Reconstruction	92%	0.57–0.69	8%	0.44–0.55	

Note: NP = Principal nest; MaW = maximum size; MiW = minimum size

workforce distribution. As colonies mature, they may shift their investment toward larger castes (Tschinkel 1988), allowing for more flexible ergonomic strategies depending on the colony’s developmental stage.

This lack of rigid specialization was particularly evident in the tending of honeydew-producing insects and in foraging. In Colony C2, minor workers performed the majority of these tasks, contrasting with the patterns observed in C1 and C3. This divergence indicates that task allocation in *A. chartifex spiriti* is potentially plastic and context-dependent. Rather than being strictly dictated by morphology, workers may assume roles based on immediate environmental needs or resource constraints. This flexibility is further highlighted by the predatory foraging in C2, where minor workers assumed roles typically requiring greater physical force.

The division of labor associated with polymorphism in ants has been a long-standing topic of interest (Möglich & Hölldobler 1974). Wilson (1978) noted that the degree of specialization varies between species, with *Solenopsis invicta* exhibiting less rigid caste specialization than *Solenopsis geminata*. Our results suggest that *A. chartifex spiriti* follows a similar pattern of flexibility. While nest

defense shows clear polymorphism-related division of labor, other behaviors such as nest reconstruction and Hemiptera tending display context-dependent task allocation.

Such behavioral plasticity likely contributes to the ecological dominance of *A. chartifex spiriti* in cacao agroecosystems (Delabie et al. 2024), as it alters the composition of the arthropod community on the host plant (Majer & Delabie 1993; Majer et al. 1994). This dominance is maintained through their ability to constantly patrol the occupied territories. These colonies promote a cascading effect on the diversity of arthropods on the plant and on the level of herbivory as seen in the closely related taxon, *A. chartifex* (Soares et al. 2022). The ability to dynamically allocate different subcastes to patrolling, reconstruction, and tending tasks allows the species to maintain its complex polydomous networks. Its success in fluctuating arboreal environments appears to be driven not only by aggression but by this capacity for behavioral adjustment to varying conditions.

A limitation of this study was the absence of a whole-colony demographic baseline, as non-destructive sampling of arboreal carton nests is logistically challenging.

However, the comparison between behavioral groups provides evidence that, except for nest defense, this species maintains a high degree of flexibility. Our results suggest that *A. chartifex spiriti* does not strictly adhere to a model of rigid specialization based on size, but instead utilizes a more adaptable social organization to meet the demands of its environment (Dornhaus 2008).

Conclusions

This study indicates that, despite the evident bimodal distribution in worker morphology in *Azteca chartifex spiriti*, both polymorphic castes may exhibit overlapping specialization in several key behaviors. While major workers were confirmed to be highly specialized in nest defense (over 85% participation), other tasks such as Hemiptera tending and nest reconstruction were performed by both subcastes with significant variation between colonies. These patterns likely reflect colony-specific factors, such as ontogeny or population density, rather than a strict relationship between shape and task.

Further studies on the division of labor in *A. chartifex spiriti* could benefit from exploring task allocation within the internal chambers of the primary nest, particularly regarding brood care. This area remains less understood due to the high defensive intensity of workers under natural field conditions.

Acknowledgements

We gratefully acknowledge CAPES for the master's scholarship support; the Graduate Program in Zoology (PPGZOO) at the Universidade Estadual de Santa Cruz (UESC); the Laboratório de Artrópodes Sociais at UESC; and the Laboratório de Mirmecologia of the Centro de Pesquisas do Cacau (CEPEC/CEPLAC) for the logistical support that made this study possible. We also thank Dr. Iara Oliveira Fernandes for expertly producing the study map. JHCD acknowledges his research grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and VLM thanks CNPq for his Junior Postdoctoral Fellowship (PDJ).

Disclosure statement

No potential conflict of interest was reported by the author(s).

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