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RESEARCH ARTICLE

Role of accelerated developmental pathway and limited nurturing capacity on soldier developmental instability in subterranean termite incipient colonies

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Abstract In the subterranean termite *Coptotermes gestroi* (Wasmann), soldiers developing in incipient colonies display strong fluctuating asymmetry when compared with soldiers developing in mature colonies. This strong asymmetry may arise from two different types of stress factors on individuals. First, the accelerated development of nanitic (small) soldiers may impose a direct physiological stress as *Coptotermes* soldiers produced in incipient colonies have two less molting events than soldiers produced in mature colonies. Second, the environmental conditions in incipient colonies present a major constraint with limited access to resources and small numbers of workers to care for the developing brood. In this study, 459 soldiers from 73 incipient colonies (6-month-old) displaying only nanitic soldiers were investigated in a range of nurturing capacity scenarios. Nanitic soldiers developing in incipient colonies with high nurturing capacity displayed more symmetrical traits than the ones developing in colonies with low nurturing capacity. In addition, the first soldiers to emerge in the colony were the most asymmetrical individuals, showing that as the conditions improve rapidly with the growth of the colony, newly produced nanitic soldiers manifest the lessening of stress in normalization of their morphology. However, the nurturing capacity of the colony only partially explained the developmental instability variability, implying that the accelerated development of nanitic soldiers remains an important stress factor in incipient colonies, in comparison with soldiers developing in mature colonies with two additional molts and homeostatic environmental conditions.

Keywords Juvenile trait · Fontanelle · Setae · Termite · Colony development

Introduction

Stress factors can interfere with the optimal development of organisms, resulting in individuals with morphologies displaying asymmetrical traits (Markow 1995). Fluctuating asymmetry can be used as a way to determine the importance of stress factors, such as a limited access to resources, epigenetic interactions, and unsuitable environmental conditions (Parsons 1992; Graham et al. 1993; Møller and Swaddle 1997). In social insects, mature colonies provide homeostatic conditions for the developing brood, with stable temperatures and humidity levels inside the nest (Wood 1988; Schmickl and Crailsheim 2004; Hughes et al. 2008) and a large worker cohort to provide for a range of caring duties (Du et al. 2016). However, in young colonies, such optimal conditions have not yet been achieved (Oster and Wilson 1978) and individuals produced in the early life of the colony can be exposed to stresses that may result in morphologies with asymmetrical traits (Rabitsch 1997).

The first emerging brood of an incipient colony is nurtured only by the primary reproductives, after which the first

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Table 1 Developmental pathways for *Coptotermes gestroi* soldiers in incipient and mature colonies Modified from Chouvenc and Su (2014)

	Incipient colonies (6-month-old)	Mature colonies (>7-year-old)
Colony size	<100 individuals	>250,000 individuals
Nurturing capacity	Limited	Extensive
Soldier type	"Nanitic soldier" (S_1)	"Mature soldier" (S_3)
Primary developmental pathway	Egg → L_1 → L_2 → PS_1 → $S_1^{(12)}$	Egg → L_1 → L_2 → W_1 → W_2 → PS_3 → $S_3^{(14)}$ (two additional molts)

Numbers in parentheses are the representative number of antennal segments of the soldier morphotype

L_1, L_2 first and second instar larvae, W_1, …, W_n worker instars, PS_n presoldier from developmental pathways, S_n soldier from developmental pathways

few workers produced from this initial brood quickly take over all nurturing tasks (Nutting 1969; Oster and Wilson 1978). This early colony life stage represents a major bottleneck where the colony is susceptible to environmental adversities, which often results in colony failure (Nutting 1969; Tschinkel 1992; Cronin et al. 2013). In addition, incipient colonies with such limited nurturing capacity may not provide optimal conditions for individuals to develop properly (Chouvenc et al. 2015a). We here define "nurturing capacity of the colony", as the cumulative capacity of all individuals within the group for providing care and nutrition to all dependent individuals within the colony. In the subterranean termite *Coptotermes gestroi* (Wasmann) (Isoptera, Rhinotermitidae), it was shown that soldiers produced in incipient colonies display strong fluctuating asymmetry when compared with soldiers produced in mature colonies (Chouvenc et al. 2014).

In termite colonies, individuals develop through a range of possible developmental pathways that result in different castes and morphologies for a given species (Noirot 1985). Soldiers produced in *Coptotermes* colonies represent a distinct morphological caste that focus on colony defense against predators and competitors. A soldiers' head capsule is heavily sclerotized with modified mandibles and an exocrine gland producing defensive secretions exuded through the fontanelle, a circular structure opening frontally (Wasmann 1896; Prestwich 1979). In *Coptotermes*, soldiers can be produced from different developmental pathways, which are colony age-dependent (Chouvenc and Su 2014). Early in the life of a colony, all soldiers are produced via an accelerated developmental pathway, with only two molts after the second instar larva. Such soldiers are small and poorly functional, and are defined as "nanitic soldiers" (Noirot 1985; Chouvenc et al. 2015a). Nanitic soldiers (S_1) were shown to be a cost-efficient way for the colony to produce the required number of soldiers needed to reach a soldier proportion equilibrium (Haverty 1977), so that the incipient colony could achieve optimal initial colony growth (Chouvenc et al. 2015a). In contrast, soldiers produced in mature colonies emerge from a more extensive developmental pathway (S_3), with at least four molts after the second instar larva (Table 1), resulting in larger and fully functional soldiers that benefited from more resources and developmental time than nanitic soldiers (Chouvenc et al. 2014).

While it is established that nanitic soldiers display strongly fluctuating asymmetry in comparison with soldiers from mature colonies (Chouvenc et al. 2014), it is unclear if asymmetrical traits result from the accelerated developmental pathway (i.e., two less molts than soldiers in mature colonies), or if it is due to the intrinsic limited nurturing capacity (small number of workers that provide for the developing brood) of the incipient colonies. The nurturing capacity of the colony represents the ability of the workers to perform a series of tasks that provide for the needs of the dependent castes, i.e., eggs, larvae, soldiers, king and queen (Su and La Fage 1987; Du et al. 2016). The nurturing capacity therefore defines the quality of the developing environment for the brood. Unfortunately, the production of nanitic soldiers is inherent to incipient colonies and the previous study (Chouvenc et al. 2014) did not separate the influence of the two confounded stress factors on developmental asymmetry.

The current study aims to determine how poor initial nurturing capacity (small number of workers) influences the expression of asymmetrical traits in developing soldiers, using a sample of 73 *C. gestroi* incipient colonies of the same age (6-month-old), but with a wide variability in their initial colony growth (colony size of 40–95 workers). Therefore, all soldiers were produced through the accelerated developmental pathway (nanitic soldiers, fixed factor), but developed in colonies with a variable quality of initial care (variable number of workers). We hypothesized that nanitic soldiers produced in colonies with low initial nurturing capacity (relatively small number of workers) would display stronger asymmetrical traits than nanitic soldiers produced in colonies with high initial nurturing capacity (relatively large number of workers). In addition, we tested if the soldiers produced within the first 3 months were subjected to more developmental stresses than soldiers emerging between 3 and 6 months, as the nurturing capacity may have improved. Our results suggest that both stress

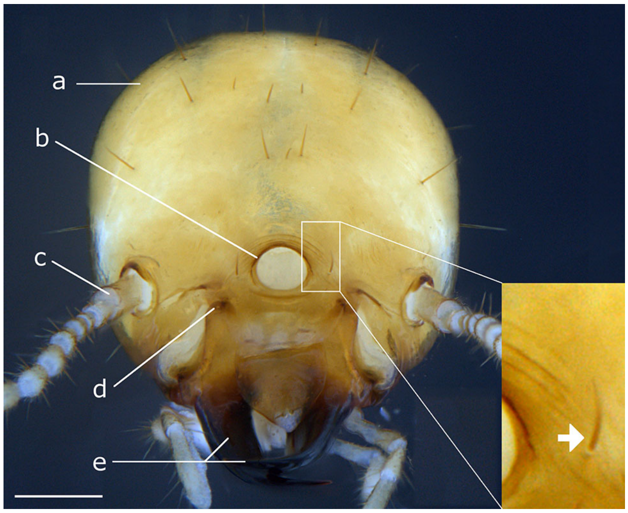

Fig. 1 Frontal view of a soldier from a *Coptotermes gestroi* mature colony, displaying a single pair of setae around the fontanelle. *a* Soldier head capsule, *b* fontanelle, *c* antenna, *d* primary point of articulation of the mandible, *e* mandibles. The *arrow* indicates the area of interest in this study, with the position of setae on each side of the fontanelle

factors are involved in soldiers' developmental instability and discuss how each factor potentially stresses developing individuals at different times in an incipient colony.

Materials and methods

Soldier morphology

Coptotermes soldiers possess an opening on the frontal part of the head: the fontanelle (Fig. 1). Defensive secretions exude from this opening and while all soldiers in *Coptotermes* species possess a fontanelle, the number of setae on each side of the structure varies within the phylogeny of the genus. Most species display a single pair of setae around the fontanelle, although *C. testaceus* (L.) displays three pairs of setae and *C. elisae* Oshima and *C. formosanus* Shiraki display two pairs of setae (Chouvenc et al. 2016). The role of the setae around the fontanelle remains unclear, although its role may be to maintain a secreted droplet stable while involved in agonistic activities (Chouvenc et al. 2014). *Coptotermes gestroi* soldiers from mature colonies characteristically display a single pair of setae (Scheffrahn and Su 2005), but nanitic soldiers from incipient colonies display a range in the number of setae, predominantly a double pair of setae phenotype, which was suggested to be a vestigial trait (Chouvenc et al. 2014). In the current study, because of the high variability in setae symmetry in *C. gestroi* nanitic soldiers, the position of each seta in nanitic soldiers was used as a surrogate to estimate the symmetrical trait, as previously determined in Chouvenc et al. (2014).

Coptotermes gestroi incipient colonies foundation and field colonies collection

Alates from *C. gestroi* dispersal flights were collected in Broward County (Florida, USA) during evenings of April 2014 with a light trap as described by Chouvenc et al. (2015b). Dealates were paired and introduced into individual rearing units made of 37-ml cylindrical vials, containing organic soil, wood pieces (*Picea* sp.) and a layer of 3% agar, as fully described in Chouvenc et al. (2015a). Rearing units ($n = 100$) were stored at 28 °C and water was occasionally added to vials that showed signs of dryness. After 6 months of development, successful incipient colonies ($n = 73$ out of 100) were opened, all castes were determined and counted (eggs, larvae, workers, soldiers, queen and king). A colony was determined as "successful" if it contained both the primary reproductives (king and queen) and a viable brood and workforce. All soldiers were collected and fixed in 85% ethanol for measurements.

In a second experiment to determine the asymmetry of the first emerged soldiers in incipient colonies, an identical protocol for incipient colonies was setup with alates collected in March 2016 at the same original location, but colonies ($n = 28$) were opened 3 months after foundation and 60 emerging nanitic soldiers were collected (1–3 soldiers per colony). This approach was used to determine the first soldiers' asymmetry instead of repeated sampling within the first 6 months because a preliminary bioassay in 2015 using repeated sampling resulted in a massive colony collapse due to the stress of the repeated destruction of the claustral nest so early in the colony development (T.C., Pers. Obs.).

In a third experiment to determine the asymmetry of soldiers in mature colonies, three colonies of origin where used. Three *C. gestroi* field colonies located in Broward County, FL were sampled from ground monitoring stations (Su and Scheffrahn 1986). From each of the three colonies of origin, 20 soldiers were randomly selected and kept in 85% ethanol before being used for setae measurements.

Asymmetry index

All soldiers collected from incipient colonies were nanitic, with 12 antennal segments, and therefore derived from second instar larvae (Chouvenc and Su 2014). A total of 459 nanitic soldiers were collected from 73 6-month-old colonies, with the numbers of soldiers per colony ranging from 4 to 12 (soldier proportion varied from 9 to 12%). Because the soldier ratio was stable across all colonies, the "nurturing capacity" directly used the number of workers as a variable, instead of using the number of workers per soldier as a transformed variable. Observations of setae around the fontanelle were made on the microscope by setting individual soldiers in hand sanitizer gel (63% alcohol), with the mandibles facing toward the microscopic lens to obtain a frontal view of the specimens. The standardized observation angle allowed for the determination of the exact location of the point of origin of each seta around the fontanelle. Automontage (microscope Leica M205C coupled with a camera Leica DFC425) was used to obtain digital pictures of soldiers, which were re-proportioned to a unique template using the fontanelle and the primary articulation point of both mandibles for alignment (Li and Su 2009). The coordinates of the point of origin of each seta were mapped for all individuals in a standard referential plan (1 pixel $\approx$ 1 µm). For comparison with the traits of soldiers from mature colonies, 60 soldiers from three *C. gestroi* mature colonies ($n = 20$ per colony) were investigated following the same methodology.

An asymmetry index (AI, in µm) was produced for each individual. This index takes into account three aspects of the soldier setae asymmetry: the departure from symmetry of paired setae, the presence of unpaired setae from expected pairs, and supernumerary setae from the expected pairs. First, the departure from symmetry was established for paired setae from the primary pairs, i.e, setae that were present on each side of the fontanelle with a degree of equivalence from an axial symmetry, as previously determined in Chouvenc et al. (2014) (lower pair and upper pair, Fig. 2). Second, all setae that were unpaired (from the expected primary pairs) were taken into account by giving an asymmetry penalty of 20 µm plus the departure of the given setae from its equivalent among the average locations of the two primary pair of setae (Fig. 2a). Finally, supernumerary setae (excess setae beyond the expected primary pairs) were taken into account by giving an asymmetry penalty of 30 µm plus the departure of the given setae from its equivalent among the average locations of the two primary pair setae. The sum of the three values resulted in a total displacement (µm), and provided an AI for each soldier (Fig. 2b–e). Penalty values were tested from a 0 to 50 µm range with an increment of 5 for each penalty. Among all tested combinations, the 20 and 30 µm penalty values resulted in AI values reaching a Poisson distribution with the highest lambda value and lowest deviation. In addition, Q–Q plot analysis confirmed that the AI distribution was not artificially altered due to penalties, and all data points belonged to a single population. Therefore, penalties were determined to measure and reflect unpaired/supernumerary setae on the overall asymmetry of individuals. Individuals with AIs $>$100 µm were considered as individuals with "extreme asymmetry", individuals with AIs between 50 and 100 µm were considered as individuals with "strong asymmetry", individuals with AIs between 25 and 50 µm were considered as individuals with "moderate asymmetry" and individuals with AIs $<$25 µm were considered as individuals with "low asymmetry".

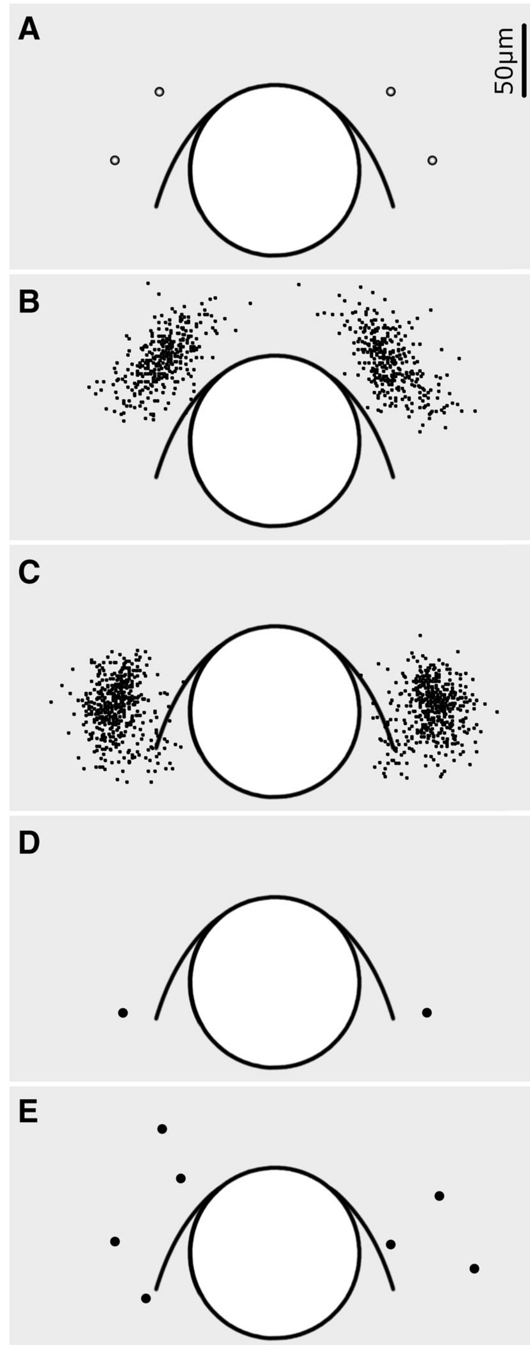

Fig. 2 Location of setae around the fontanelle of 459 *Coptotermes gestroi* nanitic soldiers sampled from 6-month-old colonies. The *circle* represents the fontanelle from a frontal view, as in Fig. 1. **a** Average locations of the two primary pairs of setae (*upper* and *lower*) found in nanitic soldiers, as established by the 459 individuals. **b** Combined locations of all individuals for the upper pair of setae only. **c** Combined locations of all individuals for the lower pair of setae only. **d** Example of the most symmetric individual in this study, with AI = 0 µm (perfect symmetry). **e** Example of the most asymmetric individual in this study, with AI = 321.4 µm

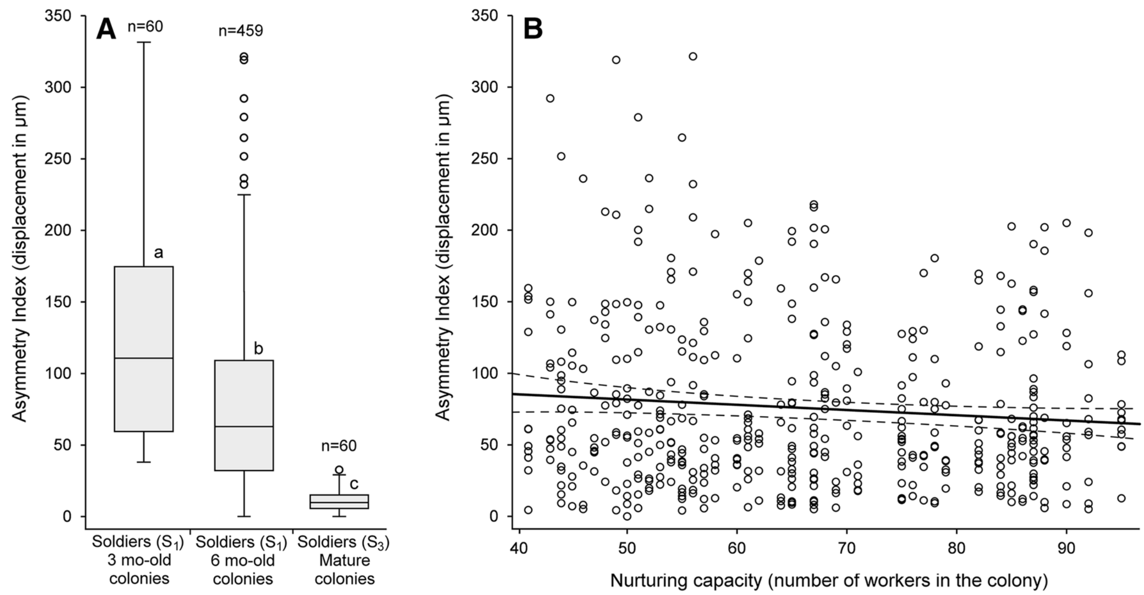

Fig. 3 Asymmetry index (AI in µm) in *C. gestroi* soldiers. **a** Comparison of soldiers' asymmetry observed in 3-month-old colonies, 6-month-old colonies and mature colonies. *Letters* indicate significant difference among groups (ANOVA, Tukey's HSD, $p < 0.001$). **b** Effect of the nurturing capacity on the asymmetry index estimated on 459 soldiers sampled from 6-month-old colonies ($\beta = 6.468 \times 10^{-5}$, $t = 2.085$, $p = 0.038$), with the model prediction and its 95% confidence intervals indicated by the *bold* and *dashed lines*, respectively

To test for the role of the nurturing capacity (number of workers available for developing soldiers) on the nanitic soldiers' asymmetry, the AI was regressed against the number of workers. To account for the right-skewed distribution of the AI (as it is bounded by zero, Fig. 3), we used a generalized linear model (GLM) with a Gamma distribution and an inverse link. Residuals were then visually inspected to assess possible violations of linear model assumptions, and a measure of goodness of fit was computed using McFadden's pseudo R^2, given by $[1 - \ln(LM)/\ln(L0)]$, where LM is the likelihood of the full model, and $L0$ is the likelihood of the model with no predictor. Finally, the asymmetry index values obtained from nanitic soldiers of 6-month-old colonies ($n = 459$), 3-month-old colonies ($n = 60$), and from soldiers collected in mature colonies ($n = 60$) were compared with an ANOVA (Tukey's HSD post hoc). Values are presented in the results as mean ± SE.

Results

Soldier asymmetry from 3-, 6-month-old and mature colonies

Soldiers sampled from mature *C. gestroi* colonies (developmental pathway S_3) displayed minimal setae asymmetry around the fontanelle (AI = 10.16 ± 0.91 µm, $n = 60$). In comparison, most nanitic soldiers sampled from 6-month-old colonies (developmental pathway S_1) displayed strong development instability (AI = 74.85 ± 2.76 µm, $n = 459$). However, the relatively low standard error from this sample was due to its large size and does not reflect the wide variability observed in the developmental instability of nanitic soldiers collected from 6-month-old colonies (Figs. 2b–e, 3a, b), with 26% individuals displaying extreme asymmetry (AI >100 µm).

Collecting all soldiers from 6-month-old colonies did not take into account that soldiers from each colony did not emerge at the same time and therefore each soldier was produced at a different degree of nurturing capacity during the growth of the colony. To discriminate soldiers produced within the first 3 months after foundation from those produced between 3 and 6 months, a second experiment investigated soldiers from 3-month-old colonies. All were nanitic soldiers (S_1) and most individuals displayed strong or extreme developmental instability (AI = 123.04 ± 10.17 µm, $n = 60$). All 28 3-month-old colonies had between 8 and 14 workers. In 3-month-old colonies, more than 54% of nanitic soldiers displayed extreme asymmetry (AI >100 µm).

All three groups had significant differences in displayed asymmetry ($F_{(578,2)} = 56.9$, $p < 0.001$, Tukey's HSD, Fig. 3a). The comparison between soldiers collected from 3- and 6-month-old colonies confirmed that soldiers displaying extreme instability (AI >100 µm) in the 6-month-old colonies were primarily produced in the early growth (<3 months), while most soldiers were produced between 3 and 6 months had improved symmetry (AI <100 µm).

Effect of the nurturing capacity on soldier development from 0 to 6 months

Individuals with a wide variability of asymmetry index were observed in the large pool of soldiers sampled from 6-month-old colonies. Many soldiers displayed extreme asymmetrical traits (AI >100 µm), while others displayed asymmetrical traits at a similar degree to mature colonies (AI <25 µm) (Fig. 3a). Soldiers developed in colonies with a range of nurturing capacity (40–95 workers), which negatively affected their asymmetry index ($\beta = 6.468 \times 10^{-5}$, $t = 2.085$, $p = 0.038$) (Fig. 3b). Therefore, soldiers produced in the presence of numerous workers developed in better conditions than soldiers produced in the presence of fewer workers. This effect, while significant, was weak and only explained less than 1% of the observed variance (McFadden's pseudo $R^2 = 0.009$).

Discussion

Our results confirmed that *C. gestroi* soldiers produced in incipient colonies display strong asymmetrical traits when compared with soldiers from mature colonies (Chouvenc et al. 2014). Developing conditions are not optimal in newly established colonies and the stress imposed on individuals is therefore reflected in their strong asymmetry (Parsons 1992; Markow 1995). However, the current study showed that most of the soldiers produced in the first 3 months display extreme asymmetrical morphotypes, while in comparison, 6-month-old colonies produced soldiers with a wide range of asymmetry, including individuals with relatively weak asymmetry. The two experiments show that during the early growth of a colony, when the nurturing capacity is critically limited and contingent mostly on the primary reproductive and a few workers (8–14 workers), 90% of the produced soldiers displayed strong or extreme asymmetry (AI >50 µm). Between 3 and 6 months, the colonies initiated their exponential growth (40–95 workers) and some of the soldiers produced during this time displayed reduced asymmetry. The wide variability of asymmetry observed in Fig. 3b depicts how each colony initially produced poorly symmetrical individuals, but as the nurturing capacity improved, produced soldiers that were more symmetrical.

Independently of the timing of the production of soldiers in each colony, all 73 6-month-old colonies had inherently different degrees of success (in term of initial colony growth), implying that the fecundity and the initial quality of the care by the parents and the first few workers differed. The growth rate of 6-month-old colonies reflects the overall nurturing capacity of a given colony and soldiers produced in the most successful colonies (>80 workers) displayed less extreme phenotypes than the least successful colonies (<60 workers). The negative effect of the nurturing capacity on the asymmetry index therefore confirms that the quality of brood care improves as the colony grows, and that better the initial growth, the more symmetrical the soldiers.

While the results support the importance of the quality of care for developing individuals in termite colonies, soldiers produced in mature colonies displayed far more symmetrical traits than a majority of nanitic soldiers produced in incipient colonies. Therefore, despite an improvement of developing conditions as the incipient colony grows, nanitic soldiers (S_1) are still inherently more asymmetrical than soldiers produced in mature colonies (S_3). Nanitic soldiers, having been produced with at least two less molts than soldiers from mature colonies, are therefore affected not only by the relatively low nurturing capacity of incipient colonies, but also by the accelerated development of such individuals.

Termite colonies have an internal regulation system for soldier production (Korb et al. 2003; Itano and Maekawa 2008), which allows colonies to maintain a stable soldier proportion, often in a species-specific manner (Haverty 1977). In incipient *C. gestroi* colonies, the production of soldiers and the maintenance of the soldier proportion come with an important cost on colony growth, as the initial investment in workers (care providers) and soldiers (dependents) affect the original growth and can impact the chances of colony success (Chouvenc et al. 2015a). Because of the inherent soldier cost in incipient colonies, nanitic soldiers were compromised by the soldier proportions imposed by physiological rules ($\approx$10%), with colonies limiting the initial investment into "cheap" soldiers (Chouvenc et al. 2015a). The current study shows that this limited investment comes in two different forms: as reduced brood care and in accelerated development, both resulting in significant developmental stresses on soldiers that manifests in their morphology. As the colony grows, the nurturing capacity improves and the colony invests in "better" soldiers with additional molts (Chouvenc and Su 2014; Chouvenc et al. 2014). As the colony invests more time and resources toward the defensive caste, it results in individuals displaying strong symmetrical traits (Supplementary Figure S1), and fully functional soldiers can now take part in defending the expanding colony.

This study confirms that the incipient phase in social insect colonies is a critical bottleneck where important stresses are imposed on developing individuals. These stresses are particularly strong during the first few months after foundation, as individuals are produced in a limited brood caring environment and are subjected to accelerated developmental pathways. As the colony initiates its exponential growth with the acquisition of a critical mass of workers, the stressful forces progressively attenuate. Once the colony has reached maturity, individuals mostly express symmetrical traits, reflecting the homeostatic and optimal developmental conditions for the brood. Finally, Du et al. (2017) showed that as a young termite colony develops, complex brood care behaviors and task division progressively emerge. Such an observation confirms that the quality of brood care in incipient colonies is suboptimal when compared with that of mature termite colonies, and that this limited brood care quality can be directly measured on the level of soldier head asymmetry.

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