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RESEARCH ARTICLE

Incipient colonies of the neotropical termite *Cornitermes cumulans* (Isoptera: Termitidae): comparing monogamy and polygamy as reproductive strategies

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Abstract

A termite colony is generally founded by a monogamous pair of alates during swarming. However, primary polygyny resulting from pleometrotic associations has been recorded for some termites. These multiple queens may continue to be associated during colony lifespan or be dissociated by conflicts that result in colony fragmentation or death of some reproductives. To date, primary polygyny in the termite *Cornitermes cumulans* has occasionally been observed in the field but no records in the literature are available. Due to its irregular incidence, this study aimed to investigate the proximate factors involved in colony development and the rare occurrence of polygamous colonies of *C. cumulans*. Forty monogamous colonies and 20 polygamous colonies (10 polygynous colonies: two females and one male; 10 polyandrous colonies: one female and two males) were set up in the laboratory. The initial development was followed for a period of 100 days, during which time censuses of the colonies were performed. Polygynous colonies laid more eggs than monogamous ones, but not twice as many, as expected, until day 60. Conversely, monogamous colonies produced more larvae than polygynous colonies until the appearance of workers, when larvae started to molt to workers and decreased in number. Larvae were rarely observed in polygynous colonies, which may be associated with cannibalism of these individuals by one of the two females. Due to these factors, primary polygyny seems to be unlikely in *C. cumulans* during colony foundation, which is in accordance with observations of natural colonies that mostly contain only a single queen.

Keywords Colony foundation · Eggs · Hatching · Higher termites · Reproduction

Introduction

The foundation of a new colony in termites generally occurs with the mating of a pair of alates after a brief swarming event (Nutting 1969). The future queen and king provide all of the genetic contribution to colony members during the initial development, resulting in high relatedness among nestmates, following the concept of inclusive fitness by Hamilton (1964, 1972). However, more than two individuals of the same sex can found a new colony in some termites. These polygamous associations may cause conflict among reproductives (Nutting 1969; Roisin 1993), though such cooperation among individuals may represent an advantageous strategy in the early development of colonies (Darlington 1988; Roisin and Pasteels 1985; Thorne 1985), when the incipient colonies are fragile and require exploiting a new area without a worker force.

Polygamy, including polygynous and polyandrous colonies, may be established through several mechanisms such

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as pleometrotic colony foundation (Chiu et al. 2018; Costa-Leonardo and Espírito-Santo-Filho 2004; Thorne 1982, 1984, 1985), by producing neotenics (Fougeyrollas et al. 2015; Fougeyrollas et al. 2017; Fournier et al. 2016; Haifig et al. 2016; Luchetti et al. 2013; Matsuura et al. 2009; Vargo et al. 2012), or by merging of different colonies (Grube and Forschler 2004). These mechanisms may also include non-regular colony foundation by individuals of the same sex, as has been reported for some lower termites (Matsuura and Nishida 2001; Matsuura et al. 2002, 2004; Mizumoto et al. 2016). However, the establishment of a new colony by a single pair of reproductives, that is monogamy, seems to be more likely in these insects (Nutting 1969).

Cornitermes cumulans (Kollar, 1832) is a mound-building termite species that occurs in Brazil, Paraguay and Argentina. This termite is considered a key-stone species in Brazilian Cerrado vegetation due to its large nests which harbor several other species (Costa et al. 2009; Marins et al. 2016; Redford 1984). Many studies involving this species (see Fernandes et al. 1998; Pereira da Silva et al. 1979; Torales et al. 1999), and our own experience in collecting nests and extracting their entire populations, have never recorded the occurrence of more than a single primary queen. However, a voucher with more than one *C. cumulans* primary queen is deposited in the collection at the MZUSP—Museu de Zoologia da USP (EM Cancello, personal communication) and two primary queens were collected in a nest at Mato Grosso do Sul, Brazil (JT Lima, personal communication).

Polyandry is not common in termites (Wu et al. 2013) and considering the rare occurrence of imaginal polygyny in *C. cumulans*, we analyzed the early development of colonies of this termite in both monogamous and polygamous scenarios aiming to understand the possibility of pleometrotic colony foundation and the near absence of polygyny found in natural colonies. Though there is no evidence of polyandry in *C. cumulans*, we tested both polygamous scenarios to understand the dynamics of pairs of alates with one extra male or one extra female. This test allowed us to determine whether there were aggressive interactions among reproductives in the polygamous associations. We hypothesized that multiple reproductives would exhibit agonistic behavior against each other and/or against non-related offspring, leading to the survival of only a single pair of reproductives or to a slower growth of the colony.

Materials and methods

Termite collection

Alates of *Cornitermes cumulans* (Isoptera: Termitidae: Syntermitinae) were collected during swarming in the city of Rio Claro, São Paulo, Brazil (22° 23′ S, 47° 31′ W). The termites were collected from three different swarming sites, separated by a minimum distance of 30 m (sites A and B) and a maximum distance of 2 km (sites A and C). Following collection, the termites were all grouped in the same vial to be sexed and paired.

Incipient colonies

Laboratory colonies of *C. cumulans* were initiated from alates, which were sexed, de-alated and randomly paired. The experimental arenas were composed of 9 cm diameter Petri dishes filled with moistened aged *Pinus* sp. sawdust. The couples were placed in a 3-cm diameter cleared space in the center of each dish.

A total of 40 colonies were set up and maintained in a dark room at 25 ± 2 °C. Water was added to the sawdust when necessary to keep sufficient moisture throughout the experiment. The colonies' development was followed during the first 100 days. The number of eggs, larvae, workers and soldiers was determined every day during the first 20 days and at 8-day intervals from day 28 to 100. When one of the reproductives died, the colony was removed from the census from that interval forward.

Polygamy tests

Two different tests were performed to evaluate the tolerance of *C. cumulans* to polygyny and polyandry during a colony's initial development. Similar experimental arenas as described for the incipient colonies were used. In test 1, two female alates were combined with one male, and in test 2, two male alates were combined with one female. Each test was replicated 10 times. These 20 polygamous colonies were observed for the same periods as the incipient monogamous colonies, and the number of eggs, larvae, workers and soldiers of each unit was recorded. In the case of the death of any reproductive, we inspected it for signs of aggression and removed the entire replicate from our analysis. The individuals were checked for signals of agonistic behavior, which was detected by the presence of injuries to the head, abdomen, antennae and legs. We estimated the intensity of aggression in one individual from 0 to 1: 0 equal to no aggression, 0.1 one injured antenna (total 0.2), 0.1 one injured leg (total 0.6), 0.1 for injury to the head, and 0.1 for injury to the abdomen, totaling 1 (considered full aggression). We also examined the same number of dead individuals from monogamous incipient colonies for statistical comparison.

Data analysis

Differences in survival between the monogamous and polygamous colonies were analyzed using the function *survdiff* of the library survival in R. The level of agonistic behavior based on the aggression rate was compared between polygamous and monogamous colonies through statistical analysis by the Wilcoxon rank-sum test.

The number of eggs laid by monogamous colonies during days 3 to 44, right before larvae start hatching, was compared to that laid by polygamous colonies using a multivariate analysis of variance—MANOVA. We excluded days 1 and 2 because none of the colonies presented eggs at this time. The number of laid eggs by monogamous colonies was also hypothetically doubled to verify whether the polygynous colonies with two females laid twice the number of eggs laid by one female from monogamous colonies. These data were also analyzed using MANOVA. We performed MANOVA rather than repeated measures ANOVA because data showed strong departure from sphericity (Mauchly's sphericity test: $W<0.0001$; $P<0.0001$). The number of larvae and workers was also compared between monogamous and polygamous colonies using MANOVA. In all comparisons, a significance level of $\alpha=0.05$ was used. The analyses were performed in the program R, version 4.1.1 (R Core Team 2020).

Results

Incipient colonies

The successful establishment of incipient colonies occurred in 36 out of the 40 (90%) monogamous pairings of alates. From those 36 colonies, 28 survived for the entire experimental period (100 days), with losses of two colonies each at days 10 and 13, and one colony each at days 40, 62, 70 and 92.

Oviposition started on the 3rd day after the alates were placed together in the experimental arenas (Fig. 1). On this date, only three colonies initiated egg laying, but by day 7, 35 out of the 36 colonies produced eggs. The number of eggs produced was 26.81 ± 2.37 (mean ± se) on day 20 (Fig. 1), and this number increased until day 40, with 35.94 ± 1.53 eggs per colony. Larvae were observed in some monogamous colonies on day 44 (Fig. 2), and on day 52, larger larvae probably of 2nd instar were observed. The number of larvae increased continuously until day 68, when the larvae started molting to workers. The workers were observed in the first colonies on day 68 of development, and were characterized by sclerotized mandibles and the presence of food in their gut, which was seen through the translucent abdominal cuticle. This differentiation was conspicuous and the color of their abdomen changed from whitish in larvae to dark brown and gray in workers. As expected, the number of workers increased as the number of larvae decreased, especially after day 76 (Fig. 2). Workers carrying and grooming the eggs were observed on day 84.

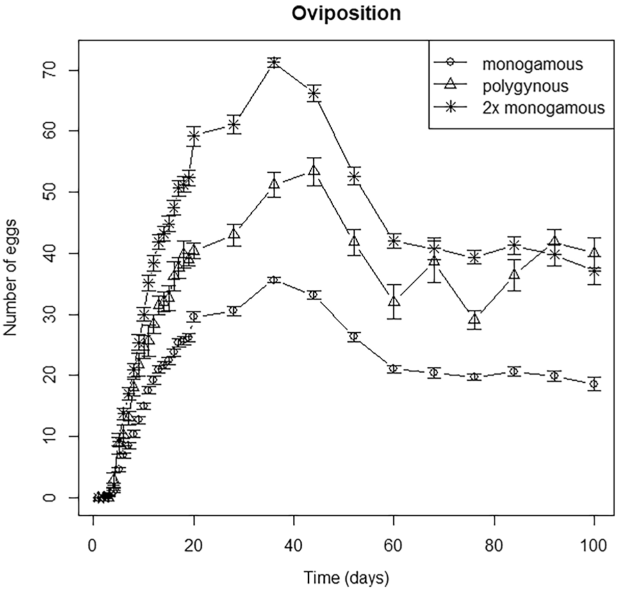

Fig. 1 Cumulative number of eggs in monogamous and polygynous colonies of *Cornitermes cumulans*. Mean (± SE)

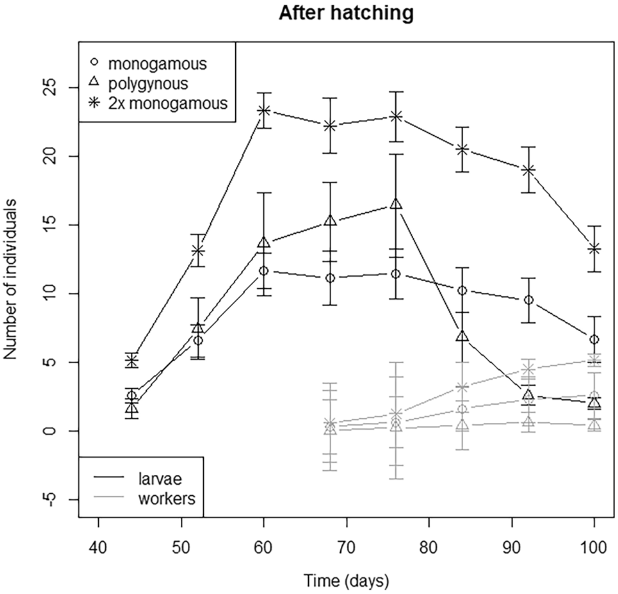

Fig. 2 Appearance of larvae and workers in monogamous and polygynous colonies of *Cornitermes cumulans*. Mean (± SE)

The first pre-soldiers appeared concomitantly with workers on day 76 of development, in two colonies, one in each. One of the pre-soldiers differentiated to soldier after 16 days, on day 92, and this soldier was removed from the colony to confirm the taxonomic identification of the species. The same procedure was performed with all soldiers available at the end of the experiment ($n = 5$).

Polygamous tests

We observed dramatic differences compared to the monogamous colonies on the first day. One or both males died in nine out of 10 polyandrous colonies, leaving only one colony with both males alive. One of the colonies that became monogamous with a surviving male–female pair remained alive during the 100 day period. Five out of ten polygynous groupings failed to establish polygamous colonies because three lost one of the females and two lost the male, though one surviving male–female pair was able to establish a monogamous colony. The other five polygynous colonies retained all three reproductives during the entire 100-day period. Within the first month, at day 20, both males of the single polyandrous colony that remained alive died. Overall, the polygamous colonies experienced a higher mortality of the reproductives during the first days when compared to monogamous colonies ($\chi^2 = 16.3$; $df = 1$, $P < 0.0001$). Only the data of the five polygynous colonies were used for comparison with the monogamous colonies.

The agonistic interactions were high among the reproductives, and the intensity of aggression was higher in polygamous colonies ($W = 26$; $P < 0.0001$), in which males ($n = 13$) exhibited more injuries than females ($n = 3$). The most affected structures were the legs of the opponents, representing approximately 71% of the attacks, followed by 23% in the antennae and 6% in the abdomen. There were no signs of aggression on the head including the mandibles, maxillae, palps and their segments.

During the first 44 days of development, the number of eggs laid by the two queens increased at each count. The number of eggs was greater than that laid by monogamous colonies within this period ($F = 27.11$, $df = 14, 21$, $P < 0.0001$), but never reached twice as many as the monogamous colonies in the same period ($F = 15.233$, $df = 14, 21$, $P < 0.0001$), as expected for the presence of two egg-laying queens. After the larvae appeared in these polygynous colonies, the number of eggs oscillated, decreasing from day 44 until day 60, then increasing at day 68, decreasing again and finally increasing until day 100 (Fig. 1).

The number of larvae also varied, increasing in the beginning, from the 44th day until the 76th day, but then decreasing without the appearance of workers. Only one worker appeared on the 76th day of development, two workers on the 84th day, three on the 92nd day, and again only two workers were observed on the 100th day (Fig. 2). The number of larvae was significantly higher ($F = 3.5932$, $df = 3, 30$, $P = 0.0249$) in monogamous colonies on days 84, 92 and 100 when compared to the polygynous colonies. No significant differences were observed comparing the number of workers of monogamous and polygamous colonies ($F = 0.5863$; $df = 5, 29$; $P = 0.7102$) (Fig. 2).

Discussion

The incipient colonies of *C. cumulans* started laying eggs by the third day after alate pairing. This is similar to other Termitidae species which laid eggs at faster and higher rates than non-Termitidae species that may take several days to lay few eggs (Nutting 1969). This was also observed in *Trinervitermes trinervoides* and some species of the genus *Macrotermes*, which started oviposition within the first week after pairing (Adam and Mitchell 2009; Mitchell 2020; Okot-Kotber 1981). The early oviposition in this group allows rapid production of a workforce, thus serving to reduce the dependence on the alate energy reserves to fuel colony development (Adam and Mitchell 2009). The *C. cumulans* colonies also showed a decrease in the number of eggs around day 44 to 52. During this period, larvae start hatching from the eggs, which were not replaced in number, suggesting that the queen stopped ovipositing. Torales et al. (1999) observed eggs in 70% of the nests and immatures in different stages of development during the entire year, suggesting that oviposition is continuous throughout the year in this species, but they analyzed mature colonies. Our results indicate that the *C. cumulans* queen might interrupt egg laying around 45 days after colony establishment, when the incipient colony still lacks a workforce. In addition, egg laying activity does not seem to resume until day 100. Interruption of egg laying was also observed in some termites, especially in non-Termitidae species (Nutting 1969).

Our results showed that when two queens were associated in the polygynous test the total number of eggs was greater than in monogamous colonies, although the number of eggs laid per queen was smaller than in monogamous colonies during the first 60 days. This was also the case for *Macrotermes michaelseni*, in which the number of eggs laid per queen was smaller in polygynous colonies than in monogamous colonies (Kaib et al. 2001). More eggs may result in a larger worker force that will help with colony success, as has been seen in hymenopterans (Bartz and Hölldobler 1982) and this was expected for the polygynous colonies in our study. However, after hatching started, we observed the number of larvae decreased without the concomitant appearance of workers in the polygynous colonies, which resulted in a significantly higher number of larvae in monogamous colonies. Although we did not observe cannibalistic behavior during our evaluations, we only briefly inspected the colonies for censuses and the disappearance of larvae suggests that cannibalism may have occurred in the polygynous colonies. This scenario would explain the slower growth observed for polygynous colonies compared to monogamous ones and when compared to double values of monogamous colonies.

The high mortality of one or more reproductives when placed in polygamous conditions indicates that *C. cumulans* is a species that presents little tolerance to polygamy. This is also evident in nature, when we collect mature colonies of this species and census the population. Although multiple queens have been observed in other species of *Cornitermes*, e.g., *C. snyderi* (Fernandes et al. 1998), the records for this occurrence in *C. cumulans* are very rare and no empirical study has been conducted to analyze this frequency in nature. Furthermore, similar results were found in *Nasutitermes corniger*, where reproductives were more likely to die in colonies founded by pleometrosis than in those founded by monogamous pairs (Hartke and Rosengaus 2013).

Nalepa and Jones (1991) suggested that monogamy in termites might be related to ecological constraints, such as low-quality food and high costs of searching for a mate. In addition, in the case of two or more same sex alates initiating a new colony, there would be competition among them, which probably leads to intraspecific agonism and only one male and one female survives. According to Chiu et al. (2018), pleometrosis in *Odontotermes formosanus* is beneficial during colony founding, due to increased nest excavation and rapid colony growth. However, there are risks associated with higher density of individuals, such as space limitations, disease transmission and intraspecific aggression. In the present study, agonistic interactions were predominantly observed between males of *C. cumulans* in the polyandrous colonies that resulted in the death of all units, indicating that the presence of one extra male is not tolerated. Polyandry is indeed rare in termites, hitherto it has only been described in one non-Termitidae species (Wu et al. 2013). Agonistic interactions were also observed between females, which caused the mortality of half of the experimental polygynous colonies. Conflicts resulting in mutilations of the queens were observed in polygynous colonies of the termite *M. michaelseni* (Brandl et al. 2001). Hartke and Rosengaus (2013) also documented that pleometrotic colony foundation was unfavorable when compared with monogamous foundation in *N. corniger* due to higher colony mortality. Therefore, the low survival of the group along with low colony growth suggests that pleometrosis is not a viable strategy for colony foundation in *C. cumulans*.

In conclusion, our results indicate that during the initial development of monogamous colonies in *C. cumulans*, there was an interruption in the production of eggs after around 45 days following colony establishment, concomitant with the hatching of larvae, which increase in size and become workers after some weeks. In polygynous groups, the colonies produce significantly more eggs than monogamous colonies, but less than their expected potential. The two females do not produce twice as many eggs until day 60. Larvae appeared at the same time in the polygynous colonies, but a decrease in the number of larvae, which did not molt to workers, was observed through time. Cannibalism may be a reasonable explanation for those observations. In summary, our results indicate that overall colony growth is lower and relatively rare in polygamous groups, which confirms the rare polygyny records for *C. cumulans* observed in natural colonies. Further studies may analyze natural populations and their reproductive strategies concerning the number of reproductive individuals within colonies to support our findings.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00040-022-00852-w.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by LHBDS, CJ and IH. The first draft of the manuscript was written by IH and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Availability of data and material The data that support the findings of this study are available in the supplementary material.

Code availability Not applicable.

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