ALESSANDRA MARINS

AGRESSIVIDADE EM *Cornitermes cumulans* (KOLLAR) (INSECTA: ISOPTERA) SUBMETIDOS A ESTRESSE

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

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À minha mãe por ter me ensinado
que a curiosidade é a chave da sabedoria,
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de saciar minha curiosidade.

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RESUMO

MARINS, Alessandra, M. Sc., Universidade Federal de Viçosa, julho de 2007. **Agressividade em *Cornitermes cumulans* (Kollar) (Insecta: Isoptera) submetidos a estresse**. Orientador: Og Francisco Fonseca de Souza. Co-orientadores: Angelo Pallini e José Henrique Schroeder.

Os insetos sociais possuem a habilidade de reconhecer indivíduos do mesmo ninho e evitar invasões de intrusos no ninho. No entanto, ninhos de cupins são freqüentemente invadidos por artrópodos, principalmente insetos, incluindo outras espécies de cupins denominados inquilinos. Os mecanismos que determinam a invasão são pouco conhecidos. Para entender como os indivíduos da espécie construtora do ninho reconhecem esses intrusos, é necessário entender o processo de reconhecimento entre indivíduos com mesma morfologia e comportamento, porém de outro ninho. Ainda não está esclarecido se os inquilinos enfraquecem a espécie construtora, visando invadir o ninho, ou se em uma colônia previamente enfraquecida, o estabelecimento de inquilinos ocorre mais facilmente. Dessa maneira, é plausível supor que em uma colônia submetida a algum estresse externo, o processo de estabelecimento de inquilinos seja favorecido. Sendo assim, espera-se que o sistema de defesa desta colônia seja menos eficiente, quando comparado a uma colônia sem estresse. Nesta tese, a principal hipótese testada foi que a agressividade dos indivíduos da espécie construtora varia em função ao estresse a que estão submetidos. Para isso, indivíduos de *Cornitermes cumulans* (Kollar, 1832) foram submetidos a diferentes intensidades de estresse, dependendo do tempo que permaneceram fora do ninho. Posteriormente, foi mensurada a agressividade e a sobrevivência desses indivíduos em grupos formados por apenas indivíduos do mesmo ninho e em grupos formados por indivíduos de ninhos diferentes. Nas situações de baixo estresse *C. cumulans* foi mais agressivo com indivíduos de outro ninho do que com indivíduos do mesmo ninho. No entanto, na situação de alto estresse indivíduos do mesmo ninho foram tão

agressivos quanto indivíduos de diferentes ninhos. Esses resultados podem indicar que a saúde da colônia é um fator importante na defesa da colônia contra invasores.

ABSTRACT

MARINS, Alessandra, M. Sc., Universidade Federal de Viçosa, July, 2007. **Agressivity in *Cornitermes cumulans* (Kollar) (Insecta: Isoptera) submitted to stress**. Adviser: Og Francisco Fonseca de Souza. Co-Advisers: Angelo Pallini e José Henrique Schroeder.

Social insects can recognize nestmates and avoid nests invasion. However, termite nests are frequently invaded by arthropods, mainly insects, including other termite species called inquilines. Mechanisms that allow nest invasion are not completely understood yet. In this work, we focus on intruders which are termite species, and how the colony builder can defend its nest from such intruders. In order to understand how builder individuals may recognize intruders, we need first to comprehend how they can distinguish themselves from other individuals with same morphology and behaviour (non nestmates). Some termite species are able to recognize non nestmate and other species do not. We do not know if inquilines may harm the original builder, or if a weak colony allows inquilines to enter. If it is true that in a stressed colony the process of inquiline's settlement is favored, we expect the colony defense system to become less efficient when the colony is subjected to some kind of stress. We tested the hypothesis that the aggressiveness of builder individuals varies with the stress that the colony is subject to. To do so we submitted *Cornitermes cumulans* workers to different amount of stress, changing how long they spent away from the nest. We checked workers aggressive behaviour and survival in groups only with nestmates or with non-nestmates. In low stress situation *C. cumulans* was more aggressive against non nestmates than against nestmates. In a high stress situation there was a increase in aggressiveness only in nestmates. This findings may be a indication that colony health is an important factor mediating colony defense against intruders.

1 INTRODUÇÃO

Interações ecológicas entre espécies podem ser positivas, negativas, neutras, ou ainda um contínuo entre esses extremos (Price, 1984). Essas interações resultam de um balanço entre custos e benefícios para as espécies envolvidas. Esse balanço não é fixo, mas pode ser alterado quando certas condições são modificadas. Essas condições podem ser: disponibilidade de recurso, abundância de cada uma das espécies envolvidas, e a presença (ou abundância) de uma outra espécie nova ao sistema (Begon et al., 2006). Quando se observa alguma alteração nestas interações, é difícil de identificar quais dessas condições foram alteradas.

Ninhos de cupins são freqüentemente habitados por indivíduos de outras espécies de cupins denominados inquilinos (Grassé, 1982). As relações entre a espécie construtora do ninho e as espécies que o coabitam, ainda não estão elucidadas. Pode existir uma relação negativa, se a espécie inquilina prejudicar a construtora, por exemplo, enfraquecendo a estrutura do ninho por se alimentar de suas paredes internas (Eggleton & Bignell, 1997); ou positiva, se a espécie inquilina auxiliar a construtora formando um sistema integrado de defesa que aumente a proteção contra predadores de todas espécies coabitantes do ninho (Redford, 1984); ou mesmo, um contínuo entre os extremos.

Existem vários registros de ocorrência de inquilinos (Araujo, 1970; Lacher Jr. et al., 1986; Domingos & Gontijo, 1994; Collins, 1980, entre outros), no entanto poucos trabalhos investigam quais são os fatores que determinam sua ocorrência. Sabe-se entretanto que, a riqueza desses inquilinos aumenta: (i) com o aumento do volume do ninho (Coles, 1980; Redford, 1984; Costa, 2005); (ii) na ausência de alados (Costa, 2005); e (iii) quando a espécie construtora do ninho não está presente (Redford, 1984; Costa, 2005).

O aumento da riqueza de inquilinos com o aumento do volume do ninho pode ser resultado de alguns fatores, não necessariamente independentes. Um maior volume de ninho implica em maior espaço, o que pode facilitar o estabelecimento de inquilinos, caso a limitação de espaço seja um fator importante para a co-ocupação em cupinzeiros. Além disso, um ninho demasiadamente grande pode implicar em menor eficiência de patrulhamento pelos construtores, e assim facilitar a invasão por inquilinos. Estes dois efeitos pressupõem que a invasão resulta de interações entre coabitantes de ninhos mas, mesmo na ausência de tais interações, um maior volume de ninho pode facilitar a invasão. Ninhos grandes são necessariamente mais velhos e, assim, estão há mais tempo disponíveis para a colonização por inquilinos. Assim, se a invasão não se dá por interações negativas entre coabitantes, então a maior riqueza de inquilinos em ninhos grandes pode ser consequência simples da idade do ninho.

Costa (2005) coletou diversos ninhos (durante um mês no Parque Nacional das Emas - GO) e verificou que algumas colônias estavam produzindo alados, e outras não. Nas colônias sem produção de alados a riqueza de inquilinos foi maior. Se uma colônia não está investindo em reprodução, em uma época favorável a isso (indicada pela presença de alados em outras colônias), significa que determinados fatores ecológicos (tais como predação ou competição) podem estar prejudicando a reprodução (Begon et al., 2006). Isso pode indicar uma relação de enfraquecimento da colônia com estabelecimento de inquilinos (Costa, 2005).

O fato da riqueza de inquilinos aumentar na ausência da espécie construtora (Redford, 1984) é um indicativo que de alguma forma a espécie construtora inibe o estabelecimento de pelo menos algumas espécies de inquilinos.

Resumindo, o fato de inquilinos ocorrerem em ninhos sem alados, associado ao fato de a riqueza de inquilinos aumentar na ausência do construtor, nos leva à suspeita de que de fato a invasão de cupinzeiros (pelo menos por algumas espécies de inquilinos) é produto de interações negativas com o construtor. Não se sabe, entretanto, os mecanismos que envolvem tais interações. Inquilinos podem forçar sua entrada no ninho, estabelecendo uma relação quase parasítica com o construtor, ou podem ocupar o ninho de forma oportunista, valendo-se de um enfraquecimento da colônia do construtor por motivos alheios à propria invasão ou ao inquilino.

Se a ocupação de ninhos ocorre em situações nas quais a colônia do construtor original encontra-se enfraquecida por fatores externos, é plausível supor que em uma colônia submetida a algum estresse externo, o processo de estabelecimento de inquilinos seja favorecido. Sendo assim, espera-se que o sistema de defesa desta colônia seja menos eficiente, do que de uma colônia sem estresse.

O entendimento dos possíveis mecanismos que garantem o estabelecimento de coabitantes em ninhos de *Cornitermes cumulans* necessita como passo inicial definir a capacidade de reconhecimento de intrusos pelo construtor. Por isso, foram testadas as hipóteses de que:

1. *C. cumulans*, é mais agressivo com indivíduos de outras colônias do que com indivíduos de sua própria colônia;
2. Os indivíduos tem sua agressividade alterada quando sujeitos à algum tipo de estresse.

Esse entendimento permitirá futuras inferências a respeito do reconhecimento de coabitantes do ninho.

2 NESTMATE RECOGNITION IN *Cornitermes cumulans* TERMITES (INSECTA: ISOPTERA)

Alessandra Marins & Og DeSouza

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2.1 Introduction

Nest construction by temites requires a great amount of time, energy and building materials, but brings the benefit of providing a safe environment to the colony that builds it. Therefore, to achieve a better benefit/cost ratio, it is imperative to protect the nest against intruders. Despite of that, some termite species are able to invade other species' nests (Wilson, 1971), establishing their own colonies in the nest along with its builder, or even staying in the nest after the original builder dies.

In the Neotropics, mounds of *Cornitermes cumulans* (Kollar) termites are well known to shelter an enourmous diversity of intruders, either vertebrates or invertebrates. Among those, inquiline termite species are also abundant and diverse (Redford, 1984), some nests holding as much as seven other termite genera (pers.obs.). Differently from the interactions between ants and their social parasites (see Thomas et al., 2005), the strategies that termite inquilines use to break into and inhabit other termites' nests are mostly unknown. Therefore, any work on that should start from the basics to minimize confounding results. Based on such a premisse, we propose that to understand termite-termite invading strategies, it would be desirable to understand whether nest builders distinguish themselves from other individuals sharing similar morphology and behaviour (that is, conspecifics) but potentially presenting differing colony-specific labels.

In this study, we have tested whether *C. cumulans* (Kollar) workers would be able to recognize and display agonistic behaviour towards non-nestmates individuals, and whether such aggressiveness would increase with the distance between their nests. We have based our reasoning on the idea that individuals from different colonies would present different colony-specific labels which allow the distinction between 'self' and 'non-self'. Moreover, because the probability of sharing genetic relatedness and environmental cues should decrease as the nests are farer apart, similarity between such labels should decrease with increasing inter-nests distance.

2.2 Material & Methods

The experiments were performed using workers (third instar and beyond) collected from five field colonies of *C. cumulans* (Kollar) (Isoptera, Termitidae), in Viçosa, state of Minas Gerais, in southeastern Brazil. *Cornitermes* spp. are Neotropical termite species occurring in several habitats, including forests, "cerrados" (Brazilian savannas) and man-modified habitats, such as pastures or even gardens within cities, where they feed on living and dead grass and herbs (Cancello, 1989). Several species of this genus (among them *C. cumulans*) build large epigeous nests which are simultaneously inhabited by inquilines, such as other termite genera, ants, beetles, birds, snakes, etc (Redford, 1984).

Experiments consisted of lab assays that measured the agonistic behaviour and consequent survival times of termite workers confined together in petri dishes. Workers have been assayed because they are known to be the main responsible for termite-termite interactions, including recognition, alarm and agonistic behaviour (Thorne, 1982).

2.2.1 Collection

Fragments of *C. cumulans*'s nest were collected from five wild colonies in November 2006, in Viçosa, Minas Gerais, Brazil. The nests were marked from 1 to 5 and the distance between them measured in meters. The nest fragments have been extracted from the original nest, placed in a plastic bag, taken to lab, and kept in a constant temperature of 25°C. In the lab the nest fragments were kept in a plastic tray for c.a. 4 hours. Workers (third instar and beyond) used for the experiment were taken from nest fragment just before experiments began. Soldier's samples were collected for identification and voucher specimens inclusion in the Termitology Section of the Entomological Museum of the Universidade Federal de Viçosa. Specimens were identified to genus following Constantino (1999), and to species following Cancello (1989).

2.2.2 Experiment

Agonistic behaviour was considered as bites towards another individual which resulted in injury. We tested all pairwise combinations of the five colonies (nests 1×2, 1×3, ..., 4×5), resulting in five combinations for nestmates and ten combinations for non-nestmates. Termite workers were grouped within Petri dishes

(9 cm of diameter) lined with filter paper to ease mobility of individuals. To start trials, one experimenter placed individuals (10 from each colony or 20 from the same colony) into the Petri dish and passed it on to an observer that did not know if individuals were nestmates or non-nestmates. After one minute had elapsed the observer recorded how many individuals were in agonistic behaviour in that moment. Subsequent instant readings were done every one minute during 15 minutes. For the analysis we used the total sum of agonistic behaviour in 15 readings. This total ranges from 0 (none individuals in agonistic behaviour) to 300 (all 20 individuals in agonistic behaviour in all 15 readings).

After the observation period, Petri dishes were protected from light in order to carry out the survival test, which consisted of checking the number of dead individuals in 2 hours intervals (except from 10 PM to 8 AM), until 32 hours had elapsed or all individuals were dead.

2.2.3 Analyses

Analyses of agonistic assays aimed to check whether grouping type (nestmate or non-nestmate) affected aggressive behaviour. Data were subjected to generalized linear modelling and Quasipoisson errors with log link. Additional analysis on the effect of the distance between nests and aggressiveness between termites has been performed using the same statistical procedure. In the survival analysis we checked whether grouping type (nestmate or non nestmate) affected individual survival. To do so, data was subjected to survival analysis under Weibull distribution. Details on such analytical procedures are described in Crawley (2007).

In all cases, statistical significance ($P < 0.05$) was achieved by extracting explanatory terms from the model, and inspecting the consequent change in deviance by Analysis of Deviance with F tests. After that, residual analyses have been performed to verify error distribution and the suitability of the models employed, including test for over-dispersion. All statistical analyses have been performed in R (R Development Core Team, 2006).

2.3 Results

C. cumulans termite workers presented more aggressiveness towards non-nestmates than to nestmates (Fig. 1, $p = 0.018$). This differential aggressivity seemed effective enough to lead to mortality as the proportion of nestmates still found alive was higher than the proportion of non-nestmates (Fig. 2, $p < 0.001$).

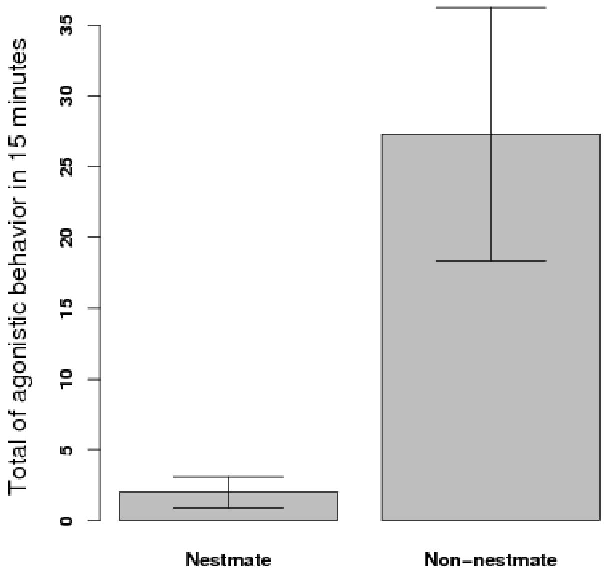

Figura 1: Total number of aggressive contacts between termites in two groupings: nestmate individuals and non-nestmate individuals ($p = 0.018$).

The distance between nests ranged from 5 to 128 meters, and such a range did not affect the pattern of aggressiveness between termite workers (Fig. 3, $p = 0.54$).

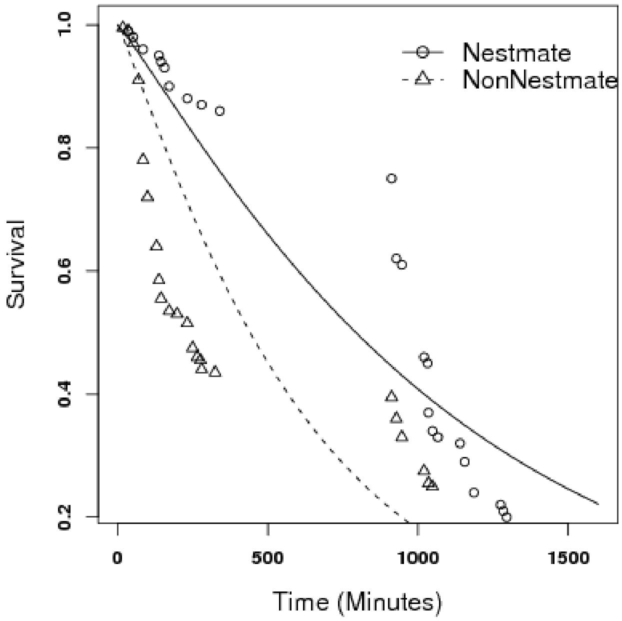

Figura 2: Proportion of termite individuals still alive as a function of time spent after submitted to the agonistic assays presented in Fig.1 ($p < 0.001$).

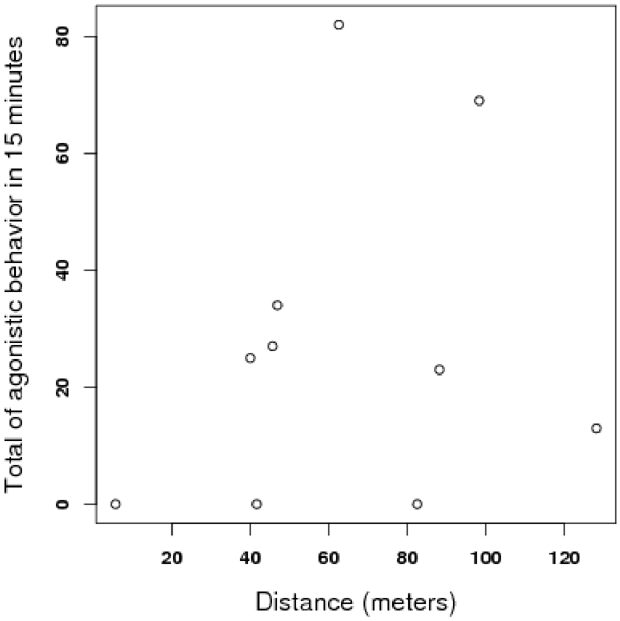

Figura 3: Total number of aggressive contacts between termites, as a function of the distance between their original nests in the field ($p = 0.54$).

2.4 Discussion

As expected *C. cumulans* was more aggressive towards non-nestmates than to nestmates (Fig. 1), and this aggressiveness resulted in a higher mortality rate in non-nestmate groups (Fig. 2). This seems to evidence that such termites do have the ability to recognize and repel 'non-selves'. The ability to recognize non-nestmates has been already recorded for some termite species (e.g. Thorne, 1982; Husseneder et al., 1998; Kirchner & Minkley, 2003; Uva et al., 2004; Kaib et al., 2004, among others), and is generally accepted that genetics (Adams, 1991; Husseneder & Grace, 2001), diet (Florane et al., 2004), and even endossimbionts (Matsuura, 2001; Kirchner & Minkley, 2003) would play a role in nestmate recognition. Such factors would assure the colony-specific hydrocarbon profiles which are known to be used as labels for termite-termite recognition (Kaib et al., 2004) but there are reports on the absence of correlation between hydrocarbons and interindividual aggressivity in termites (Florane et al., 2004; Uva et al., 2004).

These findings evidence that *C. cumulans* are able to recognize non-nestmates and attack them fiercely enough as to provoke the emergence of mortality beyond that expected from lab assay's stress only. Interesting enough, aggressivenness, albeit existent, was not modified by the distance between nests Such a recognition and repellence, being not dependent upon nest neighbourhood, seem to indicate that termite workers assayed here either (i) presented no similarity whatsoever or (ii) were intolerant to any difference in colony-specific labels, no matter how subtle these differences could be. If this is so, we might expect that the enourmous diversity of inquilines known to inhabit *C. cumulans* nests (Redford, 1984) are not promptly and pacifically accepted into such nests, if detected by the builder. Conversely, the absence of the builder may correlate with and increment in the diversity and abundance of inquilines, a pattern already noted by Costa (2005) for mounds of *C. cumulans* in 'Cerrados' (Brazilian savannas).

Concluding, is is plausible to suspect that the strategies for invasion of a termite nest may involve either disguise or contest, in a manner possibily similar to the strategies employed by inquilines of ant nests (Thomas et al., 2005). Further experiments should focus on this issue, preferably under field conditions.

3 DOES STRESS INDUCE AGGRESSIVE BEHAVIOUR IN THE TERMITE *Cornitermes cumulans*?

Alessandra Marins & Og DeSouza

3.1 Introduction

Termitophiles and inquilines, are nest invaders that use the environment built by termites. This association may be only with the nest structure itself or with termites individuals (Collins, 1980). It is plausible to suspect that the process of invading the host's nest in termites would be similar to the process known for ants. To enter and stay in the host colony, intruders of ants nests must bypass chemical recognition of their host (Akino et al., 1999; Lenoir et al., 2001). To do so, two strategies are known: (i) use of offensive chemicals to provoke panic, or decrease the aggressive response of the defenders (Ruano et al., 2005), or (ii) use of visual and olfactory cues, similar to the host, to disguise itself (Dronnet et al., 2005).

Different from the interactions between ants and their social parasites (see Thomas et al., 2005), the strategies that termite inquilines use to break into and inhabit other termites' nests are mostly unknown. Therefore, any work on that should start from the basics to minimize confounding results. Based on such a premise, we propose that to understand termite-termite invading strategies, it would be desirable to understand whether nest builders distinguish themselves from other individuals sharing similar morphology and behavior (that is, conspecifics) but potentially presenting differing colony-specific labels.

The ability to recognize non-nestmates has been already published for some termites species (eg. Thorne, 1982; Husseneder et al., 1998; Kirchner & Minkley, 2003; Uva et al., 2004; Kaib et al., 2004, among others). So far, these papers have not found a coherent pattern that allows to understand the process of recognition in termite-termite interaction. Apparently termites use a 'buquet' of components that allow them to be recognize as equals (Thorne, 1982), probably that is why is so difficult for researchers to find which factors are promoting termite identification.

It is plausible to suppose that nestmate recognition occur via relatedness, i.e. the more related two individuals are, more likely for them to be recognized as nestmates. When two individuals share a great amount of hydrocarbons, endossimbionts, diet and nesting site, their probability of being related relatives is increased, and consequently their agonistic behavior should be diminished (Kirchner & Minkley, 2003; Kaib et al., 2004; Florane et al., 2004, and papers therein)

Cornitermes cumulans and the species that live inside their nests present one of the most common cases of termite-termite cohabitation in neotropics (often call as inquilines) (Araujo, 1970; Redford, 1984; Lacher Jr. et al., 1986; Costa, 2005). It is known that inquiline richness is increased when: (i) increase nest volume (Coles, 1980; Redford, 1984; Costa, 2005); (ii) alates are absent (Costa, 2005); and (iii) original builder are absent (Redford, 1984; Costa, 2005).

The relationship between inquiline richness and nest volume, may exist due to some factors not necessarily independent. A larger nest volume implies more space, therefore it can ease establishment if space is an important limitation. Besides, the increase in nest volume may decrease patrolling efficiency of builder individuals, which may lead to intruders invasion. Both of these effects presuppose a negative interaction between co-habitants. Nevertheless, bigger nests are necessarily older and, therefore, exposed to invasion for a longer period. Thus, if nest invasion does not happen by negative interaction among co-habitants, then a higher inquiline richness in bigger nests may be a simple consequence of nest age.

Costa (2005) collected several *C. cumulans*'s nests (during a month in a National Park in Goiás state - Parque Nacional das Emas) and found that some builder colonies had alates and others did not. In the colonies without alates production the inquiline richness was higher. If a colony is not investing in reproduction in a favorable season (shown by the presence of alates in others colonies), imply that some ecological factors (such as predation or competition) may be affecting reproduction (Begon et al., 2006). This may indicate a relationship with a weaken colony and the inquiline establishment (Costa, 2005). The fact that inquiline richness increases in the absence of the original builder (Redford, 1984) is a clear indication that somehow, the builder restrain establishment of at least some inquiline species.

In conclusion, the fact that more inquilines are found in nests without alates, and the fact that inquiline richness increase in the absence of the original builder, leads us to suppose that termite nest invasion (at least for some inquiline species) is a consequence of negative interactions with the original builder. Nevertheless, it is not known which mechanisms are involved in such interactions. Inquilines may break into the nest actively facing the builder, or may occupy the nest in a opportunistic way, when the colony is subjected to some kind of stress, therefore deviating energy otherwise used in nest defence.

This last possibility of nest invasion by a opportunistic way we called the stress hypothesis, and it predicts that aggressiveness of termites individuals would be changed by stress inflicted on them. *C. cumulans* is able to recognize and attack conspecific workers individuals from other nests (Marins & DeSouza, 2008). However, according to our stress hypothesis, this ability to discriminate nestmate from non-nestmate would change if individuals were subjected to some kind of stress.

The central aim of this paper is to test the hypothesis that the aggressiveness of builder individuals varies with the stress that they are subjected to. This understanding will allow future inferences about the process of recognition in the termite nest.

3.2 Material & Methods

Due to the difficulty to measure workers stress in the field, we choose to test our hypotheses in lab experiment. In order to simulate different amount of stress in termites individuals, we left the nest fragments in the lab for 16 hours (eight hours longer than Marins & DeSouza (2008)).

Stress was inflicted on termites by keeping individuals away from their nests (albeit within a fragment nest) for a known amount of time, until the assays began. Individuals on which low stress was inflicted spent from 240 to 322 minutes away from their nests. Individuals under high stress spent 960 to 1065 minutes away from their nests.

The material collection and experiment procedures, including how we measure aggressivity and survival, were done according to (Marins & DeSouza, 2008).

3.2.1 Analyses

In the aggressive behavior analysis we checked if both of the explanatory variables (grouping type and stress) affected the response variable aggressive behavior. The explanatory variables were: (i) Grouping type: nestmate (all 20 individuals in the Petri dish were nestmates) and non-nestmate (10 individuals from one colony and 10 from a different one); and (ii) Stress: time away from the nest (amount of time each group of individuals in a Petri dish spent away from nest, ranging from 240 to 322 in low stress and 960 to 1065 in high stress). The data were subjected to generalized linear modelling and Quasipoisson errors with log link (Crawley, 2005).

We also checked if grouping type had influence in survival, using survival analysis with Weibull frequency distribution. Details on such analytical procedures are described in Crawley (2007).

Model simplification was achieved by extracting non-significant terms ($p > 0.05$) from the model according to their respective complexity, starting from the most complex one. When two non-significant terms presented the same complexity, the one explaining less deviance was extracted first. Each term deletion was followed by an ANOVA with F test, in order to recalculate the deviance explained by remaining terms. All statistical analyses have been performed in R (R Development Core Team, 2006).

3.3 Results

As anticipated by our hypothesis, stress (induced by the time spent away from the nest) did change the patterns of aggressiveness between termite workers.

When we analyse the time effect on agressivity we can see that, nestmates were affected by time away from the nest(Fig. 4 and Fig. 5), and non-nestmates did not (Fig. 7 and Fig. 6). Nestmates were not aggressive in low stress, but when stress was increased they increase their aggressivity. However, non-nestmates already presented high levels of aggressivity in low stress and this aggressivity did not increase with stress.

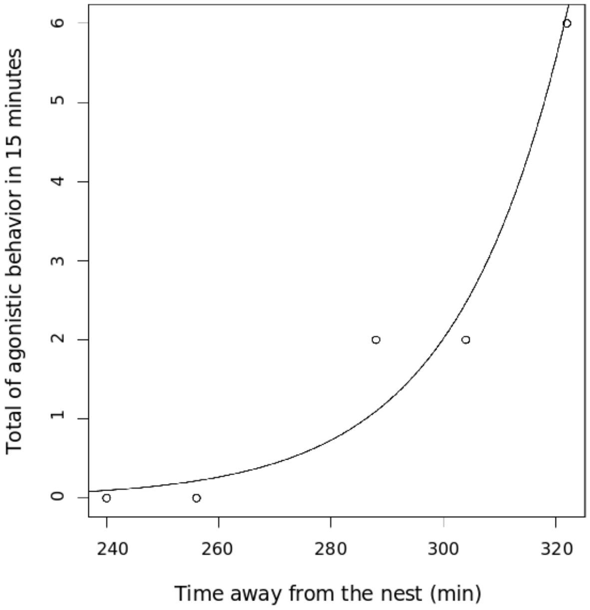

Figura 4: Relationship between total sum of aggression and time individuals had spent away from the nest (in minutes) in a low stress situation $p < 0.011$.

When we analyse only the grouping type effect on aggressive behavior in high stress situation, we saw that there is no statistically difference between nestmate and non-nestmate aggression (Tab. 1).

The pattern of aggressivity cause by stress, did not change workers survival. In both situations non-nestmates died faster than nestmates individuals (Fig. 8 and Fig. 9).

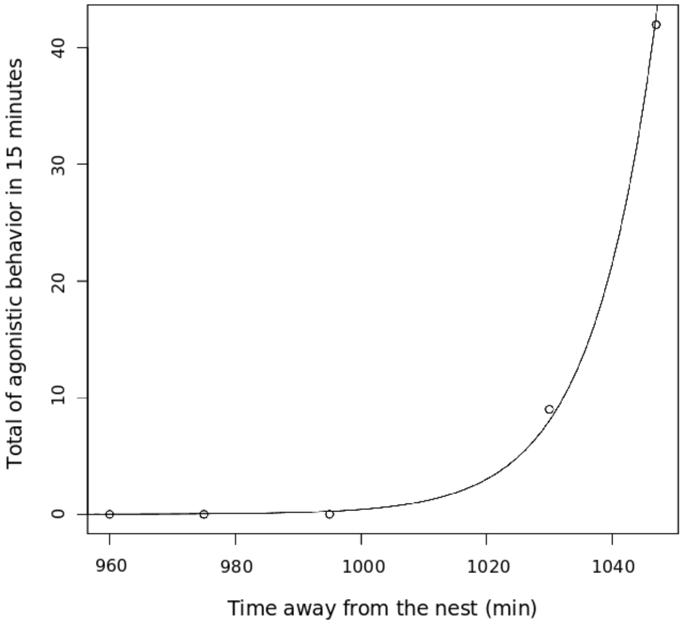

Figura 5: Relationship between total sum of aggression and time individuals had spent away from the nest (in minutes) in a high stress situation $p < 0.001$.

Tabela 1: Analysis of deviance for the effects of Grouping (Nestmate or non-nestmate) on the total of agonistic behaviour in the first 15 minutes of termite workers in a Petri dish in lab, using Generalized Linear Models with Quasipoisson errors and logit link function. In a high stress situation.

	Df	Deviance	Resid. Df	Resid. Dev	F	Pr(>F)
NULL			14	397.27		
Colony	1	48.55	13	348.72	1.8766	0.194

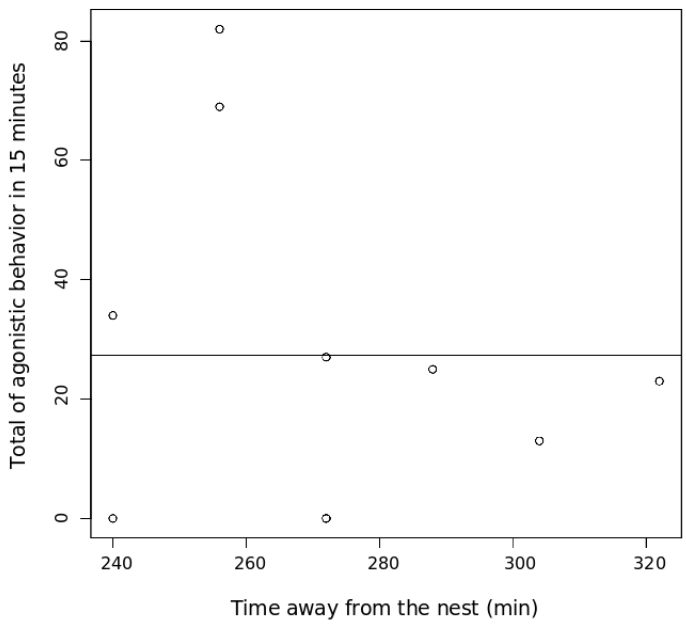

Figura 6: Relationship between total sum of aggression and time individuals had spent away from the nest (in minutes) in a low stress situation, the line was plotted on the mediam value $p = 0.427$.

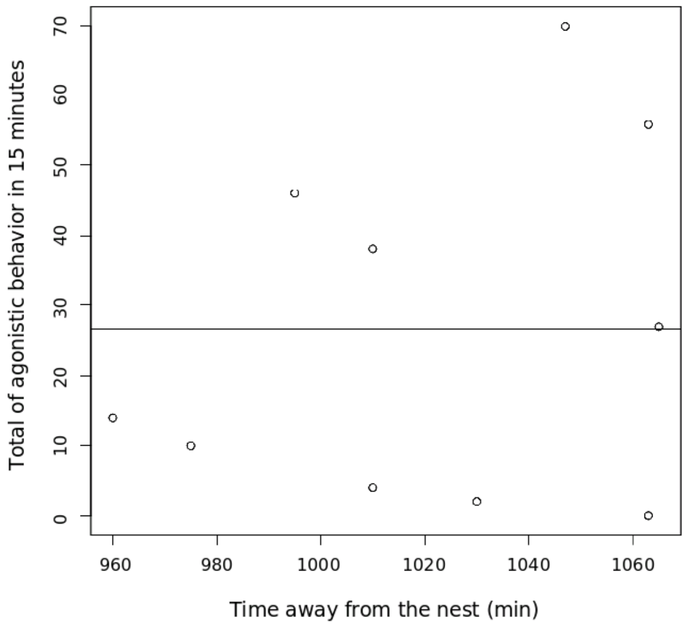

Figura 7: Relationship between total sum of aggression and time individuals had spent away from the nest (in minutes) in a high stress situation, the line was plotted on the mediam value $p = 0.867$.

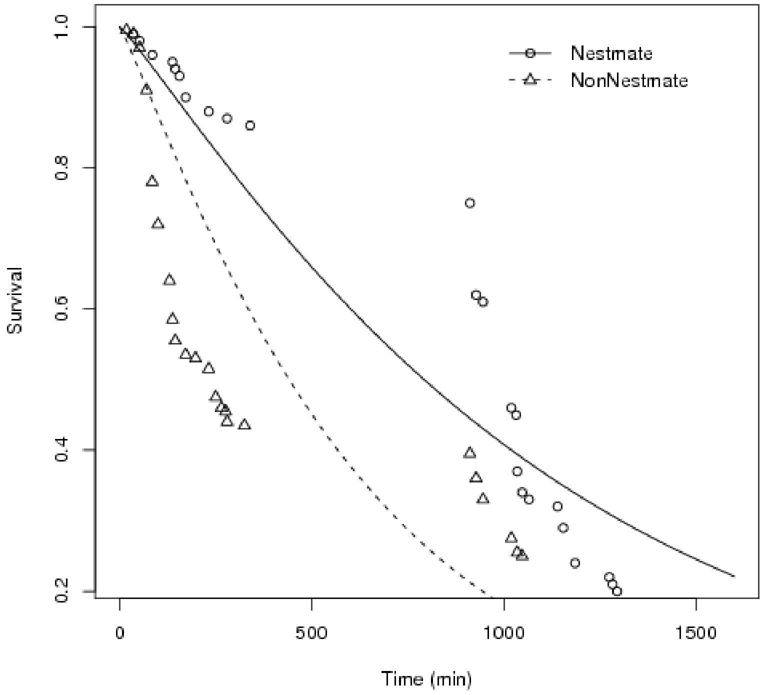

Figura 8: Proportion of termites individuals still alive as a function of time spent in Petri dish after submited to agonistic assays, in low stress $p < 0.001$.

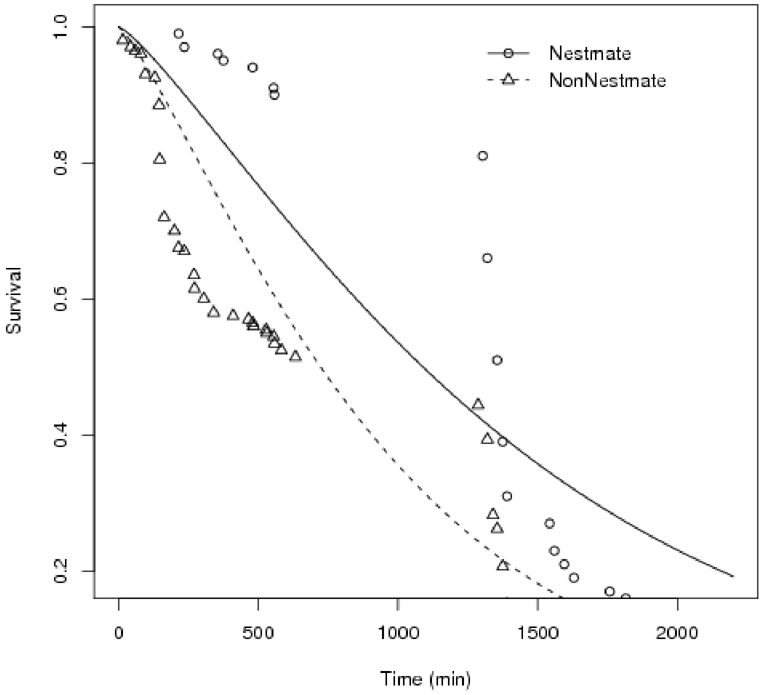

Figura 9: Proportion of termites individuals still alive as a function of time spent in Petri dish after submited to agonistic assays, in high stress $p < 0.001$.

3.4 Discussion

Marins & DeSouza (2008) confirm that *C. cumulans* is able to recognize and attack conspecific intruders. In this article we found that *C. cumulans* had their aggressive behavior changed by the stress they were subjected to. However aggression in low and high stress differed among grouping type, namely nestmates and non-nestmates. Nestmates increased their aggressivity with stress increment, and non-nestmates kept their aggressivity high no matter how stressed they were. These results point that natural stress in individuals may brake social cohesion avoiding nestmates to be recognize as equals.

Although the aggressivity in high stress among nestmates and non-nestmates were statistically similar (Tab. 1), there were changes in survival according to grouping type. Nestmates survived longer than non-nestmates, in both high stress and low stress (Fig. 8 and Fig. 9). This results suggest that nestmates became more aggressive when subjected to some stress, but this aggressivity did not cause high levels of injury as it seems to be the case for non-nestmates.

Some studies suggest situations which could enhance inquiline richness (eg. Redford, 1984; Da Cunha et al., 2003; Costa, 2005), but to understand the process of nest invasion it is necessary to know how nestmate recognition works. Such a knowledge on termites is still full of gaps, especially concerning factors capable of changing the recognition process. Copren & Geard (2005) simulated a model to test if social stimulus, induced by interindividual contact, is an important factor in defensive behavior in termites. The authors found that social stimulus is more important to similar individuals. When the intruding and defending individuals were closely related, social stimulus enable a higher aggression level, but when individuals were less related, social stimulus was less important and rejection occurred rapidly anyway (Copren & Geard, 2005). The study of Copren & Geard (2005) agrees with ours results, since it shows that it is apparently easy to brake nestmate recognition.

The strategies that termite inquilines use to brake into the nest are mostly unknown. Among ants, nest invasion may occur in two ways: (i) the establishment of alates from other colonies in the host nest, or (ii) the arrival of workers from a neighboring colony. In the first case, alates must first isolate themselves in the nest and them carry on with the colony foundation. In the second situation, the isolation also must occur with subsequent transference of the colony to the new environment (Wilson, 1971). Anyway, if the area to be occupied by intruders was in use by the host conflicts may happen.

As we can see in figure 4 and 5, stress cause by time away from the nest did increase aggressive behavior in nestmates. Although this agressivity did not cause injury enough to provoke death to individuals (Fig. 9) it can be enough to distract nestmates and allow intruders to enter the nest. When the host's social cohesion is disrupted by some kind of stress (external or produce by intruders) it may represent a mechanism that improve nest invasion.

4 CONCLUSÕES

1. Em situações de baixo estresse (tempo longe do ninho de 240 a 322 minutos) *Cornitermes cumulans* foi capaz de reconhecer a atacar indivíduos da mesma espécie porém de outro ninho.

   Esse ataque resultou em uma menor sobrevivência no grupo com indivíduos de ninhos diferentes.

2. Em situações de alto estresse (tempo longe do ninho de 960 a 1065 minutos), a agressividade manteve-se alta para indiíduos de ninhos diferentes, e aumentou para indivíduos de mesmo ninho.

Os resultados obtidos nesta dissertação implicam que em situações de baixo estresse, a espécie *C. cumulans* é capaz de reconhecer intrusos, mas não há uma escala de similaridade entre os indivíduos de colônias mais próximas e mais distantes.

É esperado que o aumento da agressividade acarrete em uma menor sobrevivência. Isso foi observado para os indíviduos de ninhos diferentes, ou seja, quem brigou mais, morreu mais rápido.

De maneira geral, os indivíduos de mesmo ninho ficam mais agressivos quando mais estressados. Essa alteração no sistema de reconhecimento pode facilitar o estabelecimento de intrusos em situações de muito estresse.

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