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Table 1. List of the morphospecies of the sampled arboreal termites in State Park of Rio Doce, MG, Brazil 2004.

Subfamily	Morphospecie
Nasutitermitinae	<i>Nasutitermes corniger</i> Motschulsky
	<i>Nasutitermes minor</i> Holmgren
	<i>Nasutitermes</i> sp. 1
Termitinae	<i>Microcerotermes strunckii</i> Sörensen

# Predation and Interference Competition Between Ants (Hymenoptera: Formicidae) and Arboreal Termites (Isoptera: Termitidae)

by

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## ABSTRACT

One of the most apparent biological interactions affecting termites is predation by vertebrates and invertebrates. Ants are the most important predators of other invertebrates and are the most active and effective predators of termites. Also, ants and termites might heavily compete for nesting space. Considering the potential of ants as competitors and predators of termites and the scarce knowledge of how they interact we tested the effects of the presence of ants on the activity of arboreal termites. Predatory ants had a negative effect on arboreal termite activity, and non-predatory ants had no effect. Specialized predatory ants are an important disturbance factor in resource exploitation by termites. Perhaps competition with non-predatory ants did not occur in our study because the foraging territories of ants and termites maybe do not overlap. Hence, it is clear that predation has a big impact on activity of termites, but the role of competition in shaping termite communities still needs further study, especially the competitive interaction between termites and ants.

Keywords: arboreal termites, asymmetrical interactions, determinants of tree exploitation, *Microcerotermes*, *Nasutitermes*, Isoptera.

## INTRODUCTION

Besides being affected by the availability and quality of resources, resource use also depends on habitat structure (Bell *et al.* 1991; Cornell & Lawton 1992) and biological interactions (Begon *et al.* 1990; Chesson 2002). Likewise, resource use by termites is affected by resource quantity (Waller & La Fage 1987; Waller 1988; Hedlund & Henderson 1999), resource quality (Miura & Matsumoto 1997, 1998; Traniello & Leuthold 2002) and biological interactions, such as predation by

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vertebrates and invertebrates (Abensperg-Traun 1998) and competition, specifically for foraging territories (Adams & Levins 1987; Leponce *et al.* 1997).

Ants are the most important predators of other invertebrates and are the most active and effective predators of termites, and a major factor of termite mortality (Abe & Darlington 1985), at least six genera of ants exist that are specialized in termite predation (Wilson 1971). In fact, risk of predation by ants is an important factor affecting resource exploitation by termites (Korb & Linsenmair 2002).

Besides predation, competition may also determine resource use by termites. Competition for space can occur among conspecific or heterospecific and between termites and non-termites. Territoriality is an important and widespread form of asymmetric competition (Adams 2001) and is very common among termites (Adams & Levins 1987; Jones & Trosset 1991; Thorne & Haverty 1991) including arboreal termite species (Leponce 1997; Leponce *et al.* 1999). Especially considering that termites and ants are both eusocial, live in colonies and have similar needs for nesting space, ants are expected to be important competitors for space with termites, particularly termites living in trees. Indeed, it is known that ants and termites may compete for nesting sites, especially on leaves and twigs (Hölldobler & Wilson 1990). Several species of termites, including various Neotropical species (Constantino 1999), inhabit trees (Noirot 1969). And arboreal-nesting ants are able to dislodge mature termite colonies from trees by progressively invading the nests (Leponce *et al.* 1999). Further indications for competition between ants and termites in trees comes from a study of the fauna associated with canopy epiphytes (Ellwood *et al.* 2002), showing that termites and ants never co-occurred inside small-sized epiphytes.

Little is known on the determinants of tree exploitation by termites, and besides some architectural aspects of trees (Gonçalves *et al.* 2005), biological interactions, particularly with ants, seem to be an important determinant of termite activity, especially because ants are the dominant arthropod family in lowland tropical forest canopies (Tobin 1995). Considering the potential of ants as competitors and predators of termites and the lack of knowledge of the interactions between ants and termites (Leponce *et al.* 1999), we tested the effects of the presence of ants on tree exploitation by termites. Specifically we tested the hypothesis that the presence of ants has a negative effect on the activity (number of termite individuals active inside the tunnels, see methods) of arboreal termites, either for competition or predation.

## MATERIAL & METHODS

### Study area

The study was carried out in the Rio Doce State Park, Minas Gerais, southwestern Brazil, between January 15 and February 15 (summer season) of 2004. This park is the largest relict of Atlantic coastal rain forest in the state of Minas Gerais (35.976 ha), and is located between 19° 48' 18" - 19° 29' 24" S and 42° 38' 30" - 42° 28' 18" W. To the east it is bordered by the river Doce and to the south by the Piracicaba river. This biome is one of the most important "hot-spots" of global biodiversity (Myers *et al.* 2000). The local altitude varies from 230 to 515 m above sea level (SOCT 1981). The area is characterized by the Aw Köppen climate type (Tropical warm semi-humid), a rainy season from October to March and a dry season from April to September. Mean rainfall is 1480.3 mm/year and the mean temperature 22° C (Gilhuis 1986). Vegetation is mainly stationary semideciduous (Lopes 1998), with a moderate to high percentage (20 to 50%) of deciduous trees (Veloso *et al.* 1991).

### Definition of terms

"Arboreal termites" were defined as termites that build earthen tunnels on living trees, such tunnels serving as a shelter for foragers. This is not a trivial definition of such termites, since most authors tend to (implicitly or not) use this term when referring to termites that do build nests on the tree (see Noirot & Darlington 2000 for a review on the nesting behavior of termites). However, because our data do not allow us to distinguish whether termites were searching for food, nesting on the tree, or merely using the tunnels as connections to other trees, we find it advisable to make such a warning in order to prevent any misconception. "Termite activity" is the amount of termites within the tunnel, which was taken as a surrogate of the degree of suitability of the tree to the termite.

### Sampling design & Data collection

We sampled 23 trees with a minimum circumference at breast height (1.3 m from the soil), of 15 cm. The trees were situated in four regions of the park, known as the Mata do Gambá, Mata do Macuco-Lagoinha, Mata da Tereza and Mata do Vinhático. Trees were arbitrarily selected, but a minimum distance of 50 m from the forest edge was kept for minimize edge effects.

Tunnels with active termites were present in all trees. Termite activity was accessed by simultaneously interrupting both extremities of a 15 cm long portion of the tunnel and capturing all termites found therein.



Further inspection on the remainder of the tunnel allowed catching additional soldiers, thereby guaranteeing secure identification of the species. These additional inspections also allowed us to confirm that tunnels were used by termites, when no termites were encountered in the 15 cm long portion of the tunnel. Termites were put in 80% alcohol, labeled and identified to genus or morphospecies. The identification was confirmed by comparison to specimens from the section of termitology of the Entomological Museum of the Federal University of Viçosa, where voucher specimens are deposited.

Trees were climbed using the single rope technique (Moffet & Lowman 1995) and ants were collected from tree crowns using an entomological umbrella. The ants were identified to species and morphospecies where appropriate, by comparison to specimens from Community Ecology Laboratory of the Federal University of Viçosa. The feeding habits of the ants were determined according to Brown Jr. (2000). The ant specimens are deposited in the entomological reference collection of Federal University of Ouro Preto.

### Data Analysis

All analyses were processed under R (R Development Core Team 2005). We tested whether ants had a negative effect on activity of arboreal termites using a generalized linear model (*Termite activity* = *Ants* + *Termite genus*), followed by analysis of residues to check for the error distribution and model adjustment. A minimal adequate model (MAM) was obtained by extracting non-significant terms ( $p > 0.05$ ) from the full model and difference between levels of the categorical explanatory variable *ants* were tested through *a posteriori* contrast procedures (Crawley 2002). In the presented full model (*Termite activity* = *Ants* + *Termite genus*), *Ants* is a categorical variable with three levels: presence of predatory ants; presence of non-predatory ants; and absence of ants. The variable *Termite genus* is also categorical, identifying the genus of the termites (*Microcerotermes* or *Nasutitermes*). The error distribution used was negative binomial with log link function.

### RESULTS

We found four termite morphospecies of the family Termitidae, comprising two subfamilies and two genera (Table 1), and 40 ant morphospecies of 12 genera from six subfamilies (Table 2). Among the genera of ants, four were essentially predatory ants: *Ectatomma* Fr. Smith; *Gnamptogenys* Roger; *Pachycondyla* Fr. Smith; and *Pseudomyrmex* Lund (Hölldobler & Wilson 1990; Brown Jr. 2000).

The activity of termites was influenced by the presence of ants (Table 3, Fig. 1). Compared to the absence of ants, termite activity was

Table 1. List of the morphospecies of arboreal termites collected in the State Park of Rio Doce, Minas Gerais, Brazil, 2004.

Subfamily	Morphospecies
Nasutitermitinae	<i>Nasutitermes kemneri</i> Snyder & Emerson <i>Nasutitermes</i> sp. 1, sp. 2
Termitinae	<i>Microcerotermes</i> cf. <i>exiguus</i> Hagen

lower in the presence of predatory ants ( $\chi^2 = 6.11$ ,  $P = 0.0134$ , Fig. 1), whereas non-predatory ants did not affect arboreal termite activity ( $\chi^2 = 0.77$ ,  $P = 0.3814$ ). Colonies of the genus *Nasutitermes* were more active than colonies of the genus *Microcerotermes* (Table 3, Fig. 1).

### DISCUSSION

We hypothesized that ants may have negative effects on termite activity through predation and through competition for space. Our results show that predatory ants, but not non-predatory ants, have a negative effect on termite activity (Table 3, Fig. 1), suggesting that predation is an important source of disturbance of termite activity, but competition is not. Nevertheless, we cannot rule out that predatory ants species also competed for space with termites.

Table 2. List of the morphospecies of ants collected with an entomological umbrella in the State Park of Rio Doce, Minas Gerais, Brazil, 2004.

Subfamily	Morphospecies
Dolichoderinae	<i>Azteca</i> sp. 1, sp. 2 <i>Dolichoderus</i> sp. 1, sp. 2, sp. 3, sp. 4
Ectatominae	<i>Ectatoma tuberculatum</i> Olivier <i>Gnamptogenys</i> sp. 1
Formicinae	<i>Camponotus sericeiventris</i> Guérin-Ménéville <i>Camponotus</i> sp. 1, sp. 2, sp. 3, sp. 4, <i>Camponotus</i> sp. 5, sp. 6, sp. 7, sp. 8, sp. 9
Myrmicinae	<i>Cephalotes atratus</i> Linnaeus <i>Cephalotes borgmeieri</i> Kempf <i>Cephalotes</i> sp. 1 <i>Crematogaster</i> sp. 1, sp. 2, sp. 3, sp. 4 <i>Leptothorax</i> sp. 1, sp. 2 <i>Procryptocerus</i> sp. 1, sp. 2 <i>Trachymyrmex</i> sp. 1
Ponerinae	<i>Pachycondyla magnifica</i> Borgmeier <i>Pachycondyla</i> sp. 1, sp. 2, sp. 3
Pseudomyrmecinae	<i>Pseudomyrmex</i> sp. 1 <i>Pseudomyrmex</i> sp. 2, sp. 3, sp. 4, sp. 5, sp. 6

Table 3. Analysis of deviance of the minimal adequate model (MAM) showing the effect of ants (predatory, non-predatory and absence) on the activity of arboreal termite genera (*Microcerotermes* and *Nasutitermes*), using a generalized linear model and Negative Binomial errors and log link function. Contrasts between levels of the variable ants are denoted by vs.

Source of variation	df	$\chi^2$	P
MAM	2	12.35	0.002
Termite genus	1	7.92	0.005
Ants	1	7.42	0.006
predatory ants vs ants absent	1	6.11	0.013
non-predatory ants vs ants absent	1	0.77	0.381
predatory ants vs non-predatory ants	1	7.68	0.006
Error	20		
<b>Total</b>	<b>22</b>		

The coevolutionary relationship between termites and ants dates back more than 100 million years, with ants mostly acting as aggressors and termites as victims (Hölldobler & Wilson 1990). A majority of ant species prey on termites if given the opportunity and some ant genera are specialized in termite predation (Wilson 1971), including the collected *Pachycondyla* Smith (Table 2). The strategies of termite capture by ants are diverse. There is a guild of specialized predatory ponerine ants which organize raids on termite mounds, whereas other ants hunt solitarily or steal eggs and nymphs from the colonies (Hölldobler & Wilson 1990). Yet other ant species, like *Megaponera foetens* Fabricius, only attack termites on the surface (Hölldobler & Wilson 1990), whereas doryline ants attack underground nests (Darlington 1985). The raid strategy seems to be the most important factor on termite colony survival and is especially adopted by *Pachycondyla* Smith (Acosta-Avalos & Esquivel 2001). The specialized predatory ants are an important disturbance factor in resource exploitation by termites. Especially doryline ants and *Megaponera foetens* Fabricius can prey on high proportions of the foraging population and reduce production of termite colonies (Lepage & Darlington 2002). Thus, our results confirm the important pressure that ants exert on termites as predators.

It is surprising that we found such strong effects of predatory ants on termite activity, whereas we did not find effects of competition, because competition between ants and termites is considered much more common than predation (Sennepin 1996). Competition for space, which has often been reported between ants and termites (Hölldobler & Wilson 1990; Sennepin 1996; Leponce *et al.* 1999), seems not to occur in our study; we found no relationship between non-predatory

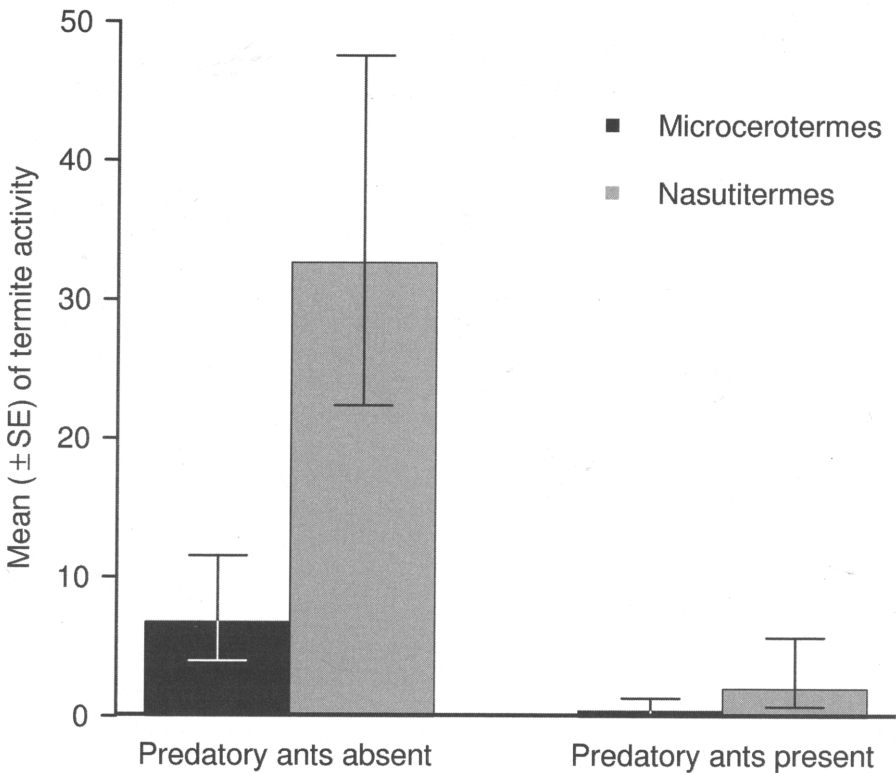


Fig. 1. Effect of the presence of predatory ants on the activity of arboreal termites (*Microcerotermes* and *Nasutitermes*). Bars were grouped following the statistical contrasts of Table 3, in which the effect of non-predatory ants does not differ from the effect of ants absent, and these differ from the effect of predatory ants. Therefore, bars grouped under the term "predatory ants absent" refer to samples without ants plus samples with only non-predatory ants.

ants and termite activity (Table 3). Thus, why is competition for space with ants not of importance for arboreal termites?

Perhaps termites and ants do not compete for space because their foraging territories do not overlap. Termites are cryptic organisms, generally foraging in protected environments (Noirot 1969), and seldom leave the shelter of their tunnels and nests (Leponce *et al.* 1999), whereas ants possess quite diverse foraging strategies. Although on the same tree, the foraging territories of ants and termites maybe separated in space, circumventing contact between them and avoiding competitive battles.

Besides competing for foraging territories, ants and termites are known to compete for nesting sites (Hölldobler & Wilson 1990), an

aspect that was not supported by our data. This maybe due to the low number of termite nests observed (in five out of the 23 observed trees), suggesting that termites do not use the trees of our study for nest or that nest construction had not started yet.

Ants and termites also may interact in non-antagonistic ways, such as in commensalism, mutualism and inquilinism (Hölldobler & Wilson 1990; Leponce *et al.* 1999). Our results show no evidence for commensalism and mutualism because the effect of the presence of non-predatory ants was the same as that of the absence of ants (Table 3). Also, the lack of interaction between non-predatory ants and termites may be due to the fact that the large majority of ant species in forest canopies consists of inconspicuous species with small colonies and limited foraging territories (Tobin 1995), which probably do not disturb termite activity.

Besides a strong effect of predatory ants on termite activity, activity levels also varied with the genus of termites. The activity of *Microcerotermes* was lower than *Nasutitermes* (Table 3, Fig. 1). Thus, despite the equal response of the two studied termite genera to the presence predatory ants, termite *taxa* differ in the intensity of that response.

Our results show that the presence of predatory ants decreases the activity of arboreal termite colonies and no evidence was found for any effect of competition. It is known that competitive interactions between termites are determinants of termite community structure (Adams & Levins 1987; Jones & Trosset 1991; Thorne & Haverty 1991; Leponce *et al.* 1997, 1999). Termites and ants do not completely compete for resources because termites are mostly detritivorous (Wood & Sands 1978; Grassé 1982) and ants are not (Hölldobler & Wilson 1990; Agosti *et al.* 2000) And that may be a reason for the absence of competition! If the resources are less used, the competition may not occur. Thus, we suggest that competition with "real" food competitors, could be more important than competition for space *per se*, and that the presence of predatory ants can be an important local factor limiting resource use of arboreal termites in tropical rainforest environments.

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