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# Feeding substrate selection is not affected by the temperature during the foraging of *Constrictotermes cyphergaster*

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**Abstract**
Termites are known as wood consumers, although some species eat other substrates. Assessing resource selection is important to understanding their biology. The present study provides information on the foraging behavior of *Constrictotermes cyphergaster* (Blattaria, Termitidae) in a dry forest area of Caatinga in Brazil. We aimed to verify the frequency of resource exploitation by termites as a function of environmental and soil temperatures. We found no significant differences in resource exploitation as a function of temperature, which is interesting because this variable is often reported as modulating foraging activity in some other termite species. This species forages on open trails at high temperatures in the Brazilian semiarid zone. Environmental changes may affect the dynamics of their behavior and, consequently, the ecosystem, since *C. cyphergaster* influences the carbon cycle and can modify the soil. Our study provides a basis for future research intending to understand the adaptations of this termite to live in the drylands.

*Keywords:* Foraging; trails; consumption; Termitidae; dry forest.

# Seleção de substrato alimentar não é afetada pela temperatura durante o forrageio de *Constrictotermes cyphergaster*

**Resumo**
Os cupins são conhecidos como consumidores de madeira, embora algumas espécies se alimentem de outros substratos. Avaliar a seleção de recursos é importante para compreender a sua biologia. O presente estudo fornece informação sobre o comportamento de forrageio de *Constrictotermes cyphergaster* (Blattaria, Termitidae) numa área de floresta seca de Caatinga no Brasil. O nosso objetivo foi verificar a frequência da exploração dos recursos pelos térmitas em função das temperaturas do ambiente e do solo. Não encontramos diferenças significativas na exploração de recursos em função da temperatura, o que é interessante porque esta variável é frequentemente reportada como moduladora da atividade de forrageio em algumas outras espécies de térmitas. Esta espécie forrageia trilhas abertas em temperaturas elevadas na zona semiárida brasileira. As mudanças ambientais podem afetar a dinâmica do seu comportamento e, consequentemente, o ecossistema, uma vez que *C. cyphergaster* influencia o ciclo do carbono e pode modificar o solo. O nosso estudo fornece uma base para futuras investigações que pretendem compreender as adaptações destes cupins para viver nas terras secas.

Palavras-chave: Forrageio; trilhas; consumo; Termitidae; floresta seca.

Termites forage through the synchronized and integrated action of individuals in search of food resources (Traniello & Leuthold, 2000); seasonal changes like temperature and humidity seem to be determinants of foraging and colony survival since even small variations can affect the activities of termite workers (Smith & Rust, 1994; Haverty et al., 2010; Clarke et al., 2013; Alamu & Ewete, 2021). However, studies on termite ecophysiology aimed to identify environmental factors limiting the foraging activity of each species with specific microclimatic requirements are still incipient (Cornelius & Osbrink, 2011).

Termites show varied foraging behaviors (Abe, 1987). Subterranean termites build extensive underground galleries of elaborate tunnels and channels for foraging food resources (Su, 2001). Some other species forage in open trails, which allows observation of their foraging behavior.

An example is *C. cyphergaster* (Silvestri, 1901), a Neotropical termite that forages on exposed trails. This species displays different foraging behaviors that may be related to the variety of resources and environments in which it forages (Oliveira et al., 2021); in Brazil, this termite is common in both Brazilian savannah (Cerrado) and semiarid environments (Caatinga) (Mathews, 1977).

Wood in different decomposition stages and the bark surface of living trees are among the most consumed resources by *C. cyphergaster*. The surface of cacti and soil bromeliads have also been reported as other consumed substrates (Moura et al., 2006). Besides, the consumption of lichens had already been indicated by Mathews (1977). Barbosa-Silva et al. (2019) recently described the consumption of 29 lichen species by *C. cyphergaster* in a semiarid environment, with seasonal variations in the richness of their ingestion. Meanwhile, it is unknown whether resource exploitation is affected by soil or environmental temperature concerning this particular termite species. Most previous studies found that temperature influences the feeding habits of subterranean termites (Fei & Henderson, 2002; Cao & Su, 2014; 2016) but not that of species that forage in open galleries in semiarid areas, showing that this variable is a strong influencer in their foraging activity.

The present study aimed to test whether *C. cyphergaster* searches for food resources based on the soil and environmental temperatures. We predicted that this termite prefers to eat on trees rather than directly on the ground soil when the soil temperature is higher. Although soil temperatures do not fluctuate as much as environmental temperatures (Ettershank et al., 1980), they still affect subterranean arthropod communities (Johnson & Whiteford, 1975; Mackay et al., 1986). Soil temperature is believed to have more effect on termite activity than environmental temperature (Ettershank et al., 1980). Our study's novelty relies on field observations about the feeding behavior of termites that consume resources on both soil and trees in open foraging trails.

Observations of the termites' behavior were performed in the Estação Experimental de São João do Cariri (EESJC), associated with the Center of Agricultural Sciences of the Universidade Federal da Paraíba, municipality of São João do Cariri (36°31'W; 7°22'S), northeastern Brazil. The area has 381 ha, altitude between 400 and 700 m, average annual precipitation between 641 and 995 mm, mean relative humidity of 70%, and temperature between 28.5 and 35 °C (Araújo et al., 2005). The region is mostly covered by open shrubby-arboreal xerophytic vegetation, with the predominance of *Poincianella pyramidalis* Tul., *Croton blanchetianus* Mull. Arg., *Combretum leprosum* Mart., *Jatropha mollissima* (Pohl) Baill., *Aspidosperma pyrifolium* Mart., and *Tacinga palmadora* (Britton and Rose) (Barbosa et al., 2007).

All the monitoring was performed at night (9:00 pm – 5 am), the period at which *C. cyphergaster* forages (Moura et al., 2006). For this, 10 nests were monitored daily for 15 days in October 2018, totalizing 80 observations. We used a digital thermometer at the start of foraging to measure temperature. The thermometer was put into the soil and also used in contact with air at the same height as the nests to measure the soil and environmental temperatures, respectively. Both temperatures were measured at a distance of ~1 m from the nests. *C. cyphergaster* colonies do not forage every day. During our observations, some nests presented intervals between the monitoring days.

To determine the types of resources consumed, we followed termites' trails from the start to the end of foraging. We considered three levels of the qualitative variable 'resources zone:' soil (leaf litter, twigs, and dead wood), trees (surface of tree barks), and both when termites explored resources of soil and tree barks at the same time or at different times during the same foraging event. The temperature monitoring was carried out at the start of the foraging, and the resource exploitation was conducted in one-hour intervals, from the start to the end of the activity.

A generalized linear model with adjustment for negative binomial distribution and analysis of deviance through the function *Anova* form package 'car' were performed to verify the significance of resource choice as a function of temperature. For the data analysis, all 80 observations were considered. Analysis and graphics were conducted on R (R Core Team, 2021).

Our results show that resource choice was not significantly influenced by soil ($\chi^2$= 00001; df=1; p=0.99) or environment temperature ($\chi^2$=0.59; df=1; p=0.44) in EESJC. However, findings close to significance were found when performing the test only with foraging results for soil and environment temperature, by removing events during which termites consumed both resources (results not shown).

The most frequent resources explored by termites were present in the soil (37 times), followed by both soil and tress (24 times), and trees (18 times) (Table 1). The mean time of foraging activity by the colonies was 5.56±0.47 hours (mean ± standard error). Contrary to our hypothesis, termites explored resources on trees regardless of soil temperatures, most frequently between 22–24°C.

**Table 1**. Frequency of the place of resource consumption by *Constrictotermes cyphergaster* (Blattaria, Isoptera) in different zones as a function of environmental and soil temperature (Temp.).

| Temp. | Environmental | | | Soil | | |
|---|---|---|---|---|---|---|
| (ºC) | Soil | Trees | Both | Soil | Trees | Both |
| 21 | 1 | 4 | 3 | - | - | - |
| 22 | 10 | 6 | 9 | 1 | 4 | 2 |
| 23 | 20 | 5 | 9 | 7 | 4 | 9 |
| 24 | 5 | 3 | 2 | 16 | 6 | 9 |
| 25 | 1 | 0 | 0 | 9 | 3 | 3 |
| 26 | - | - | - | 2 | 1 | 1 |

We found that environmental temperature was not related to the consumption of one resource over another by *C. cyphergaster* in Caatinga dry forests. Therefore, the acceptance of the null hypothesis in the present study must be disclosed. If these individuals stop consuming the bark surface of trees or resources present in the soil during the day, this will probably not be related to temperature if its range is between 21°C and 26°C (Figures 1 and 2). The resources on soil resources were most frequently consumed; since termites foraged on both soil and trees, soil foraging represented more than 75% of the frequency, suggesting that soil resources are the main items in their diet.

*C. cyphergaster* is a species with a varied diet (Moura et al., 2006; Barbosa-Silva et al., 2019), and there is still little behavioral data on termite species that feed in the open environment. Few studies have elucidated how temperature may affect foraging events under field conditions (Evans & Gleeson, 2001; Cornelius & Osbrink, 2011). Our study provides information that helps formulate new hypotheses about termite foraging dynamics in highly complex environments in the context of previous studies that have demonstrated temperature-dependent behavioral changes in subterranean termites (Fei & Henderson, 2002; Cao & Su, 2014).

In spite of the temperature influence, other factors that may lead these individuals to opt for the bark surface of living trees have not yet been clarified. It is unknown whether some other physicochemical variables are related to the consumption of these resources. To answer these questions, new studies need to be conducted. Considering this feeding habit and the ideal foraging theory by MacArthur & Pianka (1966), we can formulate some hypotheses about why these termites alternate their food preferences. If the consumption of tree parts may be related to nutrient composition, why do termites consume such resources along with those present in the soil? We observed in our fieldwork that, in order to consume both soil and tree resources, colonies need to divide their workers into many trails and on different terrains during the same foraging event, making them even more exposed to predation.

The soils and leaf litter of the Caatinga are relatively rich in nutrients such as nitrogen (Lopes et al., 2017), and this makes us think that bark surface can be consumed for other reasons. It has already been reported that the quality of resources influences their consumption by termites, leading individuals to choose those that provide greater energy amounts with less energy expenditure (Bernays, 1985; Nalepa, 1994). Plants are known to produce chemical and physical defenses that protect them against fungi and attacks from herbivorous insects (Ulyshen, 2016). The tissues of living trees have defensive substances that inhibit the digestive enzymes of organisms, hindering their digestion and thus disfavoring their choice as the main food for termites (Chrispeels & Raikhel, 1991; Peumans & Van Damme, 1995, Sá et al., 2008).

Despite these plant-imposed challenges, why do termites live on bark surfaces (Moura et al., 2006) if the soil resources are possibly better and easier to consume? If a five-degree variation in temperature had no significant influence on the choice of resources, what other variables could modify this feeding behavior? On days when termites consume only the bark surface of living trees, the nutrient cycling process must be possibly reduced since the dead organic matter in the soil is not being consumed by them. We know that *C. cyphergaster* consumes about 44.5 ± 14.7 $kg.ha^{-1}.year^{-1}$ of plant organic matter (Moura et al., 2008). Therefore, understanding how the feeding dynamics of these termites can be altered by environmental factors is a key piece to understanding the ecosystem functioning of the Brazilian Caatinga.


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