Bottom-Up Effects on Selection of Trees by Termites (Insecta: Isoptera)

by

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ABSTRACT

Several factors may limit the use of resources by animals; however, little is known about the mechanisms responsible for the use of trees by termites. In this study, we analyzed by logistic regression the prediction that termites would tend to occupy trees based on their (I) potential amount of available resources and (II) chemical traits. Termite galleries were more frequently found on large as opposed to small trees and dead as opposed to living ones. The occurrence of galleries of termites on trees was not affected by the presence of latex or by taxonomical features. We conclude that the presence of termite galleries on trees could be determined more by resource availability than resource quality.

Keywords: termite galleries, foraging, resource quantity, resource quality.

INTRODUCTION

The abundance of resources has long been recognized as an important factor limiting resource selection and use by insects. Bigger plants, as opposed to smaller ones, are prone to be more frequently selected by insects because such plants offer more feeding sites. In addition, these plants are also more apparent in space, and that eases their encounter by herbivores (Lawton 1983; Strong *et al.* 1984). In addition, insects may also be affected by resource quality: herbivores tend to prefer fast growing plants with low contents of carbon defence (e.g. secondary compounds; Grime *et al.* 1996, Schändler *et al.* 2003).

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Such bottom-up effects, however, are poorly known for detritivore insects in general and termites in particular. Evidence indicates that termites would suffer the same sort of limitations as other insects. The speed upon which termites occupy cellulosic baits in the field was shown to be heavily dependent upon the size of such baits (DeSouza *et al.* 2009). Accordingly, Evans (2005) has shown that termites are able to evaluate the size of wooden blocks in the lab, choosing to feed on the larger ones. Such results appear to validate the inference that termites can be affected by resource quantity. Resource quality may also affect termites. As shown by Grace (1997), Naga & Clement (1990), Yamaguchi *et al.* (2002), and many others, several plant species present constitutive chemical deterrents to termites. Among such deterrents, terpenes (which are normally found in plant latex; Gershenzon & Croteau 1991) play significant roles (Scheffrahn 1991).

Trees are important sources of food and nesting sites for termites (Gonçalves *et al.* 2005, Leponce *et al.* 1997, Jones & Gathorne-Hardy 1995). Cellulose, the main food item for termites, is abundant on trees, either in the form of wood and leaf litter, or as dead bark. Trees may also provide sites to attach nests and places for the accumulation of 'suspended soil' (that is, litter accumulated in the bifurcations of branches and stems). Therefore, it is not surprising that a significant number of termite species would use trees, either as nesting or as foraging sites. In spite of that, the determinants of tree exploitation by termites remain largely unknown.

With all this in mind, we inspected the determinants of tree exploitation by termites, testing the hypothesis that bottom-up effects play important roles on such an exploitation. Specifically, we tested the prediction that termites would tend to occupy trees based on their (I) potential amount of available resources and (II) chemical traits. If foragers or nesters promptly occupy the first tree they find, regardless of the quantity/quality of resources, larger trees (as opposed to smaller ones) would be more frequently occupied simply because such trees are more apparent in space. In addition, no difference should be found in termite occupation patterns among trees presenting distinct chemical traits. This would stand as our null hypotheses for the effects of resource amount and chemical traits on tree occupation by termites. Alternatively, if resource amounts dictate tree occupation by termites, among same-sized trees, those presenting more potential resources would be more frequently occupied. Similarly, if termite occupation is chemically mediated, termite presence patterns should differ on trees (I) from different botanical families - because they present distinct chemical profiles, and (II) presenting obvious chemical defences (such as latex).

MATERIAL AND METHODS

Study area

The study was carried out in the municipality of Conceição da Barra (18º2'51, 39"S, 39º52'18, 20"W; altitude 60m above sea level) in the State of Espírito Santo, Southearstern Brazil. The climate is humid tropical, with an annual mean precipitation of 1400mm and annual mean temperature of 23ºC. The area sampled consists of a fragment (190 ha) of the Atlantic Forest in advanced successional stage.

Experimental procedure

Field observations aimed to check how frequently termites would be found on trees presenting distinct (I) amounts of potential resources and (II) chemical profiles.

To do so, we recorded the presence of termite galleries on all trees (1207 individual plants) within 0.5 ha of the forest fragment described above. Resource amounts were estimated by two variables, namely, tree size (diameter at breast height, DBH) and tree condition (dead or alive). The use of these two estimators was needed to distinguish between two traits associated to tree size: conspicuousness and amount of resources offered. That is, while larger trees (i.e., having larger DBH) are more apparent in space, they also present larger amounts of potential feeding resources. Therefore, simple correlations between termites and a tree's DBH could not conclusively be attributed to either tree conspicuousness or resources offered. However, because most termites feed on dead plant material, a dead tree presents more potential feeding resources than a living tree, as long as they both are of similar size. Hence, by combining both variables (size and condition) in a single analysis of covariance, it is possible to check whether termites would 'prefer' dead trees over similar-sized live ones. In doing so, we can disentangle the effects of resource amount from those of conspicuousness of the tree on termite patterns of tree occupation. This would allow us to infer the extent to which termite presence on large trees depends on the amount of resources present or it is simply a product of random encounter of a conspicuous tree. Resource quality was also assessed by two x-vars: latex presence in the tree's cambium and taxonomical affiliation of the tree, both taken as surrogates for potential deterrents of termite use of wood. Latex directly expresses chemical deterrence because it is known to hold terpenes (among other chemicals: Esau 1965, Gershenzon & Croteau 1991), and terpenes are known to deter termites (Scheffrahn 1991). In addition, latex is easily detected in living trees in the field simply by piercing the tree trunk to expose its cambium. Other indicators of tree quality for termites would include the presence of other deterring chemicals and the taxonomical affiliation would stand as a gross measure of these. That is, trees from a given taxa would share similar traits which are prone to affect termite preference to them.

Analyses

Statistical analyses inspected the effects of resource quantity and quality on tree selection by termites, by means of Generalized Linear Modeling performed under R (R Development Core Team, 2009) with Binomial errors corrected for overdispersion when necessary. Residual analyses confirmed the choice of error distribution and the suitability of the modelling equation.

Analyses proceeded in two steps, both of them using logistic regressions where the presence of termite galleries on a tree was taken as a surrogate for tree selection, and entered the models as a qualitative binomial y-var (0 = absence, 1 = presence). First, we inspected the effects of tree size on termite occupation, distinguishing the tree's conspicuousness from resources offered, as described above. Explanatory variables included tree diameter (surrogate for tree size), tree condition ("dead" or "alive"), and the interaction of both. This analysis used all 1207 trees found in the forest fragment.

The second analytical step consisted of inspecting the relevance of resource quality on tree occupation by termites. To do so, we performed a logistic regression on tree occupation by termites (the y-var described above), including as explanatory variables the presence of latex in the tree, the tree's diameter and the interaction between such variables and also the botanical family of the trees. The diameter of the tree entered the model to avoid statistical significance due to resource quantity being spuriously attached to the variables representing resource quality. The dead trees were removed from the dataset because we cannot determine in the field whether they had latex or not, nor determine their taxonomical identity. Besides the dead trees, we removed from the analysis trees that were not taxonomically identified. This analysis was conducted in 1130 living trees.

RESULTS

A total of 1207 trees were sampled, which comprised 181 species and 42 families. The presence of latex was observed in 264 trees (21.9%) and a total of 40 (3.31%) trees were dead.

Termite galleries were recorded in 109 arboreal individuals (9.03%), belonging to 26 families. All galleries found in trees were typical of *Nasutitermes* sp. The galleries were soft and crumbly, presenting a mixture of sand, feces and bark. In fact, some *Nasutitermes* sp. soldiers were found in some galleries.

Overall, there was a trend of higher incidence of termite galleries with increasing diameter of the trees. The presence of galleries was also affected by the condition of the trees (Table 1). More galleries in dead trees were observed than in living trees (Fig 1).

Moreover, the presence of latex, the interaction between latex and diameter, and the family of the trees did not affect the presence of galleries in the trees (Table 2).

Table 1. Analysis of deviance table for effects of tree diameter and condition (live or dead) on the presence or absence of termite galleries on trees.

Source	Df	Deviance	$P > \|\chi^2\|$
Diameter	1	22.64	1.95×10^{-6}
Tree condition	1	9.91	1.64×10^{-3}
Diameter: tree condition	1	0.60	0.44
Error	1204	33.14	
Total	1207		

Table 2. Analysis of deviance table for effects of latex (presence or absence), tree diameter and tree family on the presence or absence of termite galleries on trees.

Source	Df	Deviance	$P > \|\chi^2\|$
Latex	1	0.06	0.80
Diameter	1	15.90	6.67×10^{-5}
Family	41	42.05	0.42
Latex: diameter	1	0.40	0.53
Error	1086	58.42	
Total	1130		

DISCUSSION

Termite galleries were more frequently found on large as opposed to small trees and dead as opposed to living ones (Fig 1). This seems to indicate that termite occupation of trees depends on the amount of resources present and is not simply a product of a random encounter of a conspicuous tree.

The mechanisms that determine selection of large trees by termites are not entirely known. Although there is no consensus about such mechanisms, there are several lines of evidence suggesting that these insects are selective feeders (Miura & Matsumoto 1998; Hedlund & Henderson 1999; Arab & Costa-Leonardo 2005; Gallagher & Jones 2005). In the search and recognition of resources in lab experiments, termites were able to discriminate the amount of resources through signs of acoustic vibration (Evans *et al.* 2005). To do so,

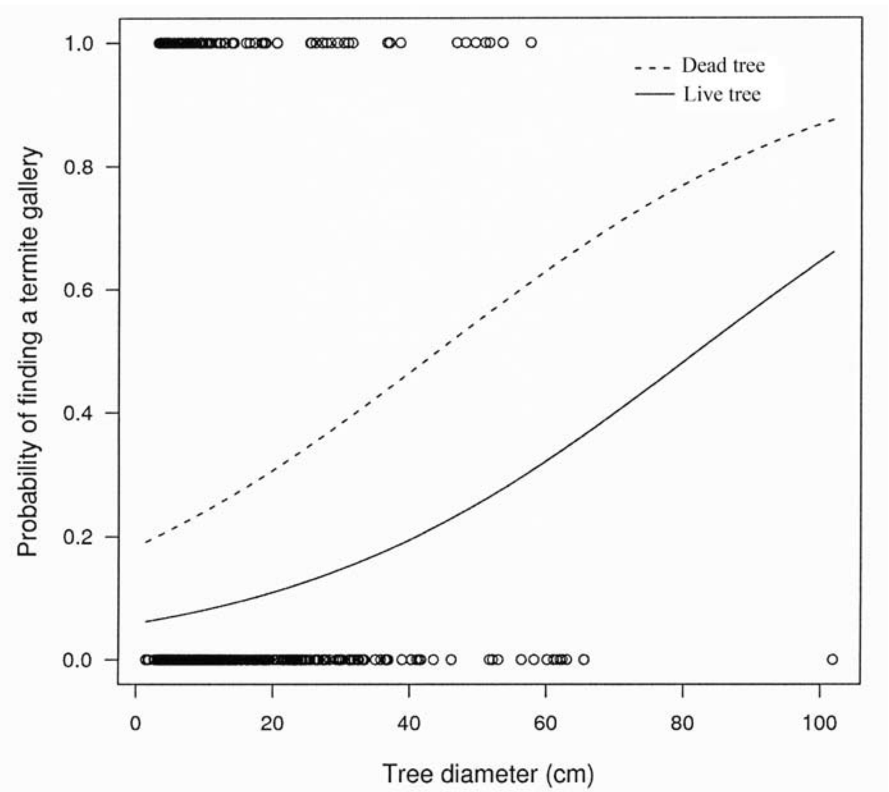

Fig. 1. Relationship between the presence or absence of termite galleries and diameter of live and dead trees in forest fragment. Generalized logistic model with binomial distribution of errors.

they provoked vibration upon potential resources and preferred large ones, apparently by evaluating their dimensions using acoustic clues. If termites are able to probe and choose larger resources in the lab, it may be that they use the same strategy in the field, evaluating the size of the tree, and opting for the larger ones. The positive effect of tree size on termite foraging was also described by Gonçalves *et al.* (2005), who found more activity of arboreal termites on trees with large diameters and more branches. Additionally, Gillison *et al.* (2003), comparing different tropical forest types, found more termite abundance and richness associated with trees presenting bigger basal areas. A plausible explanation for the selection of larger trees may be associated with large resource abundance and variety (wood, moss, lichen) provided by such trees (Jones & Gathorne-Hardy 1995; Gonçalves *et al.* 2005). Selection towards more suitable resources has also been observed in termite nesting (Shellman-Reeve 1994; Lima *et al.* 2006).

Contrarily to what was expected, neither latex content nor taxonomical identity of trees presented any effect on the probability of finding galleries on a tree. This does not conform with previous studies which have shown that termites tend to avoid chemically defended resources (Smythe & Carter 1970; Behr *et al.* 1972). As reviewed by Verma *et al.* (2009) several botanical extracts may act as arrestants, repellents and feeding deterrents to these insects. Unlike these studies, performed mostly in the laboratory, we evaluated concentrations naturally present in the trees directly in the field. This may have contributed to our acceptance of the null hypothesis that chemical traits would not affect tree occupation by termites.

Our results may shed some light on some of the mechanisms responsible for tree/resource exploitation by termites. The quantity of resources was an important factor for selection, independent of taxonomic identity and the presence of latex. We conclude that the presence of termite galleries on trees could be determined more by resource availability than resource quality. Additionally, we rule out the possibility of termites selecting large trees merely because they are easier to be encountered during random foraging.

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REFERENCES

Arab, A. & A. M. Costa-Leonardo 2005. Effect of biotic and abiotic factors on the tunneling behavior of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). Behavioural Processes 70: 32–40.

Behr, E.A., C.T. Behr & L.F. Wilson 1972. Influence of wood hardness on feeding by the Eastern subterranean termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Annals of the Entomological Society of America 65: 457-460.

DeSouza O., A.P.A. Araújo & R. Reis-Jr 2009. Trophic controls delaying foraging by termites: reasons for the ground being brown? Bulletin of Entomological Research, 99:603-609.

Esau K. 1965. Plant anatomy, 2nd . Ed. John Wiley. New York.

Evans,T.A.; J.C.S. Lai, E. Toledano, L. McDowall, S. Rakotonarivo & M. Lenz 2005. Termites assess wood size by using vibration signals. Proceedings of the National Academic Science 102: 3732-3737.

Gallagher, N.T. & S.C. Jones 2005. Effects of resource availability on search tunnel construction by the eastern subterranean termites, *Reticulitermes flavipes* (Isopera: Rhinotermitidae). Sociobiology 45:1-12.

Gershenzon, J. & Croteau, R. 1991. Terpenoids. *In:* Herbivores: their interaction with secondary plant metabolites (Rosenthal. G.A. & Berenbaum, M.R. eds), 2nd edition. vol. 1. Academic Press, New York.

Gillison, A.N., D.T. Jones, F. Susilo & D.E. Bignell 2003. Vegetation indicates diversity of soil macroinvertebrates: a case study with termites along a land-use intensification gradient in lowland Sumatra. Organisms Diversity and Evolution 3:111–126.

Gonçalves, T.T.; O. DeSouza, R. Reis-Jr & S.P. Ribeiro 2005. Effect of tree size and growth form on the presence and actitivity of arboreal termites (Insecta: Isoptera) in the Atlantic rain forest. Sociobiology 46:1-12.

Grace, J. 1997. Influence of tree extractives on foraging preferences of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Sociobiology 30:35-42.

Grime, J.P., J.H.C. Cornelissen, K. Thompson & J.G. Hodgson 1996. Evidence for causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos 77: 489-494.

Hedlund, K.A. & G. Henderson 1999. Effect of available food size on search tunnel formation by the formosan subterranean termite (Isoptera: Rhinotermitidae). Household and Structural Insects 92:610-616.

Jones, D. & F. Gathorne-Hard 1995. Foraging activity of the processional termite *Hospitalitermes hopitalis* (Termite: Nasutitermitinae) in the rain forest of Brunei, north-west Borneo. Insectes Sociaux 43:359-369.

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28: 23–9.

Lima, M.M.; T.T. Gonçalves, O. DeSouza & R. Reis-Jr 2006. Nesting site selection by *Coptotermes gestroi* (Insecta: Isoptera). Sociobiology 48:1-8.

Miura, T. & T. Matsumoto 1998. Open-air litter foraging in the nasute termite *Longipeditermes longipes* (Isoptera: Termitidae). Journal of Insect Behaviour 11: 179-89.

Naga, P. & J. Clément 1990. Terpenes from the maritime pine Pinus pinaster - Toxins for subterranean termites of the genus *Reticulitermes* (Isoptera: Rhinotermitidae). Biochemical Systematics and Ecology 18:3-16.

R Development Core Team (2006) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria. http://www.R-project.org.

Scheffrahn, R.H. 1991. Allelochemical resistance of wood to termites. Sociobiology. 19:257-281.

Shellman-Reeve, J. 1994. Limited nutrients in a dampwood termite: nest preference, competition and cooperative nest defense. Journal of Animal Ecology 63:921-932.

Smythe, R.V. & , F.L. Carter 1970. Feeding responses to sound wood by *Coptotermes formosanus*, *Reticulitermes flavipes*, and *R. virginicus* (Isoptera: Rhinotermitidae). Annals of the Entomological Society of America. 63:841-847.

Strong, D. R., J.H. Lawton & T.R.E. Southwood 1984. Insect on Plants: Community Patterns and Mechanisms. Backwell Science, London.

Verma, M., S. Sharma & R. Prasad 2009. Biological alternatives for termite control: A review. International Biodeterioration & Biodegradation *in press*

Yamaguchi, H., K. Yoshino & A. Kido 2002. Termite resistance and wood-penetrability of chemically modified tannin and tannin-cooper complexes as wood preservatives. Journal of Wood Science. 48:331-337.