1991

Feeding By *Reticulitermes* spp.

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Original Publication Citation

Waller, D. (1991). Feeding by *Reticulitermes* spp. *Sociobiology*, 19, 91-100.

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by

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INTRODUCTION

The feeding behavior of termites in the genus *Reticulitermes* (Isoptera; Rhinotermitidae) has a greater impact on the environment and human economy than that of most other animals. These termites are distributed throughout the holarctic region (Harris 1961) where they are important detritivores in natural habitats and significant structural pests in urban areas (Su & Scheffrahn 1990.) *Reticulitermes* eats primarily dead wood and occasionally damages crops (Mertins *et al.* 1971, Bournier 1977) and live wood (Kovacevic 1966.)

There are several compelling reasons to investigate feeding by *Reticulitermes*. First, measuring the rates and patterns of decomposition by *Reticulitermes* is central to assessing their nutrient cycling activities in forests. Also, *Reticulitermes* may contribute significant amounts of nitrogen to terrestrial ecosystems through nitrogen fixation by their hindgut bacterial symbionts (Breznak *et al.* 1973, Waller *et al.* 1989), but fixation rates vary according to the termite diet (Breznak *et al.* 1973.) In addition, production of greenhouse gases such as methane may be influenced by diet (Breznak 1984.) Finally, a thorough knowledge of *Reticulitermes* food preferences is required to develop environmentally benign baits for termite control. Unfortunately, little is known of the natural feeding behavior of *Reticulitermes*, and a limited number of laboratory studies have been performed. Determining consumption patterns in *Reticulitermes* will be complex because feeding may be influenced by factors associated with the colony, the environment, the food source or by interactions among these factors.

COLONY ASSOCIATED FACTORS

Food use by termites may vary with colony age, size, reproductive status or previous feeding history (Wood 1978.) For example,

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food selection by incipient colonies with small numbers of young pseudergates may be limited by the distance foragers can travel from the nest or by the density of wood they can harvest. Colonies may have higher nitrogen requirements and/or greater overall consumption rates during maturation of the sexual brood. If termites optimize the nutritional quality of the diet, they might choose foods rich in those nutrients that were deficient in a previous food source. Also, early exposure to a wood source may precondition *Reticulitermes* to prefer that species, as demonstrated for *Cryptotermes* (McMahan 1966.)

Termite feeding can be influenced by the hindgut symbiotic protozoans and bacteria, which vary among species and colonies within a species of *Reticulitermes* (Schultz & Breznak 1978, Waller, unpubl.) For example, food consumption rates of *R. lucifugus* and *R. speratus* are affected by artificial manipulations of the hindgut community (Orlova 1974), and feeding on unfavorable wood species results in the loss of gut protozoans in *Reticulitermes*, which in turn leads to starvation (Mannesmann 1972, Mauldin *et al.* 1981.) More studies of this nature could shed light on the coevolutionary associations among the termites, their microbes and different food sources, and might also identify protozoicides for termite control.

ENVIRONMENTAL FACTORS

The environment can influence feeding behavior through biotic factors such as the presence of competitors and predators or through abiotic effects such as temperature (Smythe & Williams 1972) or humidity (Collins 1969.) For example, Smythe & Williams (1972) found that *Reticulitermes* consumes more wood at 30°C than 25°C, but survivorship is decreased. Waller (unpubl.) obtained similar results and also found that nitrogen fixation by *Reticulitermes* workers is significantly lower at 30°C.

Termite colonies are often patchily distributed in forests (Waller, unpubl.), perhaps as a result of the availability of preferred foods or other environmental factors. The distribution of *R. tibialis* in Arizona appears to be limited by temperature and moisture (Haverty & Nutting 1976), and therefore food selection will be circumscribed within those limits. Termite abundance in a given habitat may be related to the dominant tree species, either directly due to its palatability or indirectly as a result of habitat modification by the tree. Gentry and Whitford (1982) noted that *Reticulitermes* is less abundant in turkey oak stands than in nearby pine habitats. Turkey oak wood is less preferred than pine, and turkey oak habitat is less favorable because of sparse tree density, lack of canopy and dry sandy soils.

FOOD-RELATED FACTORS

Wood diameter and litter particle size affect selection by several termite species (Wood 1978), and *Reticulitermes* prefers larger wood blocks in choice bioassays (Waller 1988.) Other characteristics that may influence feeding include wood density, water content, nutrients, allelochemicals and food pH. These may vary according to tree species or individuals within a species (related to genetics, age, stress or microenvironment), the section of the log consumed, the season of harvest or whether or not the wood is decayed.

Wood density

It is unclear whether density influences wood choice in termites. Preference for soft early wood over hard late wood may be related to chemistry rather than density. The conclusion of Behr *et al.* (1972) that *Reticulitermes* prefers low density wood is obscurred by the authors' method of measuring consumption (Waller *et al.* 1990.) *Reticulitermes* sometimes responds differently to sound wood and sawdust from the same source (Smythe & Carter 1970a, 1970b); this may result from changes in wood density, or because chemicals are unmasked or volatilized during sawdust preparation.

Water content

Reticulitermes is not found in very dry or very wet wood in nature (Waller, unpubl.), although it is likely that termites modify wood water content during feeding as *Coptotermes* does (Delaplane & La Fage 1989.) Rudolph *et al.* (1990) suggest that the moisture content of wood is irrelevant to the Rhinotermitidae as long as termites have access to free water in soil, and Collins (1969) reports that dehydrated termites can restore water content through drinking. Kahn (1980) found that feeding by *R. flavipes* is greatest at soil (vermiculite) moisture contents of 350-400%, but Lenz *et al.* (1987) suggest that vermiculite moisture content should be 225% for laboratory bioassays of *R. flavipes* response to decay fungi.

Nutrients

Wood nutrients probably influence food choice, although few studies have addressed this issue. Nitrogen should be limiting for *Reticulitermes* because wood is so low in this element (La Fage & Nutting 1978.) High concentrations of nitrogenous compounds appear to be detrimental to *Reticulitermes* (Mauldin & Rich 1975, Waller, unpubl.), but termites may not always be able to recognize lethal concentrations. For example, urea applied as a 5% solution (w/v in water) to filter paper resulted in increased mortality of *Reticulitermes* workers, although the termites preferred this concentration over water-treated paper. In contrast, termites ate less from paper treated with a 5% solution of uric acid than from controls (Waller, unpubl.) The ability to respond appropriately to different nutrients may be related to the range of concentrations encountered in nature.

Allelochemicals

Allelochemicals strongly influence food selection by *Reticulitermes* (Bultman & Parrish 1979, Carter 1979, Carter & Smythe 1972, Carter & Beal 1982, Carter *et al.* 1972, Floyd *et al.* 1976, Schefferan, this volume.) Toxicity does not always correlate with preference, however, because *R. hesperus* prefers toxic extracts of *Pinus ponderosa* in behavioral bioassays (Grace *et al.* 1989.) Allelochemicals vary in toxicity to different species of *Reticulitermes*, perhaps related to coevolutionary associations between the termites and different hosts (Nagnan & Clement 1990.)

Esenther (1977) noted that consumption of resistant wood by *R. flavipes* and *R. virginicus* increases when palatable sawdust is provided. This might occur because the favorable food buffers or counteracts the toxicity of the resistant wood. For example, a protozoicidal wood might eliminate gut symbionts and result in termite starvation; however, termites feeding on favorable species would maintiain viable symbionts which they could transfer via trophallaxis to nestmates ingesting the protozoicidal wood. Whatever the explanation, Esenther's (1977) finding suggests that *Reticulitermes* might ingest antitermitic foods in nature if palatable sources are available. Therefore natural wood use by termites may not always indicate the host species is nontoxic.

Food pH

Waller (unpubl.) found that *Reticulitermes* preferred filter paper treated with hydrochloric acid, nitric acid and sulfuric acid solutions adjusted to pH 2 over controls, and that levels of nitrogen fixation were decreased in termite workers fed acid-treated paper. Wood species vary widely in pH (Gray 1958), but no information exists on the pH of wood eaten by *Reticulitermes* in nature. Exploring the dynamics of wood pH, food selection and nitrogen fixation in termites will be valuable in predicting the effects of industrial acidification on nutrient cycling in natural habitats. This information will also be useful in formulating pH levels for termite baits.

Decay fungi

Infection by decay fungi may alter the density, water and nutrient content, allelochemical composition and pH of sound wood (reviewed in La Fage & Nutting 1978 and Waller & La Fage 1987.) Rotted wood is frequently eaten by *Reticulitermes* (Schultz-Dewitz 1972, Amburgey 1979, Waller *et al.* 1987), but Amburgey and Beal (1977) reported that stakes decayed by the white-rot basidiomycete *Ganoderma applanatum* are avoided by *Reticulitermes*. However, Waller *et al.* (1987) found that *Reticulitermes* attacks logs colonized by over 18 white-rot fungal species in Louisiana, and that basidiocarps of *G. lucidum* are preferred to other genera in choice bioassays. Clearly termite response to decayed wood will depend on the wood species, the fungal species and stage of decay (Amburgey & Smythe 1977.) A useful approach will be to catalog wood and fungal species consumed by *Reticulitermes* and then identify the chemical and physical parameters that underly those associations.

CONCLUSIONS

Investigations of *Reticulitermes* feeding have barely scratched the surface. More research is needed on all aspects of the colony, environment and the food source that influence wood selection and consumption rates of these important detritivores.

Although most work has focused on termite response to different wood species and their extracts, much remains to be learned about the effects of allelochemicals and nutrients on food choice. In addition, the physiology of food perception (Aksyutova *et al.* 1969), is essentially unknown. Bioassays have focused on consumption by termite groups, but individual feeding behavior has not been explored (Waller *et al.* 1990.) For example, information on how termites measure bitesize and mealsize may be required to assess preference when termites consume food sources that differ in density (Waller *et al.* 1990.)

The rewards of this research will be great. Feeding on wood is a challenge that few animals have mastered, and identifying the evolutionary processes that have shaped this unique trophic habit will reap both basic and practical benefits. A detailed understanding of *Reticulitermes* feeding pattens will provideinsight into the functioning of forest ecosystems and also facilitate the development of biologically based controls.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Jeff La Fage, whose enthusiasm for termites and zest for life were infectious. His contributions to termite biology will continue through those who drew inspiration from him. I am grateful for support provided by the Blandy Experimental Farm of the University of Virginia and by a Faculty Summer Research Fellowship from Old Dominion University.

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Jeff LaFage in a condemned playground near Jackson Square in the French Quarter of New Orleans, Louisiana, April 27, 1989. He was demonstrating the improper use of untreated wood placed directly into the soil. Photo by Michael Haverty.