Studies of Termite Wood-feeding Preferences[1]

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Introduction

Investigators of termites and termite damage have noted that certain woods appear to have greater immunity to termite attack than others. Kofoid and Bowe (1934) suggested that the factors determining woods selected by termites in nature include moisture content, amounts and chemical nature of the wood extracts, physical hardness, differences between heartwood and sapwood, and the nature and extent of pre-existing fungus attack. They suggested, for example, that the high death rate of termites in redwood may be due to the lethal effect of redwood extract on protozoa of the termite gut. Sherrard and Kurth (1934) indicated the detrimental effect of these extracts on fungal growth. Esenther et al. (1961) indicated, however, that fungus infection is not a prerequisite for termite attack. Wolcott (1946, 1953) found that some highly resinous woods are termite resistant, as are woods with a high lignin content. Marchán (1946) reported a relationship between lignin, ash, and protein content of various kinds of wood and their termite resistance.

These and other studies imply that termite choice is based on favorable characteristics of the selected wood which are correlated with increased survival and colony development, but is this the whole story? A termite colony is begun usually by a pair of primary reproductives creeping into a crevice in, or alongside, wood or some other cellulose supply. As the colony grows, its members may expand their area of feeding to include cellulose not part of the original supply. In addition to availability and favorable characteristics intrinsic in the selected wood, past feeding experience may play a role in habitat selection.

In 1958 and 1959 experiments, carried out at the University of Hawaii, were designed (1) to test the relative attractiveness to termites of different kinds of wood veneer, and (2) to see if the preference ratings so obtained would be reflected in the survival and developmental rates of incipient colonies reared in termitaries made of these different woods. Later experiments, carried out in 1964 and 1965 at the University of North Carolina, tested the effect of past feeding experience on termite wood preferences. These experiments did not supply a final answer to the question of the previous paragraph, but did provide pertinent data.

[1]A portion of this paper is based on part of a thesis submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy at the University of Hawaii in 1960.

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Preliminary Tests of Wood Preferences

Materials and Methods

Termites. *Cryptotermes brevis* (Walker), the West Indian termite, was the species tested in the experiments. It is a drywood species usually found in cured timber and furniture of human habitations and rarely in nature. A colony, when mature, numbers only a few hundred individuals live which entirely within feeding galleries. This species has no true worker caste, the work being done by immature forms of soldier and reproductive castes.

Wood Veneer. Fifteen kinds of wood veneer (commonly employed in furniture manufacture) were used to construct experimental termitaries. The untreated veneer was 1/32" thick and of the following types: (1) Spanish oak; (2), tupelo; (3) maple; (4) cherry; (5) black walnut; (6) ash; (7) white oak; (8) yellow poplar; (9) African mahogany; (10) sycamore; (11) white pine; (12) yellow pine; (13) elm; (14) korina; and (15) sweet gum. These woods were not all tested equally, nor were all possible factors affecting termite survival completely controlled. Consequently, conclusions regarding the relative "resistances" of these various woods to termite attack can be approximate only. The chief purpose of this preliminary study was to provide a basis for classifying the woods as "more preferred" or "less preferred" for use in later comparisons of colony development.

Termitaries. Two groups of termitaries, 7 in Group 1 and 8 in Group 2, were prepared (Fig. 1). In the first group, each of the 7 was composed of woods 1 through 7 listed above. In the second group, woods 8 through 15 were used in each.

In Group 1, a typical termitary consisted of 14 sheets of veneer (3" × 6" × 1/32"), two for each type of wood, and a top and bottom of plexiglass. The two veneer sheets nearest the plexiglass, were left entire, but the remaining 10 had a 1" × 2" rectangular center hole cut out to form a center chamber approximately 1" × 2" × 5/16". The two sheets of each type of wood were placed together to provide a total thickness that would permit a termite to tunnel completely within that type.

The position of the wood type was varied for each termitary. For the first termitary of Group 1, the order from top to bottom followed the list above with Spanish oak on top and White oak on the bottom. This general order was constant for all 7 termitaries, but the effect of position relative to the central chamber (sheets 3 through 12) was controlled by shifting the top wood to the bottom in consecutive termitaries. Termitary 2, e.g., had tupelo as the top two sheets and Spanish oak as the bottom two.

The 8 termitatries of Group 2 were similar in construction, except that they consisted of the remaining 8 types of veneer and consequently of 16 veneer sheets bolted together. The top to bottom arrangement of the first termitary was the same as the order listed. Position order relative to

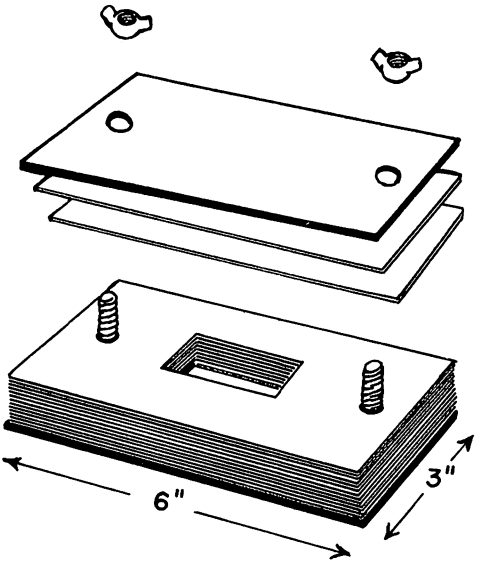

Fig. 1. Termitary composed of different kinds of wood veneer used in preliminary tests of wood preference. Top and bottom of plexiglass.

the chamber was systematically varied as in Group 1.

EXPERIMENTAL PROCEDURE

Into the central chamber of each termitary were placed 50 large *C. brevis* nymphs mostly micropterous (6 mg each or heavier) taken from infested plywood. Termitaries of Group 1 were filled on 3. II. 58 and left undisturbed for 150 days. Termitaries of Group 2 were set up on 29. VI. 58 and left for 140 days. Then the termitaries were dismantled, and each veneer sheet examined and judged on a 4-point scale. "0" meant that there was no indication of attempted feeding. A score of "1" meant very few such indications, consisting sometimes of a single hole (termite diameter) indicating that termites had merely tunneled through the sheet on their way to another region. A score of "2" meant that evidence of feeding was definitely more than in the "1" samples, and a score of "3" indicated extensive feeding and tunneling.

RESULTS

Mortality was high, approximagely 50% for the original inhabitants. Nevertheless, supplementary reproductives were produced in all termitaries, and many eggs and young nymphs were present indicating that conditions did permit colony development.

Table 1 shows the relative attractiveness of the different veneers of each termitary using weighted scores. Since feeding comparisons for the woods of Group 1 termitaries and for those of Group 2 cannot be made directly, this method of judging wood preferences can lead only to ap-

proximate rankings. It does permit the classification of these woods as "more preferred" with the higher scores, and "less preferred" with the lower scores.

Table 1. Preliminary wood preference test: Comparison of termite feeding on different types of wood veneer.

Wood	Termitaries of of Group 1							Total Score	Corrected Score (for comparison)
	1	2	3	4	5	6	7		
Spanish Oak[1]	3	1	0	2	0	0	2	8	9
Tupelo[2]	3	3	2	3	3	2	3	19	22
Hard Maple[3]	3	3	3	3	3	3	3	21	24
Cherry[4]	2	1	1	2	1	0	0	7	8
Black Walnut[5]	0	0	0	1	2	1	0	4	5
Ash[6]	1	0	3	0	2	3	2	11	13
White Oak[7]	0	0	0	0	0	0	1	1	1

	Termitaries of Group 2								Total Score
	1	2	3	4	5	6	7	8	
Yellow Poplar[8]	3	3	2	3	3	3	3	3	23
African Mahogany[9]	1	1	0	0	0	2	1	1	6
Sycamore[10]	3	3	0	3	3	3	3	3	21
White Pine[11]	1	0	0	1	2	2	0	0	6
Yellow Pine[12]	0	2	2	0	1	2	1	0	8
Elm[13]	0	3	3	0	0	0	2	0	8
Korina[14]	0	0	0	0	0	0	0	0	0
Sweet Gum[15]	2	2	3	3	1	1	1	1	14

1 *Qeurcus falcata*, 2. *Nyssa sylvatica**, 3. *Acer saccharum**, 4. *Prunus serotina*, 5. *Juglans nigra*, 6. *Fraxinus americana**, 7. *Quercus alba*, 8. *Liriodendron tulipifera*, 9. *Khaya ivorensis** 10. *Platanus occidentalis*, 11. *Pinus strobus*, 12. *Pinus echinata**, 13. *Ulmus americana*, 14. *Terminalia superba*, 15. *Liquidambar styraciflua*.
*Denotes species identification uncertain

According to these data, the woods were arranged in a descending order of "preference" as follows: maple>yellow poplar>tupelo>sycamore>sweet gum>ash>Spanish oak>cherry=yellow pine=elm>African mahogany=white pine>black walnut>white oak>korina.

Comparison of Survival and Development of Colonies Reared in "More Preferred" and in "Less Preferred" Woods

The next experiment tested the hypothesis that incipient colonies reared in termitaries composed of "less preferred" woods would have a higher mortality rate, fewer nymphs, and fewer eggs after a given interval than those reared in "more preferred" woods.

MATERIALS AND METHODS

The termitaries used were similar to the one shown in Fig. 1 except

that each consisted of 10 smaller sheets of veneer (6" × 1" × 1/32"), and all the veneer sheets composing a given termitary were of a single wood type. The central chamber was 4 sheets deep and 1/2" × 1/4" in area. A pair of new dealates (primary reproductives) was introduced into each chamber and left undisturbed for 12 to 15 months. During this period, all termitaries were kept under identical conditions of ambient temperature and moisture.

There were unequal numbers of termitaries for the various types of veneer, and yellow pine, elm, and korina were not tested.

RESULTS

Table 2 shows that the experimental results supported the original hypothesis.

Out of 41 original pairs in the "more preferred" woods, about 46% survived, while less than 4% survived of the 29 pairs in "less preferred" woods. In the former case, 83 offspring (including eggs) were produced, or about 4 per surviving pair. No eggs or nymphs were produced by the one surviving pair in the "less preferred" woods.

Table 2. Comparison of colony development in "More Preferred" and in "Less Preferred" woods

More Preferred Woods	No. of Original Pairs	No. of Surviving Pairs	No. of eggs	No. of Nymphs
Maple	10	5	5	22
Y. Poplar	7	5	1	11
Tupelo	3	2	2	8
Sycamore	8	2	2	6
Sweet Gum	11	6	2	21
Ash	2	0	0	0
Total	41	19	12	71

Less Preferred Woods	No. of Original Pairs	No. of Surviving Pairs	No. of eggs	No. of Nymphs
Spanish Oak	1	0	0	0
Cherry	3	0	0	0
African Mahogany	6	0	0	0
White Pine	1	0	0	0
Black Walnut	11	1	0	0
White Oak	7	0	0	0
Total	29	1	0	0

Effect of Past Feeding Experience on Wood Preferences

A study conducted in 1964 and 1965 on rate of colony development in *C. brevis* privided an opportunity to test the effect of the past feeding experience of termites upon their subsequent choice of wood.

MATERIALS AND METHODS

Incipient colonies were reared for one year (from the date of the original pairing of dealates) in termitaries composed of yellow poplar veneer. This wood was chosen for its easy availability and because it was in the "more preferred" category.

A total of 31 year-old incipient colonies (each consisting of a pair of primary reproductives and from 1–7 small nymphs) were placed in a choice situation and allowed to choose their subsequent food.

As each incipient colony was removed from its poplar home (a termitary similar to those previously described) it was introduced into a dual choice situation consisting of a special termitary diagramed in Figure 2.

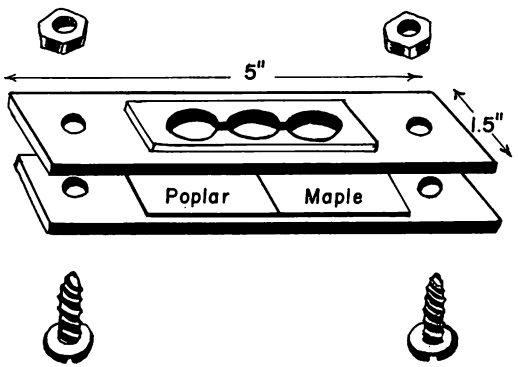

Fig. 2. Dismantled termitary of masonite, with transparent roof, used for presenting poplar-reared incipient colonies with a dual choice situation. Small squares of poplar (the accustomed wood) and another (unaccustomed) veneer were inserted between the two masonite strips to serve as floors for the connected chambers. Termites were originally placed in the center chamber and allowed to choose their food source.

It was composed chiefly of two bolted strips of masonite (a synthetic material not palatable to termites), the top strip with three circular adjoining chambers, each 1/2" in diameter, connected in series by narrow corridors. The floor of each termitary consisted of two sheets of different veneers which were slipped between the masonite strips and apposed end to end. The veneer boundaries met in the exact midline of the center chamber. This meant that one of the end chambers and half the center chamber was floored with one of the two types of wood. A glass slide was hinge-taped above the chambers to serve as a transparent roof.

Two series of tests were carried out. In Series 1, 18 incipient colonies (96 termites) were tested in termitaries with poplar and maple, both in the "more preferred" category. In Series 2, 13 colonies (69 termites) were given a choice between poplar and one of three "less preferred" woods: cherry, elm, or korina.

In a given series, each colony was transferred gently from its poplar

home of one year to a watch glass from which all members were dropped simultaneously into the center chamber of a choice-termitary. The glass roof was closed and sealed, and a black cloth placed over the top to exclude light until later examination.

Examinations were made after 1, 3, 7, and 14 days. The cloth was removed carefully from one termitary at a time and the position of each termite within the three chambers was recorded. This procedure did not appear to disturb the termites, since little movement was noticed during an examination. In fact, they tended not to move out of the center

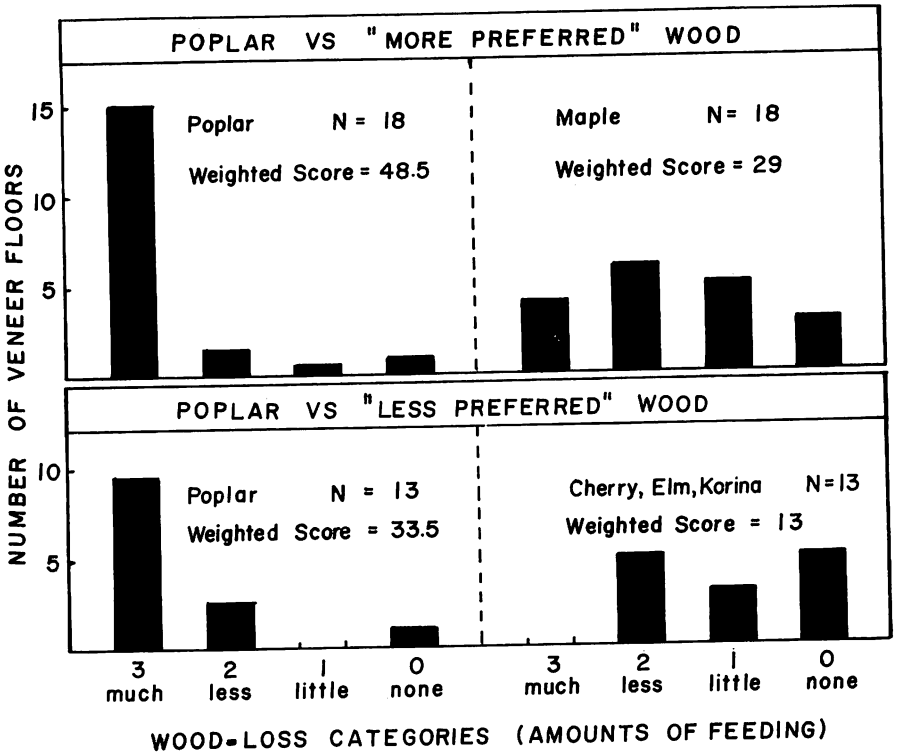

Fig. 3. Distribution of various kinds of veneer floors into categories of wood loss reflecting relative amounts of feeding by poplar-reared termites. The top histograms compare feeding when poplar was presented simultaneously with maple, a "more preferred" wood. The bottom histograms similarly compare poplar and veneers which were "less preferred" (cherry, elm, and korina). The "weighted score" in each case was obtained by adding the scores of all the floors of the particular veneer in question. The data represent averages for two judges.

chamber.

After 14 days, the termitaries were dismantled, and the 62 veneer floors examined for evidence of feeding. Again, the degree of feeding was designated by scores of "0, 1, 2, and 3." Another judage, unaquainted with

the experiment, was asked to classify all the veneer floors independently. The two judges disagreed on only 12 out of 62 judgements, and never by more than one category. Their scores have been averaged in Figure 3.

This method, involving estimates of actual feeding, was better for indicating feeding preferences than the procedure of recording termite position.

RESULTS

For Series 1, visual examination of termite position within the termitaries indicated that the termites, after one day, were more concentrated on the maple than on the poplar floors, but this apparent early preference gradually shifted until, at 14 days, the termites were about equally distributed on the two types of wood. In most instances, they clustered within the center chamber. In Series 2, the termites also tended to cluster within the center chamber, but as observation continued, they were found more and more to be concentrated on the poplar floor.

Table 3 shows termite distribution between the various veneers at different examination times in the two series of tests. In the "midline" category were placed all termites which were partially on one veneer and partially on the other in the center chamber.

Table 3. Distribution of termites on veneer flooring after four time intervals.

Days after Introduction	Poplar vs. "More Preferred"			Poplar vs. "Less Preferred"		
	Poplar	Midline	Maple	Poplar	Midline	Other[a]
1	18	6	72	22	9	38
3	27	12	57	31	11	27
7	36	17	43	38	5	26
14	36	17	43	43[b]	9	16

a Either cherry, elm or korina
b One nymph died

Figure 3 shows the results of analyses of the degree of feeding on each of the veneer floors. The termites, when given a choice, ate a greater volume of poplar, their previous food, than either maple or "less preferred" woods. About 80% of the poplar floors were in the "3" category, indicating extensive feeding, while only about 22% of the maple floors were in this category. When poplar was presented with a "less preferred" wood, about 73% of the poplar floors were in this category, as opposed to 0% for "less preferred" woods. This use of weighted scores to indicate feeding preference is on the conservative side. Woods judged to be in category 3 almost invariably exhibited a loss of wood volume much more than 3 times that of woods judged to be in category 1.

Table 4 gives the data in a slightly different way. It shows the number of times a poplar floor was judged to be in a superior, an equal, or an

inferior category, to the other floor simultaneously presented. These data all indicate the termite's preference for poplar. They also indicate that poplar was chosen more strongly when it was paired with a "less preferred" wood than when it was paired with maple, a "more preferred" wood.

Table 4. Comparison of termite feeding on accustomed (poplar) and unaccustomed wood veneer presented simultaneously

Judge	Series 1 (Poplar vs. "More Preferred" Wood[a])			Series 2 (Poplar vs. "Less Preferred" Wood[b])		
	Poplar Superior	Poplar Equal	Poplar Inferior	Poplar Superior	Poplar Equal	Poplar Inferior
E.McMahan	13	4	1	11	2	0
D. Misch	11	4	2	11	2	0
Average	12	4	1.5	11	2	0

a Maple
b Cherry, elm or korina

DISCUSSION

Food selection by termites, as by other insects, is doubtless based upon multiple genetic factors which underlie the physiological and behavioral aspects of the response (Thorpe, 1939; Cushing, 1941; Hovanitz, 1944; Dethier, 1954; Hodgson, 1964; Kovoor, 1964). Vision, phototaxis, geotaxis, and hygrotaxis may all play a part in directing insects to their food, but the chief role at close range is usually played by chemoreception (Dethier, 1954). Termites, like most other mandibulate insects, probably have contact chemoreceptors on the maxillary and labial palpi (Frings & Frings, 1949) and possibly the tarsi (Noyes, 1930). Olfactory receptors are probably on the antennae (Hartwell, 1924). Verron (1963) recently revived the suggestion that olfactory sense organs may be associated also with the tracheae.

The wood preference responses shown by *C. brevis* may have been triggered by attractant (or repellent) substances characteristic of the various woods, but not necessarily having nutritive value in themselves. A number of investigators have shown that nutritionally unimportant "token stimuli" often serve as releasers of genetically based feeding patterns (Dethier, 1947, 1953; Tinbergen, 1951; Thorsteinson, 1953; Fraenkel & Gunn, 1961). Whether nutritional aspects, toxicity factors, or some other conditions were basically responsible for the selection responses, the termites did choose to feed on woods that were shown to be most conducive to the successful rearing of a colony.

Some studies have shown that feeding preferences of certain insects can be altered through conditioning (Sladden, 1934, 1935; Sladden & Hewer, 1938; Thorpe & Jones, 1937; Thorpe, 1939; Cushing, 1941). The rearing of larvae or young on a changed diet resulted in changed feed-

ing (or oviposition) preferences of the adults or of subsequent generations. This phenomenon has been suggested as an isolating mechanism in the ecological separation of populations (Dethier, 1954; Thorpe & Jones, 1937). Preferences arising through conditioning (or habituation), whether natural or artificial, are probably not so strongly ingrained or permanently fixed as genetically fixed preferences. Dethier (1953) points out, however, that such conditioning may so alter the threshold of response in some species that substances "that normally elicit a rejection may be made to provoke acceptance" (and presumably vice versa).

Polyphagous insects may be expected to exhibit conditioning most readily, and the present tests indicate that the phenomenon does occur in *C. brevis*. These termites strongly preferred the wood to which they had become accustomed (poplar) over another to which they were unaccustomed (maple), even though the latter was shown to be just as favorable to colony development, and under more "neutral" conditions was preferred slightly over poplar. The superior strength of genetically-fixed over conditioned preferences is indicated probably by the fact that poplar-reared termites preferred poplar over woods in the "less preferred" category to an even greater degree than they preferred it over maple.

Further experiments in which termites are reared in both "more and less preferred" woods and then tested systematically in choice situations are indicated.

SUMMARY AND CONCLUSIONS

Cryptotermes brevis (Walker), a drywood termite, was tested in termitaries made of 15 kinds of wood veneer and was found to prefer some over others. A hierarchy of preference for woods was determined.

Primary reproductive pairs were placed in termitaries made of the various types of wood, each termitary composed of a given type, and left for one year to establish incipient colonies. Survival and offspring production were definitely greater in termitaries of "more preferred" woods than in those of "less preferred" woods.

Poplar and maple both ranked as "more preferred" woods, with maple being perhaps slightly above poplar, yet incipient colonies reared on poplar strongly preferred it over maple, indicating that conditioning is possible in these termites. Woods in the "less preferred" category were rejected even more strongly in favor of poplar by poplar-reared colonies. Conditioning may play a role in home selection by swarming termite reproductives or by expanding colonies in nature.

ACKNOWLEDGMENTS

The work carried out at the University of Hawaii during 1958 and 1959 was done in connection with National Science Foundation grant No. G-9581 awarded to Dr. L. D. Tuthill. The work completed at the University of North Carolina in 1964–65 was supported by NSF grant No.

GB-530.

The generous help of a number of persons and businesses was of particular importance to the work. The Ritch Veneer Company of High Point and Liberty, North Carolina provided the veneer; T. Roy Young Jr., and Melvin Gardner of Young Pest Control, Tampa, Florida, and Dr. Ralph Heal were of invaluable assistance in procuring termites; and Dr. D. W. Misch was the independent judge in the feeding preference tests. This aid is gratefully acknowledged.

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