THE SIGNIFICANCE OF THE SUBTERRANEAN TERMITE, *HETEROTERMES AUREUS* (SNYDER), AS A DETRITIVORE IN A DESERT GRASSLAND ECOSYSTEM

by

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I hereby recommend that this dissertation prepared under my direction by Michael Irving Haverty

entitled THE SIGNIFICANCE OF THE SUBTERRANEAN TERMITE, HETEROTERMES AUREUS (SNYDER), AS A DETRITIVORE IN A DESERT GRASSLAND ECOSYSTEM

be accepted as fulfilling the dissertation requirement of the degree of DOCTOR OF PHILOSOPHY

William L. Nutting — March 27, 1974

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After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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BIOGRAPHICAL SKETCH

Michael Irving Haverty was born in Fresno, California, on October 24, 1946. He attended grammar school and graduated from McLane High in Fresno.

He obtained his undergraduate education at the University of California, Davis, where he received his Bachelor of Science degree in zoology in 1968.

From 1968 to 1969 he was a graduate research assistant in the Department of Entomology, University of Arizona, and received the degree of Master of Science in 1970. His thesis involved a study on the circadian sensitivity and dosage rate response to X-irradiation in the pink bollworm moth.

He was a graduate research associate in the Department of Entomology, University of Arizona, from 1971 to 1973, supported by a grant from the National Science Foundation, through the International Biological Program, Analysis of Ecosystems, Desert Biome, for study and research toward the Doctor of Philosophy degree in entomology with a minor in zoology.

He is married to the former Marsha Ann Mead of Lindsay, California.

TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--Continued

LIST OF ILLUSTRATIONS--Continued

ABSTRACT

To evaluate the efficiency of the subterranean termite, Heterotermes aureus (Snyder), in removing superficial dead wood from a desert grassland ecosystem the following parameters were examined: 1) size and dispersion of foraging populations, 2) production and availability of wood, 3) wood consumption rates, 4) preferences in selection of wood and 5) environmental control of foraging activity.

Field experiments were carried out in a shrub-invaded desert grassland ecotone on the Santa Rita Experimental Range, ca. 40 km south of Tucson, Arizona. Fifty randomly located circular quadrats were sampled to study relationships between termite populations and wood abundance. A bait sampling technique provided information on environmental control of termite foraging activity, number of foragers, colony density and foraging territories. Laboratory wood consumption rates were established using six constant temperatures and four wood species. A simple computer model was developed to synthesize results and to evaluate this termite's role as a detritivore in this ecosystem.

From circledrat data it is estimated that there were 160 foraging groups or colonies per hectare and an average of 68,918 foraging termites per hectare at any given moment during the year of study. There were an estimated 181 colonies and an average of 37,800 foraging termites per hectare as determined by the bait sampling

technique. Average colony foraging territory was 13.14 m^2. Foraging groups consisted of 97.2 percent larva-workers, 1.5 percent soldiers and 1.3 percent nymphs, larvae and pre-soldiers. Numbers or biomass of termites was generally not correlated with amount of wood available.

Standing crop biomass of superficial dead wood on the study site is 2127 kg per hectare. Five plant species represent 97.6 percent of the biomass. Six plant species account for 96.4 percent of the 450 kg per hectare of superficial dead wood produced annually.

Wood consumption by H. aureus is best described as a linear or quadratic function relative to temperature. Maximum consumption occurred between 28 and 32°C regardless of wood species and a significantly greater amount of blue palo verde, C. floridum, was consumed than the other three wood species.

H. aureus is a general feeder yet appears to prefer cholla, mesquite and catclaw over blue palo verde and other less abundant woods. This contrasts with its ability to consume significantly greater amounts of C. floridum in compulsory feeding trials.

Surface foraging occurs throughout the year between 7 and 47°C, extreme temperatures between the food-soil interface and 15 cm in the soil. Increased soil moisture increases foraging intensity. Number of foragers on the bait sampling grid at a given point in time may be predicted by the equation: $\ln Y = -0.985 - 0.0761\ T + 2.928 \ln T + 0.327 \ln R$ where Y = number of foragers at that time, T = daily mean temperature at food-soil interface and R = daily rainfall.

Total density of H. aureus is estimated at 431 to 786 per m^2 with a biomass of 0.145 to 0.264 g per m^2. Average colony size may range from ca. 23,754 to 49,125 individuals.

A simulated wood consumption model couples temperature-dependent wood consumption and foraging intensity functions to provide number of termite visits to soil surface and amount of wood consumed annually. The model predicts that H. aureus foragers made 4.61×10^{10} foraging sorties per hectare per year. In the course of these trips foragers removed surface wood at the rate of 78.9 kg per hectare per year. This represents 3.7 percent of the standing crop biomass and 17.5 percent of the annual production of superficial dead wood. Therefore, H. aureus apparently plays an important role in removing selected species of wood from the desert grassland ecosystem.

INTRODUCTION

Termites form the order Isoptera, a small, homogeneous order of approximately 2,200 species, all of which are social (Wilson, 1971). The primitive termite, Mastotermes darwiniensis Froggatt, has many morphological and physiological characters in common with the cockroaches of the genus Cryptocercus. Thus, having a close evolutionary relationship with these wood-eating cockroaches, termites may be thought of as social cockroaches. The individuals are differentiated into various morphological forms, or castes, which exhibit a division of labor, each performing a different biological function, and which live together in highly organized and integral units, societies or colonies.

The Isoptera have reached heights of eusociality that are equivalent to or surpass those of the social Hymenoptera, and from a primitive base far removed from them. Termites differ from the social bees, ants and wasps in that they are hemimetabolous, that their castes are usually bisexual and that they have no known subsocial groups (Krishna, 1969). Wilson (1971) has recently made an exhaustive review of sociality in insects with extensive comparisons of termites with the social Hymenoptera.

All termites utilize cellulose from a variety of sources as their principal energy source. They are all involved, with the

assistance of their symbiotic biota, in the comminution and decomposition of plant debris whether it be above, on or in the soil. Sometimes in the process of nutrient recycling termites can cause severe denudation of grasslands (Coaton, 1951; Watson and Gay, 1970), even competing with livestock in the removal of grass and reduction of primary productivity in grasslands (Bodine, 1973). Where they are present, wood-eating termites are an integral part of an ecosystem and are considered to be much more important in the initial breakdown of wood than are microbes and fungi (Hopkins, 1966; Lee and Wood, 1971).

Termites have long been of interest to man. Their attacks upon his man-made structures and possessions are of continuing economic concern. Many of the studies on termites involve the testing of wood or wood products, attractants and toxic chemicals and their effects on the destructive activities of various species of termites.

Because of their cryptic behavior, there are relatively few comprehensive studies which examine the ecology and demography of subterranean termites. Most such studies have concerned themselves primarily with the obvious mound building or harvesting species which forage above the ground, even though subterranean termites may be at least as numerous and ecologically more important (Sands, 1972).

There are approximately 40 species of termites in the continental United States and at least 16 of these occur in the Tucson Basin. This represents the largest number and greatest diversity of species in any area of comparable size in the country. Of the 16 species, 10 are subterranean and feed on cellulose from a

variety of sources including wood, dried vegetation, dung and humus (Nutting, 1968). Heterotermes aureus (Snyder) appears to be the most economically important of the subterranean termites in this area.

Heterotermes aureus is the only truly Nearctic species of this genus and occurs in the Sonoran Desert of California and Arizona in the United States, and Sonora, Sinaloa and Baja California in Mexico. Reticulitermes tibialis Banks replaces H. aureus in the higher elevations of the Sonoran Desert although the two species are sympatric in many of the lower canyons and along water courses. H. aureus is not as dependent on moisture as is Reticulitermes. It is probable that much of the damage attributed to Reticulitermes in certain areas of the southwestern deserts of the United States is actually caused by H. aureus (Weesner, 1970).

Since it is an economically important species in the Sonoran Desert, it was postualted that H. aureus must be an important decomposer in this ecosystem, functioning mainly in the breakdown and gradual recycling of the dead wood which is continually produced. To evaluate the efficiency of H. aureus in removing superficial dead wood it was necessary to measure the following parameters: 1) foraging populations, 2) production and availability of wood, 3) wood consumption rates as a function of temperature and wood species, 4) wood preferences and 5) environmental control of termite foraging activity.

METHODS AND MATERIALS

The field work for this study was carried out on the US/IBP, Desert Biome research site. The U. S. Forest Service provided the area on its Santa Rita Experimental Range approximately 40 km south of Tucson, Arizona, at an elevation of 950 m. The soil of this site is formed from outwash alluvium characteristic of much of the Sonoran Desert. Annual rainfall averages 330 mm, most of which occurs during the summer monsoon season. The remainder is frequently made up, less reliably, during the period from December through February. The area is a shrub-invaded, desert grassland ecotone, characterized by scattered shrubs, cacti and small trees. The shrub layer is dominated by burrow weed [Aplopappus tenuisectus (Green) Blake], the cactus by cholla [Opuntia fulgida Engel. and O. spinosior (Engel. and Bigel.) Toumey], and the small tree layer by mesquite [Prosopis juliflora var. velutina (Woot.) Sarg.] and blue palo verde (Cercidium floridum Benth.). Perennial grasses are found mainly along the water courses and beneath the crowns of trees and shrubs.

Laboratory experiments were conducted in the Department of Entomology, University of Arizona.

Circledrats

Sampling for superficial dead wood, associated termite activity and foraging group size was done on the limited destructive

sampling area of the untreated plot. From a grid, which had been used for soil moisture sampling, fifty random points were chosen and served as the centers of the 50 "circledrats" (circular quadrats).

In the beginning sampling was done both day and night to randomize the time of day in which the termite populations were observed. It was soon decided that their foraging activity should be studied separately and intensively, with detailed attention to several environmental variables (see METHODS AND MATERIALS: Bait Sampling Grid). The circledrats could then be sampled during daylight hours with primary attention to dead wood and foraging group size and density.

Using the random points as centers, fifty 50-m^2 circledrats were "drawn". All the dead wood on the ground was identified and weighed in pounds and ounces on a hand-held, Chatillon® hide scale. Weights were later converted to grams. Termite activity was broken down into three categories: 1) termites present, 2) past termite activity but no termites present and 3) no past termite activity.

While surveying some preliminary circledrats, I established criteria to determine which pieces of dead wood should be included in the circle as follows:

1. All wood wholly within the circle and on the ground was included.
2. Wood partially in the circle but on the ground was broken or cut at the perimeter of the circle and the portion within the circle included.
3. Wood on a bush or tree inside or outside the circle, but

touching the ground within only, and therefore accessible to subterranean termites, was removed and counted *in toto*.

4. Wood extending into the circle (aerially) but not touching the ground inside was not included.

These criteria may be summed up by the general rule that all wood accessible from the ground within the circle was included, and wood accessible only from without was not.

When foraging groups were encountered, they were either counted on the spot or the wood containing the termites was brought back into the laboratory and the termites were extracted from the wood and counted. All counts were exact tallies of every individual in a foraging group. None was estimated. When clean and healthy termites were brought back to the laboratory occasional samples were removed and dried to constant dry weight at 60°C for 24 hr. Weights of samples were taken to the nearest 0.1 mg on a Mettler analytical balance, Type 6H.

The 50 circledrats were sampled between May 3, 1971, and June 7, 1972. To determine dead wood production each point was resampled between May 2, 1972, and June 5, 1973.

Data Analysis

The circledrat method yielded data for determining several different pieces of information: biomass of dead wood of each species per hectare available for termites, biomass of dead wood of each species produced annually per hectare, numbers and biomass of *H. aureus* per hectare, the relationship between the amount of wood

available and the termite numbers and biomass, and wood preferences.

Wood weights obtained in the field necessarily included a certain amount of moisture, soil and miscellaneous debris. These field weights have been corrected for moisture content and adhering material as follows. Two collections of random samples of six species of wood were made just outside the IBP study area. Collections were made at two different times of year: after a wet period (October 20, 1972) and a dry period (September 24, 1973). Routine field weights were taken and the wood was brought back into the laboratory for a thorough cleaning and drying. It was brushed and washed in water, dried at 105°C for 24 hr, then reweighed on the same scale to determine biomass. A factor for correcting field weights was determined by dividing the weight of a clean, dry sample by its field weight.

No significant difference was found between the correction factors for the wet and dry periods; therefore, data for the two seasons were considered together. A significant difference ($\alpha = .01$) between correction factors for wood species was found by analysis of variance. These specific correction factors are listed in Table 1. Wood species not processed as above have been assigned a correction factor which is the average of factors determined for the six species. Field weights were multiplied by the appropriate correction factors to give the standing crop biomass of superficial dead wood and annual dead wood production.

Table 1. Factors for correcting field weights of wood for moisture content and adhering soil. Field weights of each species times its correction factor provides a reasonably accurate standing crop biomass for fallen dead wood.

Wood species	No. samples	Correction factor[a]
Acacia greggii	2	.9109 a
Prosopis juliflora	2	.9024 a
Celtis pallida	2	.8697 a
Opuntia spinosior	8	.8359 a
Cercidium floridum	2	.8174 ab
Opuntia fulgida	8	.7812 ab
O. fulgida, joints	4	.7682 ab
O. spinosior, joints	2	.6773 b
All species	30	.8122

[a]Correction factors followed by the same letter are not significantly different at the $\alpha = .05$ level as determined by Student-Newman-Keuls' test for unequal replication.

Relationships between the standing crop of superficial dead wood and termite biomass or numbers were obtained by linear correlation. Correlations between the total H. aureus numbers and biomass were examined, using the average biomass for each caste and the corrected biomass of each wood species for each circledrat.

Wood preferences were determined by tabulating the number of occurrences of each species of wood in all fifty circledrats. The counts were separated into the number of pieces of each species of wood attacked and not attacked by H. aureus. These frequencies were analysed by Chi-square. Probabilities of attack were separated at the $\alpha = .05$ level by a Student-Newman-Keuls' multiple range test.

Bait Sampling Grid

To examine the physical factors affecting or regulating foraging and to determine colony territories and densities, a grid of attractive bait was planned on the limited destructive sampling area of the chained plot. This area was chosen because most of the standing vegetation had been removed by a chaining operation 18 months before. Prior to setting out the bait all superficial and partially buried wood was raked off the grid area so as to eliminate any possible competition between natural wood and the bait.

Two types of bait material proved to be unsuccessful in preliminary trials. Birch tongue depressors, spaced at 1-m intervals on two 10 x 10-m grids and pushed half way into the soil, proved to be attractive to termites. However, when the depressors were pulled up for periodic examination, the termites were destroyed and could not be

counted. As a result this method was abandoned. Fir 2" x 4" blocks (8.4 x 3.7 x 10.0 cm) spaced at 1-m intervals on two additional 10 x 10-m grids were established but did not prove to be very attractive to termites and this method was also abandoned.

A rather novel termite bait was discovered and used on a trial basis after the two previous methods were deemed unsatisfactory. Two 10 x 10-m grids of toilet paper rolls which were spaced at 1-m intervals were set up adjacent to the tongue depressor grids. Tongue depressors were used to mark the 1-m intervals and to prevent them from blowing away. The rolls of paper were slipped over the tongue depressors and pressed onto the soil surface. Each roll of paper (Forest Park®, 650 sheets, 11.43 x 11.43 cm, single ply, white, unscented) was wrapped with 3 strips of masking tape (5.2 cm wide) to prevent raveling. This bait proved to be very attractive to H. aureus and the rolls could be lifted and the termites observed without greatly interfering with their activities.

Following the success of this method additional grids were set up. The completed plot consisted of 16 test areas, of 100 rolls of paper set at 1-m intervals. The total grid area measured 40 x 40 m, or 1600 m^2. Between some of the test areas intermediate rows occurred as a result of the chronological order in which the test areas were laid out. These intermediate rolls were checked for termite activity at the end of the experiment to aid in establishing colony boundaries. Of the 16 test areas 12 were used to observe weekly foraging activity of two species of termites, H. aureus and Gnathamitermes perplexus

(Banks). The adjacent four plots were left untouched as part of a parallel study to determine the amount of soil brought to the surface by termites as well as to estimate the amount of paper removed by termites over a period of one year.

Environmental Control of Foraging Activity

Observations on the foraging activity of H. aureus were made from October 15, 1971, to October 13, 1972. It was decided after some preliminary observations that each roll of paper should be examined no oftener than once a week to prevent undue disturbance. Observations on these test areas were made during a 24-hr period each week. A different test area of 100 rolls was examined every 24-hr, thus no single roll was checked more than once a week.

Checking for termite foraging activity involved a quick examination of the underside of each roll, and a notation of the species and approximate number of termites present or, if none were present, any evidence of past activity. In this manner, 100 rolls could be examined in about 30 minutes. The narrower, deeper and more heavily spotted galleries of H. aureus made its workings easy to distinguish from those of G. perplexus.

Prior to each 2-hourly check several environmental parameters were measured. Soil temperature at 1, 3, 5, 10, and 15 cm from the surface and temperatures in a roll and at the roll-soil interface were measured with copper-constantan thermocouples using a Leeds and Northrop single range potentiometer. Soil surface temperature was also measured with PTC® surface thermometers, model 310C (Pacific Transducer

Corp. Instruments). Soil temperatures were means of values measured at two stations within the bait sampling grid. Air temperature and relative humidity were continuously recorded by a Bendix hygro-thermograph, model 594, on the south edge of the test area. Continuous recordings for roll-soil interface temperatures were made with an Electric Auto-Lite recording thermometer, model 100. Rainfall was obtained weekly with two simple, wedge-shaped, plastic collecting gauges.

Data Analysis

Five categories were used to describe the number of termites observed at a roll: few, 1-5; medium small, 6-50; medium, 51-150; medium large, 151-250; and large, >250. The median value of each category (few, 2.5; medium small, 27.5; medium 100.0; medium large, 200.0; large, 500) was used as the estimate of the number of termites foraging at a particular roll. The closeness of the estimate was determined at the end of the study by harvesting 200 rolls from the four undisturbed test areas, assigning a size class as usual in the field, and finally counting the termites in the laboratory. When the relationship was examined by linear regression and correlation, the estimated and observed values of 35 foraging groups showed a highly significant correlation ($r = .955$). Since the numbers of termites were consistently underestimated, the resulting regression equation ($Y = 2.04 + 1.875X$) was used to adjust all estimated numbers of termites.

Seasonal trends in foraging were determined by summing the estimated numbers of termites observed at the surface for all 12 test areas (over a 24-hr period) each week for the 53 weeks of the experiment. These totals were plotted along with mean temperature (roll-soil interface) for the 24-hr observation period and cumulative rainfall for the preceding week.

The relationship between number of foraging termites, mean daily temperature and daily rainfall was determined by multiple linear (curvilinear) regression (Dixon, 1973). Independent variables were transgenerated to $\log_e$, reciprocal and square, and the dependent variable transgenerated to $\log_e$. With the transgenerated variables, models describing the above relationship were developed.

Colony Foraging Territory and Density

In addition to relating foraging behavior to environmental parameters, the toilet paper plot provided a means for estimating the size (area) and density of foraging territories of H. aureus. It was not possible to demonstrate suspected territorial limits by noting aggression (or lack of it) displayed when workers or soldiers from different areas were brought together as was done by Nel (1968) with Hodotermes mossambicus. However, it was possible to establish boundaries of what are considered to be foraging territories of individual colonies. Rolls attacked on the first week of the study and rolls with consistently large numbers of termites were considered as colony epicenters. From these epicenters the spread of foragers to

new rolls was followed weekly. Thus, from this series of observations colony boundaries were empirically determined.

Based on the assumption that each roll subtended 1 m^2 of territory, the areas of the territories thus defined were determined by summing the rolls attacked in each grouping. Unattacked rolls within such groups were included in the occupied areas since it seems unlikely that they would be attacked by other colonies of H. aureus (Greaves, 1962). Areas of the colonies on the periphery of the study plot were multiplied by two since it is assumed that, on the average, only half of each such colony fell within the plot. In determining the number of colonies per hectare, colonies wholly within the plot were counted as whole colonies but, according to the preceding assumption, those divided by plot boundaries were counted as half-colonies.

The average number of foragers per hectare per week was ascertained by summing the mean number of termites observed per roll per week for the entire 12 test areas.

Wood Consumption Rates

Termites

Three foraging groups of H. aureus were collected at the Santa Rita Experimental Range by using rolls of toilet paper as bait. After their removal from the paper all termites were held at 25°C and ca. 100 percent R. H. for three weeks on filter paper, with a piece of 4 percent agar as a moisture source.

Woods

Four species of wood were chosen which H. aureus commonly attacks on the Santa Rita Experimental Range: catclaw acacia, Acacia greggii Gray; jumping cholla, Opuntia fulgida Engelm.; mesquite, Prosopis juliflora var. velutina (Wooton) Sarg.; and blue palo verde, Cercidium floridum Benth. O. fulgida was chosen over O. spinosior because of its size, so that large uniform pieces of wood could be used.

Blocks were cut (6 x 12 x 12 mm) from sound, dead branches of each species. Before the tests, blocks were oven dried at 105°C for 24 hr and weighed to the nearest 0.1 mg using a Mettler analytical balance, Type H6. To avoid water uptake between removal from the oven and weighing, the wood was held in a desiccating jar with indicating Drierite®. Although it was not apparent whether or not this wood had been attacked by fungi, it did not appear to be altered significantly.

Test Procedures

An experimental unit consisted of 100 termites in a closed container with a block of wood on moistened sand. The caste composition of each group varied slightly to match the caste proportions of the foraging group from which it was taken. The termites for each replication were drawn from a single natural foraging group. An average dry weight for each caste, obtained in conjunction with the foraging group study, was used to estimate the dry weight of each group. The resulting composition and estimated group weight of each replication are shown in Table 2.

Table 2. Group weights and caste composition of Heterotermes aureus for each replication used in wood consumption tests. Individual caste weights are means determined by drying large numbers at 60°C for 24 hr.

Caste	Caste wt, mg	Rep 1	Rep 2	Rep 2
Larva-worker[a]	0.336	99	99	98
Soldier	0.479	1	1	2
Group wt, mg		33.743	33.743	33.886

[a]Undifferentiated larvae of at least the third instar.

Five dram, snap-cap vials were filled with 10 ml of sterile, washed sand (.246 $\leq$ particle size $\leq$ .590 mm), and 4 ml of distilled water with a block of wood gently pressed into the sand. The termite groups were then immediately added. Each experimental unit was held at an assigned temperature of 16, 20, 24, 28, 32 or 36°C in a temperature cabinet adjusted to ± 1.0°C and ca. 100 percent R. H. The temperatures used in this experiment are known to be well within the foraging limits of H. aureus (LaFage, Nutting, and Haverty, 1973). Containers were examined daily with minimal disturbance to see that the groups were still active. If all termites in a group had died prior to the completion of the 28-day test, the container was placed in a freezer to prevent microbial or fungal decay of the wood. At the end of the test period the termites of each surviving group were counted,

all wood blocks were cleaned of sand, ovendried at 105°C for 24 hr and reweighed for calculating weight loss due to feeding. Wood consumption was determined in two ways: 1) by measuring the total amount of wood removed by each group of termites during the 28-day test period, regardless of survival and, 2) by calculating the amount of wood consumed per hour per gram of dry weight of termite. The latter calculation was made by dividing the amount of wood consumed per group by the number of hours survived, then dividing by the estimated dry weight of the termites in grams. If less than 28 days, number of days was multiplied by 24 to give number of hours survived.

Data Analysis

The wood consumption data were examined by an analysis of variance utilizing a randomized complete-block design with a factorial selection of treatments. The survival percentages were transformed to arc sine before analysis. Means were tested for significance at the $\alpha = .05$ level and separated using the Student-Newman-Keuls' test (Steel and Torrie, 1960). Regression equations were determined by the method of orthogonal polynomials (Little and Hills, 1972).

Simulated Wood Consumption

One of the central questions concerning the role of termites in the detritus cycle asks how much wood a termite species can consume or remove from the ecosystem per hectare per year. A simple model has been developed to answer this question through a synthesis of the supporting data from this work and from the literature. Although it

uses data from many sources, the temperature-dependent functions of termite foraging intensity and wood consumption are most critical. The model has been designed to run on mean daily temperatures (at the food-soil interface) and daily rainfall for a period of one year. Temperature and precipitation data collected on the bait sampling grid were used. The complexity of the model may be increased by basing calculations on hourly temperatures. Since the results were not significantly changed the model was run with mean temperatures to optimize computer time.

A description of the model's operation is best illustrated by a detailed outline of the logic involved:

1. For each day of a year, 24 hourly temperatures and daily rainfall are read in and a daily mean temperature calculated.
2. It is assumed that foraging is possible every day of the year provided the mean temperature does not fall below 4.0°C (see RESULTS: Environmental Control of Foraging Activity).
3. Temperature and rainfall values are fed into an equation of the following form:

   $$\ln \text{Number of Foragers} = b_0 + b_1 \text{Temp} + b_2 \ln \text{Temp} + b_3 \text{Rain}$$

   to determine the number of foragers at some instant during the day (see RESULTS: Environmental Control of Foraging Activity).
4. Since these data come from a study area of only 0.01 hectare, the number of foragers observed must be multiplied by 100 to provide an estimated foraging force per hectare.

5. The above equation does not estimate the number of termites foraging at the surface during a day, but only the number observed at a single point in time within the day. It therefore becomes necessary to determine how fast the termites above the surface might be replaced by an equal number from below. This required one major assumption: the numbers below the surface approach infinity; that is, there will always be an ample subsurface force to replace those foraging above. This assumption has necessitated the establishment of a forager "turnover rate" based on the speed at which termites travel as a function of temperature. Skaife (1961) has measured the speed (in cm/minute) of Amitermes hastatus over the range of temperatures from 10-30°C. On the assumption that H. aureus moves at the same speed, these data have been used to develop the following equation:

Speed in cm/day = (-1.47 + (1.62 x Temperature)) x 60 x 24 to calculate the distance a forager can travel (cm/day).

To complete one circuit from the underground forager pool (estimated at 2 cm below the soil surface) to the food source (the height of a toilet paper roll) and back to the pool, a termite must travel a maximum distance of 26.86 cm. Thus the number of foraging round-trips per unit time, or turnover rate, may be expressed as follows:

Turnovers/day = Speed (cm/day) / Maximum distance (cm).

6. If number of turnovers per day is multiplied by number of foragers observed at some instant during the day, the resulting number represents the total force visiting the food source during that day.
7. Forager biomass must next be calculated from the data on size and caste composition of foraging groups. Proportional caste composition of H. aureus foraging groups is as follows:

0.1044 %	larvae
97.2277 %	larva-workers
1.5717 %	soldiers
1.0962 %	nymphs

The foraging biomass is obtained by summing the products of the numbers of a caste and the average biomass per individual. Numbers are converted to biomass because wood consumption rates have been determined as a function of termite biomass, not numbers of termites.

8. Different species of wood are consumed by termites at varying rates as a result of many factors. These rates have been determined for H. aureus on four species of wood at six temperatures (see RESULTS: Wood Consumption Rates, Figures 8-12). Since termites preferentially divide their foraging attention toward different species of wood (see RESULTS: Circledrats, Table 8) it follows that foraging biomass must also be partitioned into percentages of the total which will process each of the 11 species of wood in the system. Thus

the amount of each wood species consumed is a product of a particular consumption rate times its assigned termite biomass.

9. The temperature-dependent, daily consumption of each wood species can now be summed to give a total daily wood consumption, and these figures finally summed over a year to provide the total annual amount of wood consumed by H. aureus.

RESULTS

Circledrats

Fallen Dead Wood Available to Termites and Annual Dead Wood Production

Correcting field weights of all superficial dead wood, I estimated that the standing crop biomass is 2127 kg per hectare (Table 3). Five dominant plant species (Acacia greggii, Prosopis juliflora var. velutina, Opuntia fulgida, Opuntia spinosior and Cercidium floridum) account for 97.6 percent of the biomass.

Biomass of all superficial dead wood produced annually is estimated at 450 kg per hectare (Table 4). Six plant species (the above plus Opuntia engelmannii) account for 96.4 percent of the biomass produced annually. These production figures might be somewhat high due to the exceptionally cold winter of 1971-72, which brought freezing temperatures and snow. Many peripheral joints on Opuntia fulgida and O. engelmannii froze and dropped. The weight of snow appeared to cause many large limbs of Cercidium floridum to break and fall. Two such occurrences accounted for 92.5 percent of the annual dead wood production of C. floridum. On the basis of these alone, standing crop biomass of fallen dead wood for P. juliflora and C. floridum turnsover rapidly. The annual production of each species is 44.2 and 51.5 percent of their standing crops. This would imply that the standing crops are turned over at a rate of once every 2.26 yr for

Table 3. Standing crop biomass of superficial dead wood on the I.B.P. untreated plot, Santa Rita Experimental Range, based on fifty 50-m^2 circledrats.

Wood species	$\bar{X}$ wt/circledrat ± 95% C.I.	Est kg/ha
Acacia greggii	3.162 ± 2.312	632
Prosopis juliflora	1.801 ± 1.357	360
Opuntia fulgida	1.766 ± 1.124	353
Opuntia spinosior	1.562 ± 0.533	312
Opuntia spp. joints	1.405 ± 0.746	281
Cercidium floridum	0.688 ± 1.013	138
Celtis pallida	0.087 ± 0.147	17
Opuntia engelmannii	0.051 ± 0.050	10
Ephedra trifurca	0.041 ± 0.036	8
Gutierrezia sarothrae	0.040 ± 0.060	8
Other woods	0.034 ± 0.028	7
Total	10.636 ± 2.732	2127

Table 4. Biomass of superficial dead wood produced annually on the I.B.P. untreated plot, Santa Rita Experimental Range, based on fifty 50-m^2 circledrats.

Wood species	$\bar{X}$ wt/circledrat ± 95% C.I.	Est kg/ha
Prosopis juliflora	0.796 ± 0.971	159
Opuntia fulgida	0.415 ± 0.577	83
Cercidium floridum	0.352 ± 0.496	70
Opuntia spp. joints	0.274 ± 0.143	55
Acacia greggii	0.158 ± 0.145	32
Opuntia engelmannii	0.102 ± 0.145	20
Opuntia spinosior	0.074 ± 0.078	15
Gutierrezia sarothrae	0.045 ± 0.034	9
Ephedra trifurca	0.023 ± 0.012	5
Other woods	0.007 ± 0.006	1
Celtis pallida	0.003 ± 0.004	1
Total	2.249 ± 1.194	450

P. juliflora and 1.95 yr for C. floridum. The turnover rates for the other major wood species (Opuntia fulgida, Opuntia spp. joints, Acacia greggii and O. spinosior) are much lower at once every 4.26, 5.13, 20.00 and 21.28 yr, respectively.

Foraging Group Characters

Estimates of numbers of termites and termite biomass per hectare are based on 40 foraging groups collected while sampling superficial dead wood. Selected samples of clean termites were taken from 29 foraging groups to determine mean biomass (mg) for each caste (Table 5).

Twenty six of the 50 circledrats contained 40 foraging groups of H. aureus, an average of 0.80 foraging groups per circledrat or 160 foraging groups per hectare (Table 6). Average group size was 430.74. Larva-workers (undifferentiated larvae of at least the third instar) comprised 97.2 percent of the foraging termites collected, soldiers 1.5 percent, reproductive nymphs 1.1 percent and white soldiers and larvae 0.1 percent each. Biomass figures of individual castes (Table 5) permit calculation of an average group weight of 150.96 mg. With 160 foraging groups per hectare it is estimated that there are 68,918 foragers per hectare with a biomass of 24.154 g. This biomass figure must represent only a small portion of the colony biomass since it is an instantaneous sample of the total foraging force (Bodine, 1973).

Relationship between Wood Biomass and Termite Biomass or Numbers

One of the major questions which might be asked in a study of this nature is "Does a relationship exist between the number of

Table 5. Mean biomass of castes of Heterotermes aureus based on samples from 29 foraging groups on the Santa Rita Experimental Range.

Caste	No. individuals weighed	X biomass/indiv., mg[a]
Larva	50	0.2640
Larva-worker	11,100	0.3408
Soldier	200	0.4675
White soldier	29	0.3862
Nymph	311	1.0540

[a]Biomass determined by ovendrying at 60°C for 24 hr.

Table 6. Average composition, density and biomass of 40 foraging groups of Heterotermes aureus collected on the Santa Rita Experimental Range.

Ave. groups/circledrat (50 m^2)	0.80
Ave. group composition:	
Larva-workers	418.80 (97.2%)
Soldiers	6.28 (1.5%)
Nymphs	4.73 (1.1%)
White soldiers	0.53 (0.1%)
Larvae	0.40 (0.1%)
Total	430.74
Ave. group weight, mg[a]	150.96
Est. groups/ha	160
Est. termites/ha	68,918
Est. biomass/ha, g	24.15

[a]Biomass figures based on Table 5.

termites in an area and the amount of wood available?". Correlation coefficients of superficial dead wood biomass and numbers and biomass of H. aureus are given in Table 7. Only one plant species is significantly correlated with numbers or biomass of termites. Therefore, there does not appear to be a general relationship between termite numbers or biomass and wood biomass.

Wood Preference

Table 8 lists the number of attacks or non-attacks by H. aureus on all items of each species of superficial dead wood in fifty 50-m^2 circledrats sampled on the Santa Rita Experimental Range. The probabilities of being attacked thus provide a measure of preference for these woods. The χ^2 value for wood preference is 88.04, significant at the $\alpha = 0.005$ level. With the exception of Celtis pallida, H. aureus shows strong preferences for four of the five dominant woody plants. Celtis appears to be highly preferred, but is relatively uncommon in terms of total standing crop biomass (0.8%) and total annual production of dead wood (0.2%). Although C. floridum appears to be low on the preference list here, H. aureus consumed much more of it in laboratory wood consumption tests than it did of O. fulgida, P. juliflora var. velutina or A. greggii.

Bait Sampling Grid

Seasonal Trends in Foraging

Heterotermes aureus foraged day and night throughout most of the year in the study area of the Santa Rita Experimental Range.

Table 7. Correlation coefficients of standing crop biomass of superficial dead wood, by species, and numbers and biomass of Heterotermes aureus. Based on data from fifty 50-m^2 circledrats, Santa Rita Experimental Range.

Wood species	r Termite Numbers	Biomass
Acacia greggii	-.112	-.116
Celtis pallida	-.065	-.065
Cercidium floridum	-.065	-.066
Ephedra trifurca	-.083	-.086
Gutierrezia sarothrae	.090	.089
Opuntia engelmannii	-.120	-.122
Opuntia fulgida	.017	.018
Opuntia spinosior	.393**	.399**
Opuntia spp. joints	-.209	-.210
Prosopis juliflora	-.119	-.109
Other woods	.018	.017
Total wood	-.156	-.153

**Correlation coefficient significant at the $\alpha = .01$ level.

Table 8. Number of attacks, or non-attacks, and probabilities of attack by Heterotermes aureus on all items of 11 species of wood in fifty 50-m^2 circledrats sampled on the Santa Rita Experimental Range.

Wood species	No. Attacked	No. not Attacked	Total Observations	Probability[a] of being Attacked
Celtis pallida	8	2	10	.800 a
Opuntia spinosior	92	49	141	.652 a
Opuntia fulgida	29	22	51	.569 a
Prosopis juliflora	31	44	75	.413 ab
Acacia greggii	34	50	84	.405 ab
Ferocactus wislizeni	1	2	3	.333 abc
Cercidium floridum	6	15	21	.286 abc
Opuntia engelmannii	3	8	11	.273 abc
Ephedra trifurca	5	17	22	.227 bc
Gutierrezia sarothrae	2	16	18	.111 c
O. fulgida, joints	2	31	33	.061 c
O. spinosior, joints	0	14	14	.000 c
Other woods, 4 species	1	12	13	
Totals	282	214	496	

[a]Probabilities of being attacked following by the same letter are not significantly different at the $\alpha = .05$ level by Student-Newman-Keuls' multiple range test with ∞ d.f.

Figure 1 plots the total number of foragers observed at the surface during each of 53 24-hr observation periods from October 15, 1971, to October 13, 1972. The corresponding mean temperature (at the roll-soil interface) for each observation period and the cumulative rainfall for the week preceding each period are included for reference. On only two days were no foragers observed, December 17, 1971, and January 7, 1972, when the mean temperatures were 4.8 and 9.9°C. However, foragers were observed on a day with a lower mean temperature (December 10, 1971, at 4.0°C). Wide daily temperature fluctuations are common, so that it would be difficult to establish an upper or lower foraging limit(s) based on a 24-hr mean, and probably not particularly useful.

Foraging was minimal from December through February with usually less than 2000 foragers observed during the 24-hr period. Foraging intensity increased moderately in the spring and fall and was high but erratic during the summer months.

The number of foragers generally increased with increasing temperature (mean roll-soil interface). From October through December, when the temperature was consistently below 20°C, rainfall appeared to have very little effect on increasing the number of foragers. However, during the hot summer months of June through September, even a slight amount of rain increased the number of foragers, provided the temperature did not rise above 33°C. Above 33 degrees (June 29-July 14, July 27-August 4, August 17-25, 1972), even with precipitation, foraging numbers plummeted.

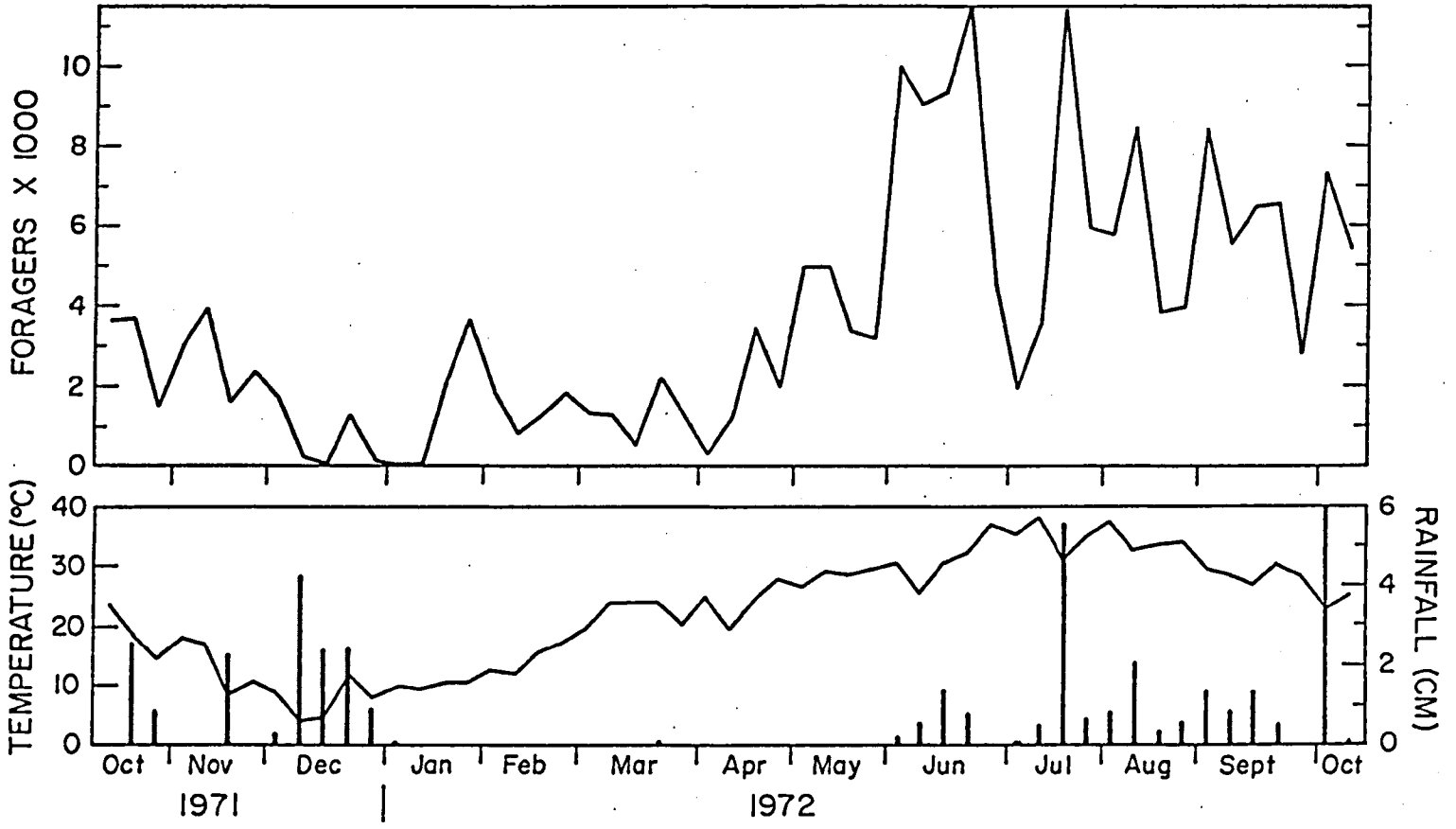

Figure 1. Seasonal foraging intensity and accompanying temperature and rainfall for bait sampling grid, Santa Rita Experimental Range. Foraging numbers represent the sum of 1200 observations each day. Temperature is the mean at the bait-soil interface over the 24-hr observation period while rainfall is a weekly total.

Environmental Control of Foraging Activity

H. aureus foraged at the rolls within a temperature range of 7.6 to 47.0°C (extremes measured in a series from under a roll down to a soil depth of 15 cm) (LaFage et al., 1973). This range apparently restricts the time which can be spent foraging. Temperature also determines foraging intensity (number of individuals at the surface per unit area).

Several equations utilizing temperature at the roll-soil interface and daily rainfall have been constructed which will predict the number of termites foraging above the soil surface (Table 9). Since all equations have similar multiple regression coefficients they were examined for C_p values (Gorman and Toman, 1966) to select the best one. Equations with C_p values larger than their corresponding p value were not chosen (equations 2, 4 and 7, Table 9) because of their bias in estimating error. The remaining are all good candidates, but the best equation must also be biologically sound. Equation 8 (Table 9) is eliminated because it does not allow for a decrease in activity once temperature passes an optimum. Equation 6, of the remaining equations, is chosen as the best equation because of its high multiple regression coefficient with only three independent variables, and low C_p/p ratio indicating a random estimate of error. This equation was used for predicting the number of H. aureus foragers at the soil surface at any given point in time.

Table 9. Equations predicting number of Heterotermes aureus foragers above the soil surface (Y) as a function of mean daily temperature at the roll-soil interface (T) and daily rainfall (R).

	Equation	p^a	$C_p{}^a$	R^b
1.	$Y = 275.278 + 8.010\ T - 2090.073/T + 291.816\ R - 2.515/R$	5	3.107	.772
2.	$Y = 116.850 + 16.323\ T + 68.772\ \ln R$	3	6.100	.731
3.	$Y = - 541.332 + 291.913\ \ln T + 274.360\ R - 2.467/R$	4	1.578	.769
4.	$Y = - 365.958 + 292.365\ \ln T + 78.870\ \ln R$	3	3.688	.746
5.	$\ln Y = 6.235 + 0.0147\ T - 17.567/T + 0.647\ R - 0.0143/R$	5	4.285	.784
6.	$\ln Y = -0.985 - 0.0761\ T + 2.928\ \ln T + 0.327\ \ln R$	4	2.656	.782
7.	$\ln Y = 0.784 + 1.580\ \ln T + 0.420\ R - 0.0126/R$	4	4.926	.770
8.	$\ln Y = 1.039 + 1.643\ \ln T + 0.282\ \ln R$	3	0.656	.771

[a] p = number of constants in an equation, $C_p = \frac{RSSp}{\hat{\sigma}^2} - (N-2p)$ where RSSp = residual sum of squares for the equation, N = number of observations and $\hat{\sigma}^2$ is the estimate of variance based on the error mean square with all variables in the equation (Gorman and Toman, 1966).

[b] Multiple regression coefficient.

Colony Foraging Territory and Density

Figure 2 illustrates the 40 x 40-m grid of toilet paper rolls where the black circles represent rolls attacked by H. aureus. This termite attacked 383 or 22.78 percent of the rolls. The distribution of the 24 complete and 13 partial (one-half) colony territories are also outlined in Figure 2. The area of these colonies averages 13.14 ± 6.71 m^2 ($\overline{X}$ ± 95% C.I.). By assuming 30.5 colonies on the study area, and extrapolating from these data, it is calculated that there would be 181.44 colonies per hectare foraging over 23.84 percent of the area. The reliability of this figure is supported by the finding of 160 foraging groups per hectare (perhaps representing individual colonies) based on their occurrence in the fifty 50 m^2 circledrats sampled.

The average, estimated number of foragers seen on the bait sampling grid was 37,800 per hectare. This is somewhat less (54.87%) than the 68,918 foragers similarly estimated by the circledrat method and may actually indicate a smaller population on the bait sampling grid. Sampling on the grid was done throughout the year over a great range in temperature, both favorable and unfavorable, whereas the natural area was sampled at times thought to be generally favorable for foraging. This might have had the effect of increasing termite foraging estimates on the natural area. On the other hand, the differences in these estimates could very well be a result of varying reliability of the sampling techniques (Sands, 1972).

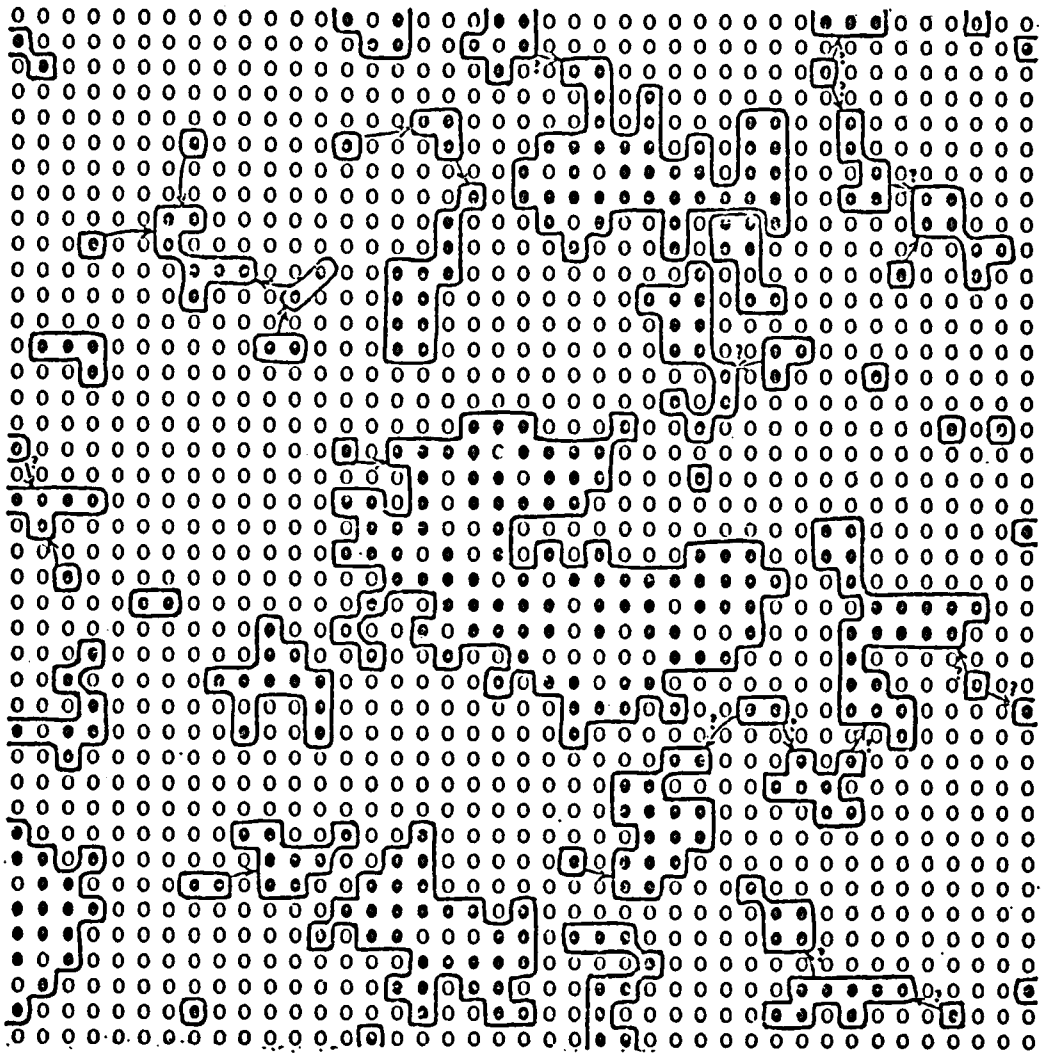

Figure 2. Foraging territory pattern and distribution for individual colonies of Heterotermes aureus on bait sampling grid, Santa Rita Experimental Range. Data provide estimates of an average 13.14 m^2/ colony and 181.4 colonies/ha.

Wood Consumption Rates

Wood consumption was measured in two ways: mg of wood consumed per group for the 28-day test period and mg of wood consumed per hour per estimated g termite biomass (per gram dry weight of termite). Differences in wood consumption, for both methods of measurement, were determined as a function of temperature and wood species.

Wood Consumption on a Group Basis

The temperature at which H. aureus consumed the most wood varied with wood species (Table 10). Maximum consumption was at 28°C on C. floridum while it was at 36°C for the other wood species and all woods combined. Although a significant difference between means of each species consumed at different temperatures was found only for C. floridum, significant response curves could be drawn for each species by the method of orthogonal polynomials (Steel and Torrie, 1960; Little and Hills, 1972). The sums of squares attributable to the linear and quadratic components of regression were removed from the treatment (temperature) sum of squares as long as they made a significant contribution at the $\alpha = .05$ level. A. greggii proved an exception to this rule in that its regression was significant only at the $\alpha = .10$ level. Response curves have been drawn on the data points separately for each species of wood (Figures 3-6) and for all woods combined (Figure 7). Except for the quadratic response curve of C. floridum, group wood consumption showed an increasing linear relationship with increasing temperature.

Table 10. Mean wood consumption (mg) and survival of groups of 100 Heterotermes aureus at six constant temperatures and on four species of wood. Duration of the test, 28 days.

Treatment	$\bar{x}$ Percent[a] Survival	C. floridum	O. fulgida	P. juliflora	A. greggii	All woods
All woods at:						
16°	26 a	105.1 b	23.5 a	21.2 a	50.9 a	50.2 c
20°	48 a	107.2 b	51.5 a	22.9 a	40.5 a	55.5 bc
24°	59 a	152.3 a	76.7 a	32.0 a	50.4 a	77.9 ab
28°	45 a	169.4 a	65.1 a	37.1 a	41.3 a	78.2 ab
32°	59 a	165.5 a	88.4 a	60.2 a	76.0 a	97.5 a
36°	56 a	145.1 ab	88.9 a	78.8 a	79.1 a	98.0 a
All temperatures on:						
C. floridum	54 a	140.8 a				
O. fulgida	59 a		65.7 b			
P. juliflora	39 a			42.0 c		
A. greggii	43 a				56.4 bc	

[a]Means in a column or diagonal followed by the same letter are not significantly different at the 5% level by Student-Newman-Keuls' Multiple Range Test.

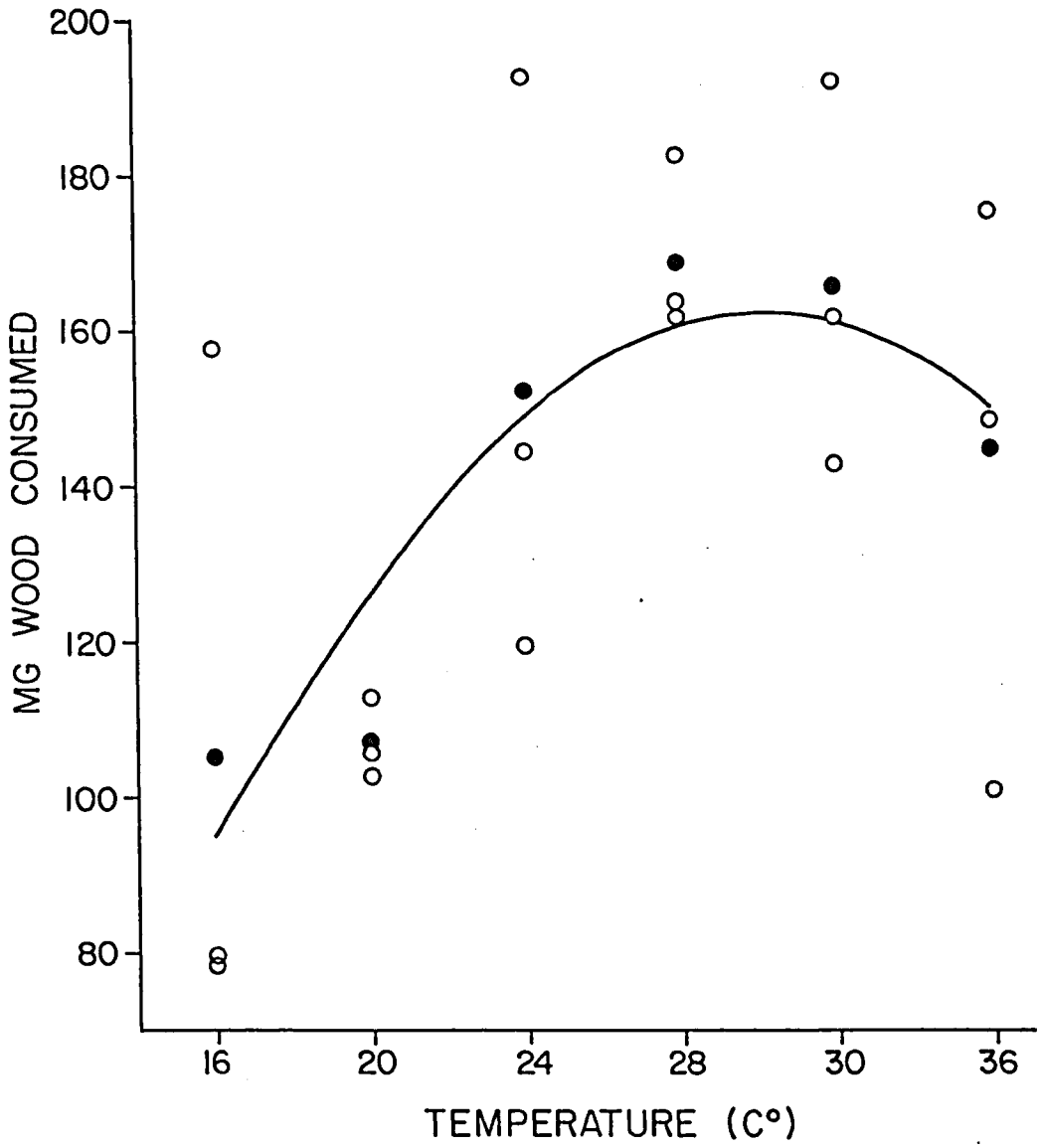

Figure 3. Mg Cercidium floridum consumed by groups of 100 Heterotermes aureus during 28-day test period at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -148.76 + 20.71 X - 0.344 X^2$, is significant at the $\alpha = .005$ level, $R^2 = .444$.

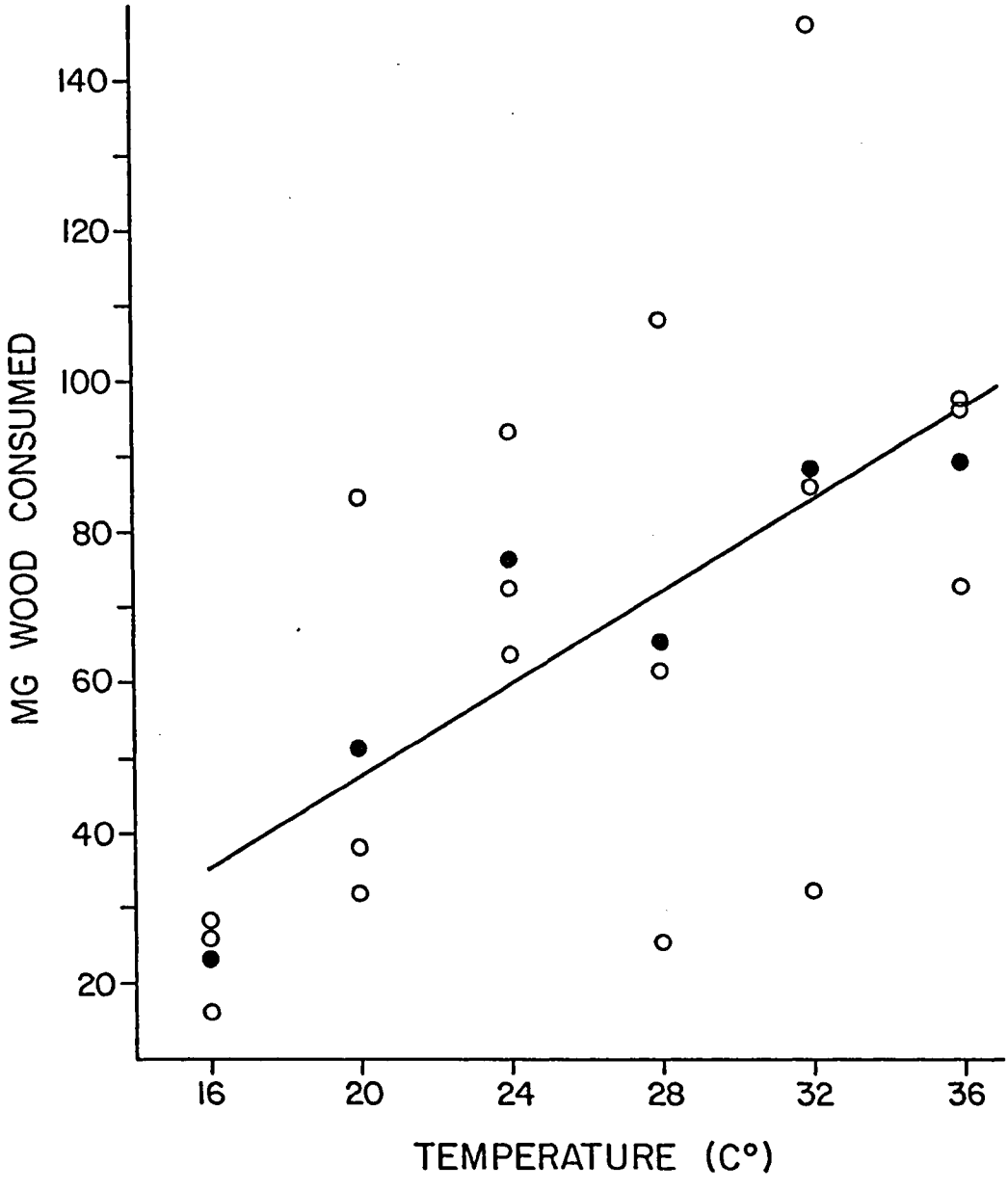

Figure 4. Mg Opuntia fulgida consumed by groups of 100 Heterotermes aureus during 28-day test period at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -13.40 + 3.40\ X$, is significant at the $\alpha = .05$ level, $r^2 = .351$.

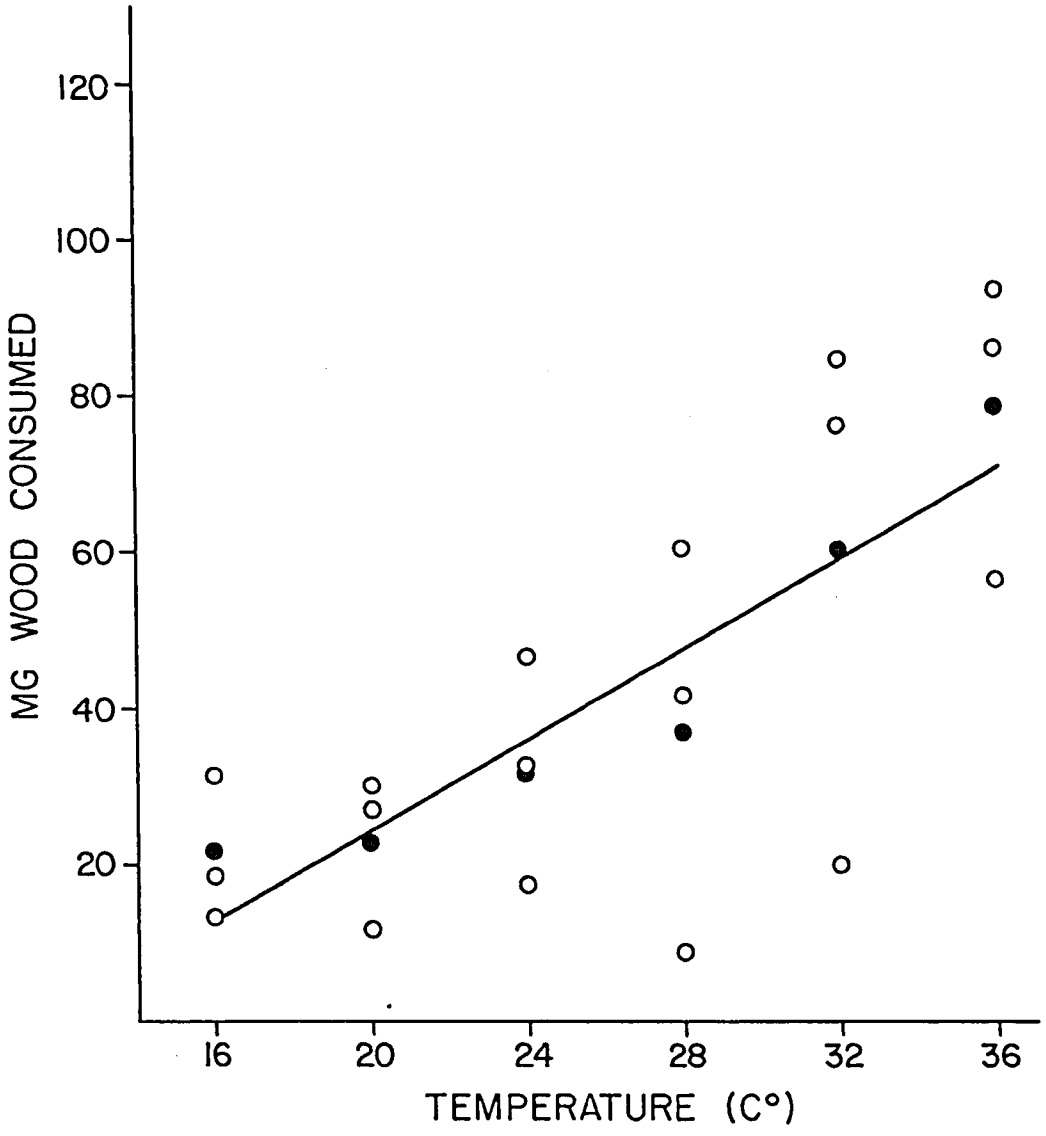

Figure 5. Mg Prosopis juliflora consumed by groups of 100 Heterotermes aureus during 28-day test period at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -33.18 + 2.89\ X$, is significant at the $\alpha = .005$ level, $r^2 = .532$.

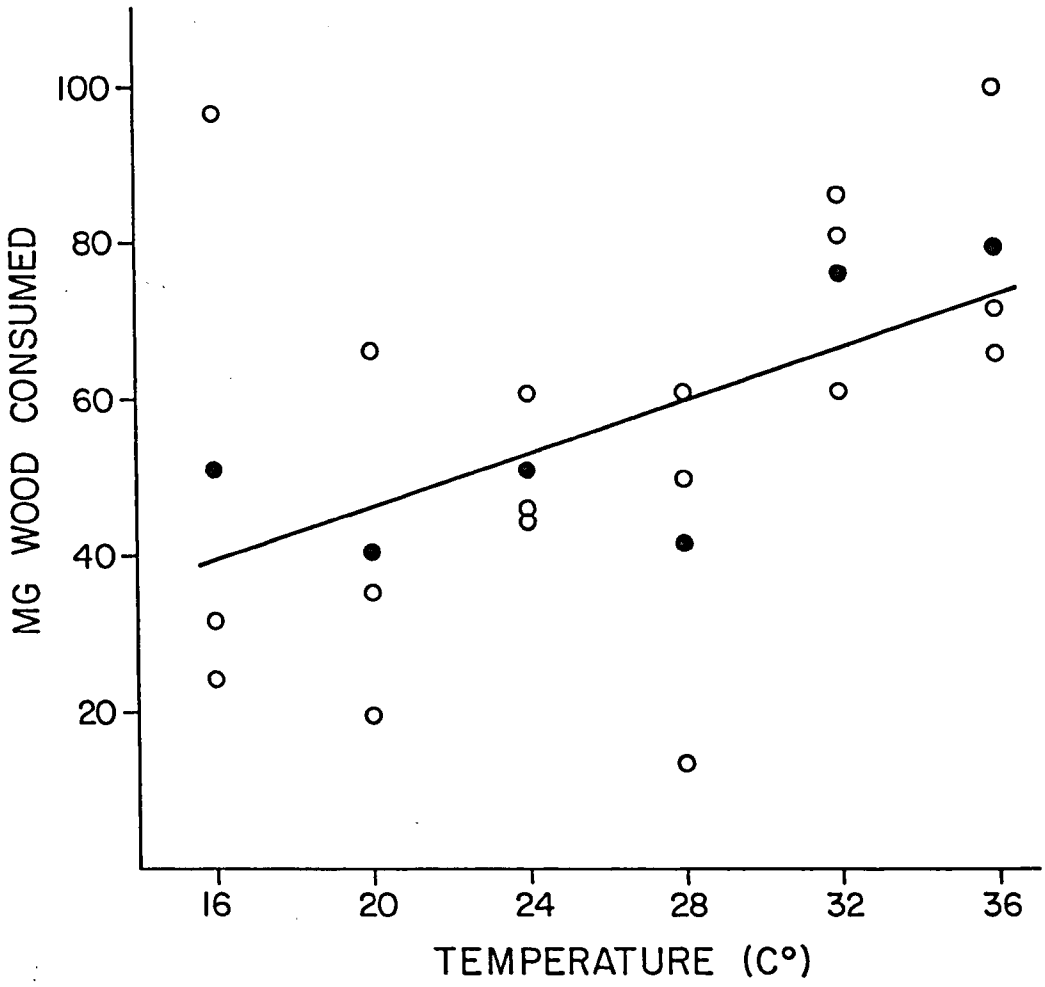

Figure 6. Mg Acacia greggii consumed by groups of 100 Heterotermes aureus during 28-day test period at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = 12.06 + 1.71 X$, is significant at the $\alpha = .10$ level, $r^2 = .220$.

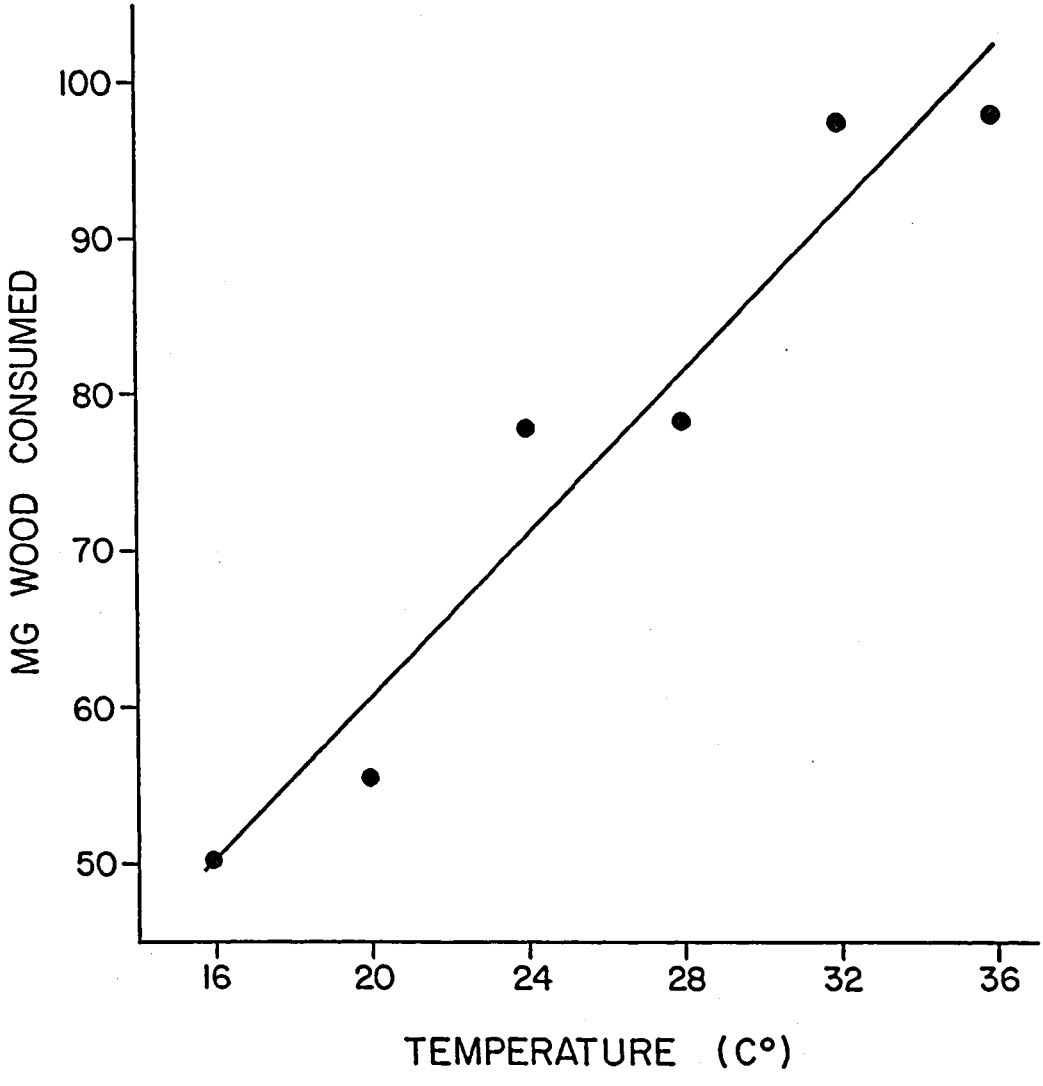

Figure 7. Mg wood (4 species combined) consumed by groups of 100 Heterotermes aureus during 28-day test period at constant temperatures. Data points are mean values for each of 6 temperatures. Regression equation, $Y = 8.37 + 2.61 X$ is significant at the $\alpha = .001$ level, $r^2 = .131$.

Wood species had a significant effect (α = .001) on wood consumption (Table 10). H. aureus was able to consume significantly more C. floridum than the other three wood species, with O. fulgida, A. greggii and P. juliflora being consumed in proportionately lesser amounts.

Survival of the termites seemed to increase with increasing temperature although no significant differences in survival were found among the termites feeding on different species of wood. However, mortality presented a problem during the course of the experiments. Active, and apparently healthy, groups occasionally died but their rather sudden demise did not seem to result from attacks by the usual mites, nematodes or fungi. Nineteen of the 72 groups of H. aureus terminated before the end of the 28-day period. Therefore, it was deemed necessary to take mortality into account in describing wood consumption.

Wood Consumption as a Function of Termite Biomass

By observing the experimental groups daily it was possible to calculate a consumption rate based on the number of hours the groups were functioning normally. Again, the temperature at which the consumption rate was greatest varied with wood species (Table 11). In all cases this temperature was either 28°C (C. floridum, O. fulgida and A. greggii) or 32°C (P. juliflora and all woods combined).

By measuring wood consumption as an hourly rate (Table 11) rather than on a group basis (Table 10), more significant differences appear between temperatures within each wood species. Significant

Table 11. Mg wood consumed/hour/termite biomass of groups of 100 Heterotermes aureus at six constant temperatures and on four species of wood. Duration of test, 28 days.

Treatment	C. floridum[a]	O. fulgida	P. juliflora	A. greggii	All woods
All woods at:					
16°	4.77 b	1.04 c	1.29 a	2.24 a	2.34 b
20°	4.72 b	2.27 bc	2.06 a	2.66 a	2.93 b
24°	6.71 a	3.68 ab	3.52 a	2.32 a	4.06 a
28°	7.46 a	5.12 a	3.83 a	3.51 a	4.98 a
32°	7.29 a	4.62 ab	5.11 a	3.35 a	5.09 a
36°	6.43 ab	3.92 ab	3.47 a	3.49 a	4.33 a
All temperatures on:					
C. floridum	6.23 a				
O. fulgida		3.44 b			
P. juliflora			3.21 b		
A. greggii				2.93 b	

[a]Means in a column or diagonal followed by the same letter are not significantly different at the 5% level by Student-Newman-Keuls' Multiple Range Test.

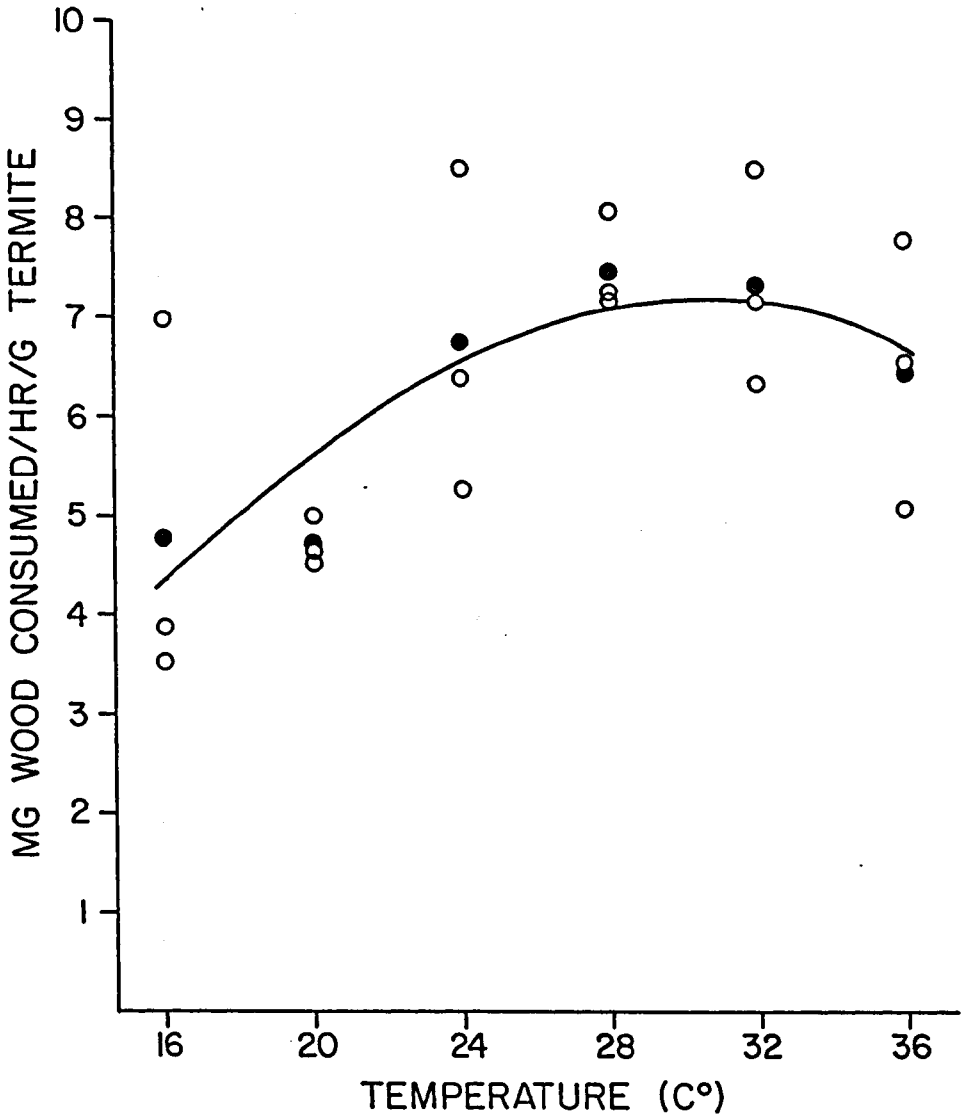

Figure 8. Mg Cercidium floridum consumed/hr/g dry wt of Heterotermes aureus at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -5.75 + 0.852\ X - 0.0141\ X^2$, is significant at the $\alpha = .005$ level, $R^2 = .431$.

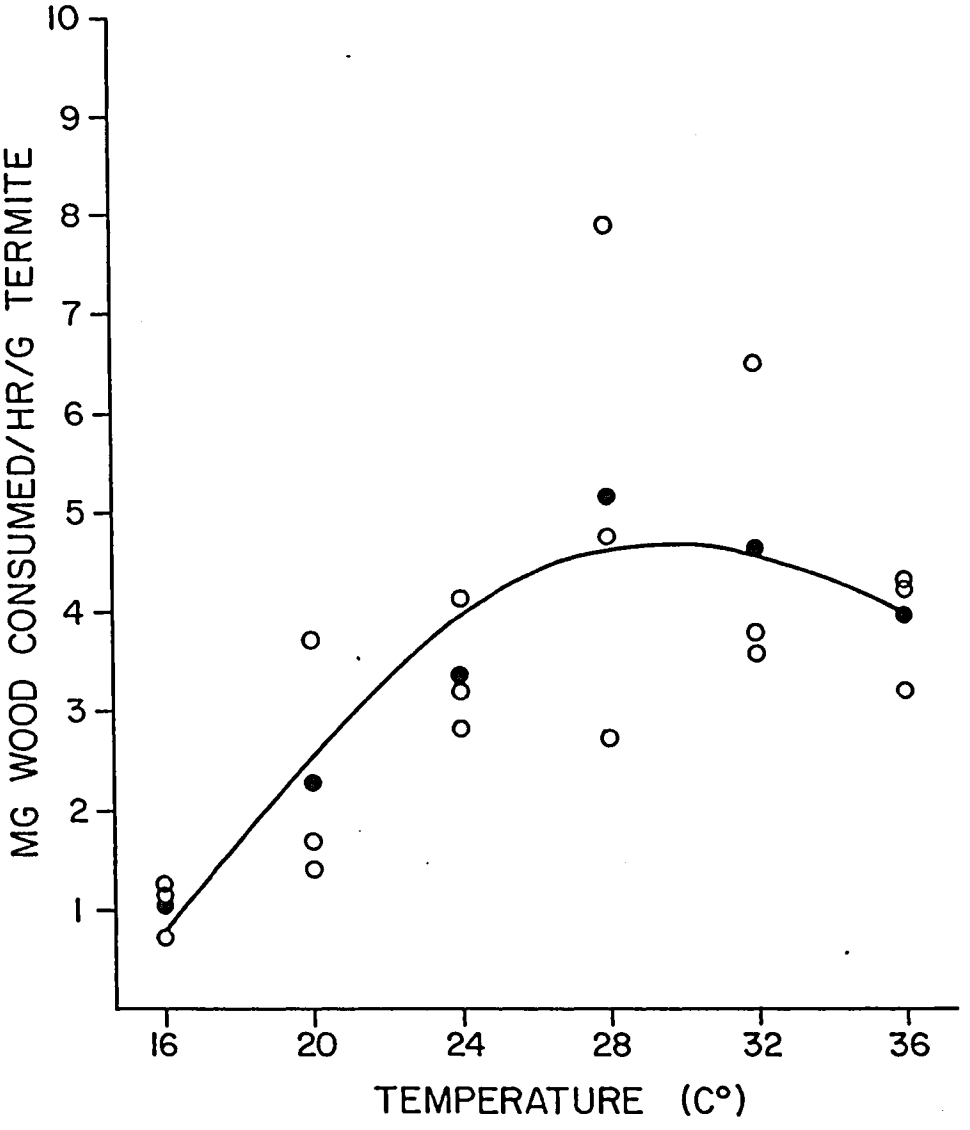

Figure 9. Mg Opuntia fulgida consumed/hr/g dry wt of Heterotermes aureus at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -12.92 + 1.165\ X - 0.0193\ X^2$, is significant at the $\alpha = .001$ level, $R^2 = .569$.

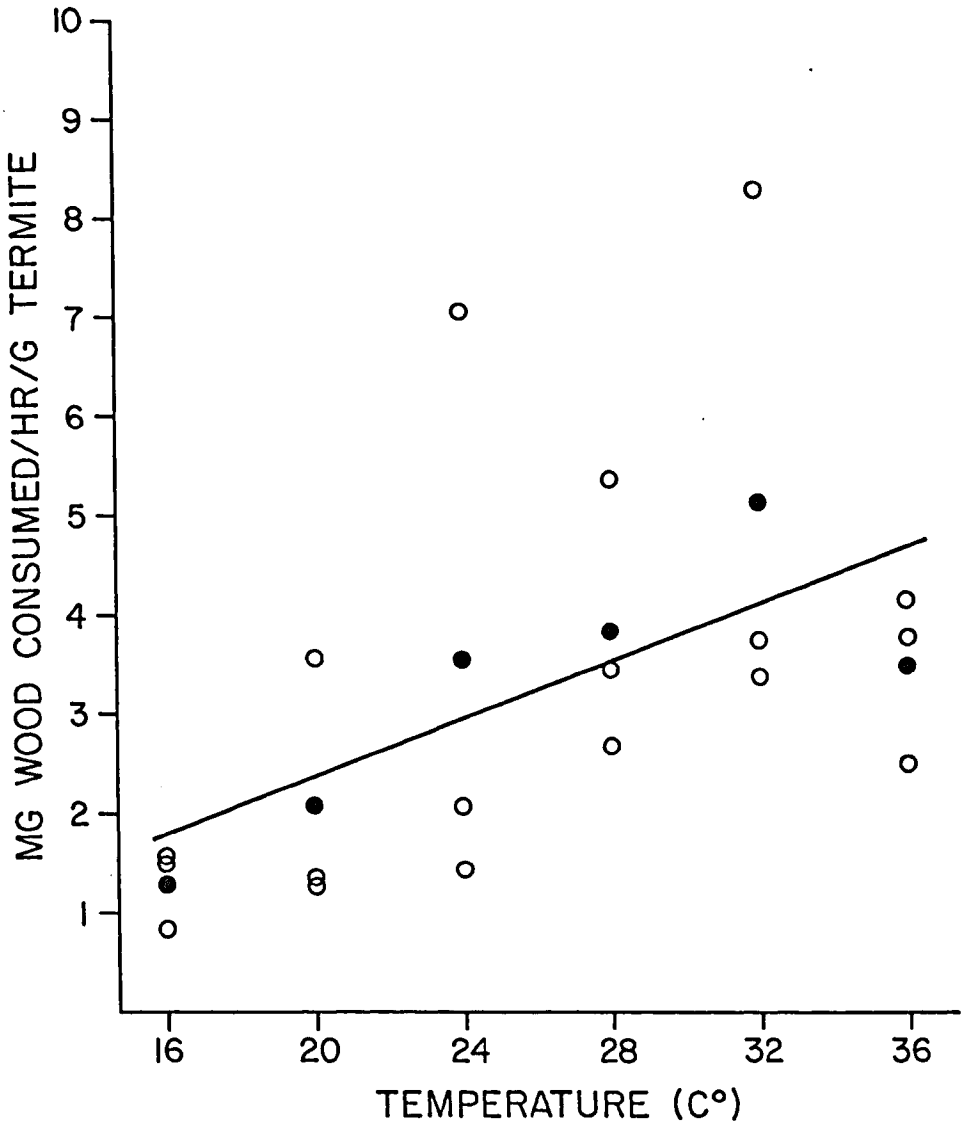

Figure 10. Mg Prosopis juliflora consumed/hr/g dry wt of Heterotermes aureus at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. Regression equation, $Y = -0.57 + 0.145\ X$, is significant at the $\alpha = .10$ level, $r^2 = .251$.

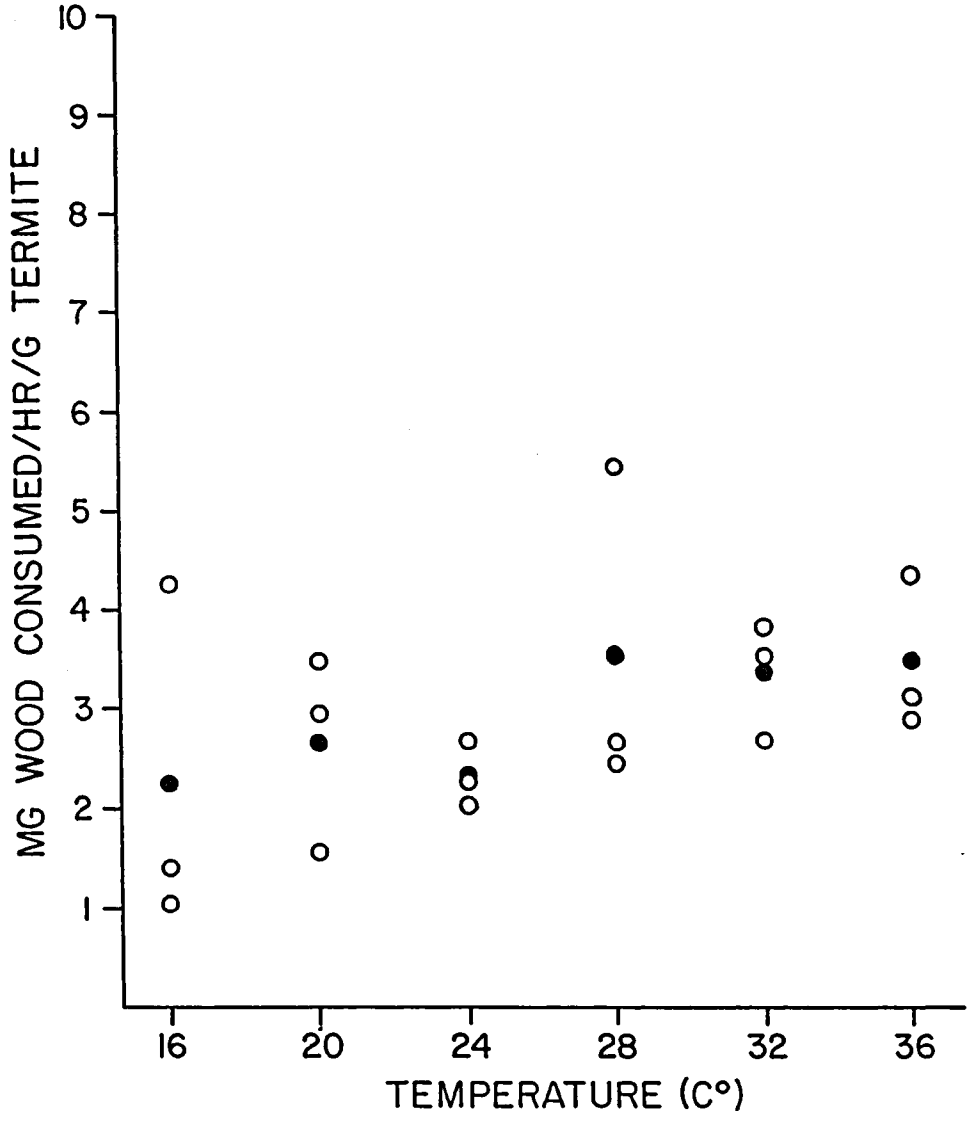

Figure 11. Mg Acacia greggii consumed/hr/g dry wt of Heterotermes aureus at constant temperatures. Open circles represent replications and solid circles mean values for each temperature. There was no significant difference between temperatures.

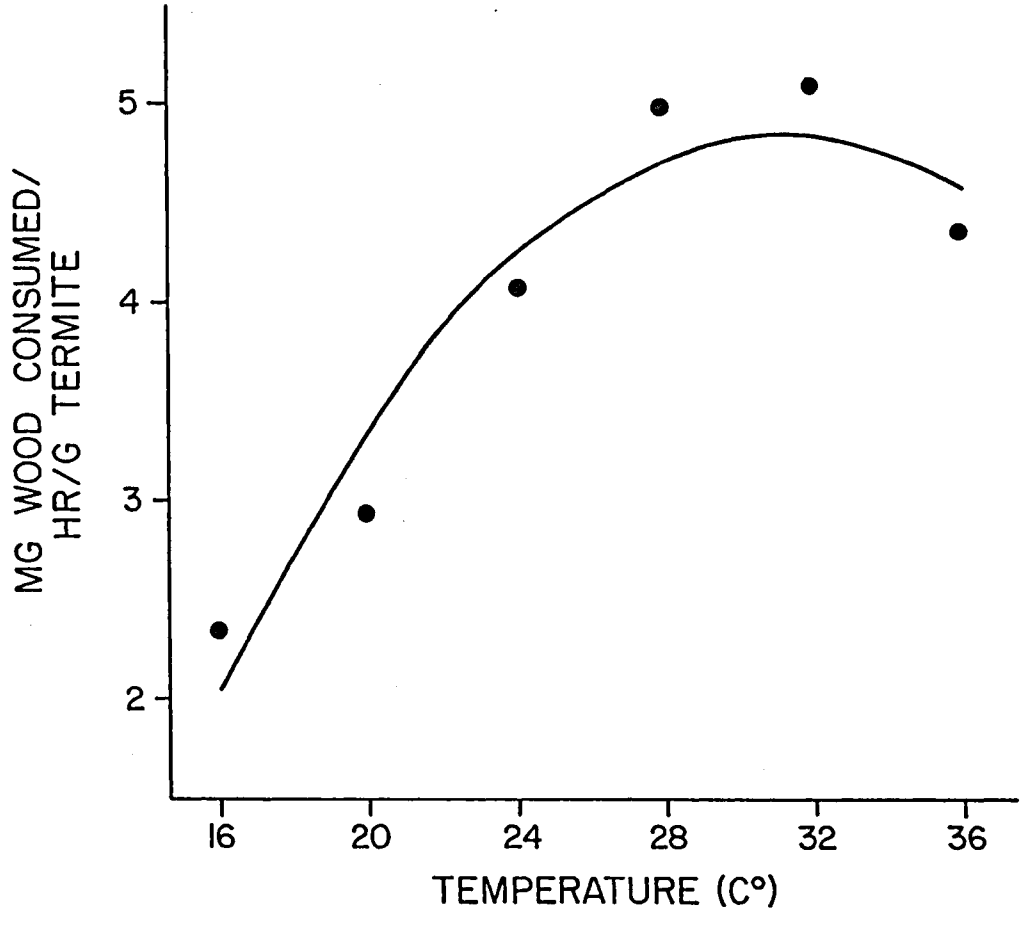

Figure 12. Mg wood (4 species combined) consumed/hr/g dry wt of Heterotermes aureus at constant temperatures. Data points represent mean values for each of 6 temperatures. Regression equation, $Y = -6.89 + 0.754\ X - 0.121\ X^2$, is significant at the $\alpha = .001$ level, $R^2 = .216$.

quadratic response curves were developed for C. floridum, O. fulgida and all woods combined (Figures 8, 9 and 12). P. juliflora showed a linear response curve ($.10 \leq \alpha \leq .05$) while A. greggii demonstrated no significant differences ($\alpha > .5$) between temperatures (Figures 10 and 11). By converting a monthly, group rate to an hourly rate as a function of biomass there was an increase in the coefficient of determination for O. fulgida and all woods combined (Figures 4 and 9, 7 and 12) while this had the effect of lowering the coefficient of determination for C. floridum and P. juliflora (Figures 3 and 8, 5 and 10).

Significant differences in hourly wood consumption were found between wood species at the $\alpha = .001$ level. C. floridum was significantly different from the three other wood species while no differences were observed between the remaining three wood species.

Simulated Wood Consumption

Predicting the amount of wood H. aureus has removed from the desert grassland by a simple computer model establishes this species as an important component of this community. Although many assumptions are made, the results and supporting evidence indicate that the assumptions are well founded.

Using equation 6, Table 9, and setting a lower limit to foraging at 4.0°C (daily mean) it is predicted that there were only seven days, all within the month of December, from October 15, 1971, to October 13, 1972, in which H. aureus did not forage. During the remainder of the year, the model predicts that this termite made 4.61×10^{10} foraging visits per hectare to the surface.

Simulated annual wood consumption for H. aureus was 78.9 kg per hectare per year, representing 3.71 percent of the total dead wood standing crop biomass and 17.54 percent of the annual dead wood production. The annual consumptions on an individual wood species basis are presented in Table 12. Of the eleven categories of wood, four species account for 83.26 percent of all wood consumed (kg/ha/yr): Opuntia spinosior (31.40), Prosopis juliflora (12.20), Acacia greggii (12.20) and Opuntia fulgida (9.89). H. aureus apparently plays an important role in removing or recycling selected species of wood. Two of the six dominant wood species were consumed by H. aureus at a rate (percent of dead wood standing crop biomass) greater than that of the over all average. Although substantial quantities of A. greggii and P. juliflora are consumed (12.2 kg/ha/yr, each) it is only a small proportion of the standing crop of each species (1.93 and 3.39 percent, respectively). The largest portion of the latter two species of wood is probably consumed by other subterranean termites: Gnathamitermes perplexus (Banks), Paraneotermes simplicicornis (Banks) and Amitermes spp.

Table 12. Simulated annual wood consumption by *Heterotermes aureus* for twelve categories of wood, and percentage of dead wood standing crop biomass consumed annually.

Wood species	Annual consumption (kg/ha/yr)	% Annual consumption of standing crop
Acacia greggii	12.20	1.93
Celtis pallida	3.43	19.71
Cercidium floridum	3.72	2.70
Ephedra trifurca	2.14	26.10
Gutierrezia sarothrae	0.86	10.75
Opuntia engelmannii	1.29	12.65
Opuntia fulgida	9.89	2.80
Opuntia spinosior	31.40	10.05
O. fulgida & *spinosior*, joints	0.86	0.31
Prosopis juliflora	12.20	3.39
Other woods	0.86	12.65
All woods, average	78.90	3.71

DISCUSSION

Termite Populations

Subterranean termites may be defined as those species that normally live in more or less diffuse nests of scattered chambers in the soil with no above ground indication of their presence in the form of a mound structure. They are difficult subjects for research and have consequently been neglected by most ecologists. The preoccupation of ecologists with mound building species is understandable since they are convenient subjects for research. The concentration of effort on the more obvious part of a community has perhaps created the impression that mound building species are ecologically more important than subterranean species, when they occur together (Sands, 1972). However, Sands concludes that subterranean species are probably the most numerous, and certainly the most significant from the economic viewpoint, in the developing countries of the topics.

The absolute density of subterranean termite populations in any particular habitat has never been estimated reliably (Lee and Wood, 1971). Relative density or intensity of foraging can be measured with baits, pits and quadrats (Sands, 1972; Lee and Wood, 1971; and Bodot, 1967a). Soil cores have been used to estimate the numbers of termites in the upper 30 cm of soil (Sands, 1972; Lee and Wood, 1971; and Bodine, 1973). However, soil core-sampling poses problems

in that subterranean termites tend to be clumped, with their distribution best described by a negative binomial (Sands, 1972). For example, during an active period, as many as 87.5 percent of the cores taken by Bodine (1973) contained no termites. Cores cannot be taken sufficiently large to overcome this problem and yet remain practical.

The number of H. aureus colonies per hectare has been estimated at 160 and 181.4 by two independent methods. Since these estimates are so close, and were taken from areas with very similar plant cover, it is assumed that they are reasonably good. There are few estimates in the literature of the number of subterranean termite colonies per unit area. Nel (1968) observed the foraging behavior of 16 colonies of Hodotermes mossambicus on a test area of 2980 m^2. Of these, 13 were wholly within the area and three were bisected by the area borders. This leaves 14.5 colonies/2980 m^2 or 48.7 colonies per hectare. Lee and Wood (1971) used Nel's data and somehow calculated 110 colonies per hectare. Their calculations are evidently in error. Any further comparisons will have to be mainly with research on mound-building termites.

Table 13 elaborates on the information given by Lee and Wood (1971) and lists most of the published records on the abundance of colonies. The densities of large mounds, which contain colonies of several millions of individuals, are usually less than 10 per hectare, while densities of the smaller mounds which contain colonies of several thousand individuals, may approach 1,000 per hectare (Lee and Wood, 1971). On this basis one might assume colonies of H. aureus

Table 13. Summary of literature records on the abundance of termite colonies per hectare.

Family and Species	Colonies/ha	Habitat and Locality	Reference
Hodotermitidae			
Anacanthotermes ahngerianus	162	Steppe, central Asia	Ghilarov, 1962
Hodotermes mossambicus	49	Veld, S. Africa	Nel, 1968
Rhinotermitidae			
Heterotermitinae			
Heterotermes aureus	160-181	Desert grassland, Arizona	Haverty, 1974
Coptotermitinae			
Coptotermes acinaciformis	5	Savanna woodland, N.T., Australia	Lee and Wood, 1971
Coptotermes lacteus	1-2	Sclerophyll forest, S. Australia	Wood and Lee, 1971
Termitidae			
Macrotermitinae			
Macrotermes bellicosus[1]	2-3	Savanna, Congo	Bouillon and Kidieri, 1964
Macrotermes natalensis[1]	4-86	Savanna, Ivory Coast	Bodot, 1964
Macrotermes spp.	3-4	Savanna, e. Africa	Hesse, 1955
Macrotermes spp.	2-3	--	Sands, 1972
Nasutitermitinae			

Table 13. Continued

Family and Species	Colonies/ha	Habitat and Locality	Reference
Nasutitermes exitiosus	4-9	Sclerophyll forest, S. Australia	Wood and Lee, 1971
N. magnus	61	Pasture, e. Australia	Wood and Lee, 1971
N. triodiae	3-7	Tree savanna, n. Australia	Wood and Lee, 1971
Trinervitermes geminatus	247-494	Savanna, Congo	Bouillon, 1969
T. geminatus[1]	59-501	grassland, woodland, W. Africa	Sands, 1965b
T. occidentalis[1]	5	grassland, woodland, W. Africa	Sands, 1965b
T. oeconomus	7-25	grassland, woodland, W. Africa	Sands, 1965b
T. togoensis[1]	2-27	grassland, woodland, W. Africa	Sands, 1965b
T. trinervius[1]	5-17	grassland, woodland, W. Africa	Sands, 1965b
T. trinervoides	534	Savanna, S. Africa	Murray, 1938
T. spp.	7-52	Savanna, Ivory Coast	Bodot, 1964
Tumulitermes hastilis	180-309	Savanna woodland, N.T., Australia	Lee and Wood, 1971
Amitermitinae			
Amitermes evuncifer	7-18	Savanna, Ivory Coast	Bodot, 1964

Table 13. Continued

Family and Species	Colonies/ha	Habitat and Locality	Reference
A. laurensis	28-210	Savanna woodland, n. Australia	Wood and Lee, 1971
A. vitiosus	196	Savanna woodland, N.T., Australia	Lee and Wood, 1971
Drepanotermes spp.	≤ 350	Semi-arid woodland, Australia	Watson and Gay, 1970
Termitinae			
Apicotermes desneuxi	238	Savanna, Congo	Bouillon, 1969
A. gurgulifex	49	Savanna, Congo	Bouillon, 1969
Cubitermes exiguus	650	Savanna, Congo	Bouillon, 1969
C. exiguus	0-652	Steppe savanna, Congo	Bouillon and Mathot, 1964
C. fungifaber	875	Steppe savanna, Congo	Bouillon and Mathot, 1964
C. sankurensis	8-550	Steppe savanna, Congo	Bouillon and Mathot, 1964
C. spp.	0-157	Savanna, Ivory Coast	Bodot, 1964

[1] Macrotermes bellicosus (as Bellicositermes bellicosus)
Macrotermes natalensis (as Bellicositermes natalensis)
Trinervitermes geminatus (as T. ebenerianus)
Trinervitermes occidentalis (as T. auriterrae)
Trinervitermes togoensis (as T. suspensus)
Trinervitermes trinervius (as T. carbonarius)

to be of medium size, perhaps 50,000 individuals, although this research can in no way validate such a figure.

Comparing the densities of colonies of different termite species from different areas is of dubious value. Even if one accepts the premise that smaller colonies are more densely distributed, different areas are quite likely to have very different termite carrying capacities. These may be modified by one or more factors such as quantity of dead wood, soil type or climate. Local, interspecific comparisons would be more worthwhile in that they express the relative importance or status of each species within a community.

Foraging Territory

The average foraging territory of H. aureus on the bait sampling grid was estimated to be 13.14 ± 6.71 m^2 which is quite small in comparison with those of other termite species. Nel (1968) measured the foraging territories of 12 colonies of Hodotermes mossambicus (Hagen) and found the mean to be 92.14 m^2. Greaves (1962) found that the foraging galleries of Coptotermes acinaciformis extended out from the mound to a maximum of 47.5 m while those of C. brunneus reached a maximum of 45.7 m. Both C. acinaciformis and C. brunneus colonies were spaced consistently at 90 m apart, each apparently controlling an area of at least 8209.8 m^2. Foraging territories of social insects, particularly those that forage for scattered food, may fluctuate but seldom overlap (Greaves, 1962) and there is often a buffer zone between them (Brian, Hibble and Stradling, 1965; Elton, 1932; Nel, 1968; and Wilson, Dillier and Markin, 1971). The colony territories

of H. aureus do not appear to overlap and neutral zones often occur between colonies. In some cases, however, colony boundaries are tangential. Since territory is dynamic, boundaries generally expanded to exploit the new, uniformly distributed food source, until apparently halted by contact with neighboring colonies. Whether or not discrete boundaries are maintained by intraspecific aggressive behavior is not known (Nel, 1968).

Interspecific overlap of foraging territory was very common between H. aureus and Gnathamitermes perplexus; their territories overlapped in 12 percent of the toilet paper rolls sampled (Nutting, Haverty and LaFage, 1973). Any aggression between these species may be avoided by their unique modes of attack on a food source. Heterotermes attacked 22.78 percent of the rolls on the 1681 m^2 grid while its foraging covered 23.84 percent of the area. Its territories occasionally included rolls which were not attacked but it is unlikely that any young colonies would be able to become established within another's territory (Greaves, 1962).

Foraging Group Size and Caste Composition

As determined by the circledrat method the average foraging group contained 430.7 individuals and was composed of 97.2 percent larva-workers, 1.5 percent soldiers, and 1.3 percent divided among nymphs, white soldiers and larvae. Nutting (1970) presented the only previous record of caste composition in a single foraging group of H. aureus in which he found 4 percent soldiers and 96 percent non-soldiers. Caste proportions in nests or foraging groups are known to

vary with time of day, season, species and colony size or age (Bodot, 1969 and 1970; Sands, 1965a; Bouillon, 1964; and Nutting, 1970). Larvae and white soldiers were seldom encountered. Nymphs were encountered only from late November through late May or early June in 27.5 percent of the foraging groups. Neither nymphs nor alates were encountered at the surface during the flight season from late June through September. Nymphs may comprise as much as 20.5 percent of a foraging group. Soldiers were encountered in 75 percent of the groups and are apparently generally included in the foraging force.

Number and Biomass of Termites per Unit Area

Estimating the number or biomass of termites per hectare is simpler with mound-building species. One need only multiply the number of colonies per hectare by the mean number of individuals or biomass per colony. Sands (1965a) estimated populations of *Trinervitermes ebenerianus* in open savanna of West Africa to be 4.94 to 12.36 x 10^6 individuals per hectare or 494 to 1235.5 per m^2. Bouillon (1969) reported densities for three species in an African savanna; *Apicotermes desneuxi* at 660/m^2, *A. gurgulifex* at 43/m^2 and *Cubitermes exiguus* at 519/m^2.

Numbers of subterranean termites per unit area are somewhat more difficult to establish. The method most often used involves taking soil cores, usually to a depth of 15 or 30 cm, and counting the termites. Lee and Wood (1971) present a summary of data from tropical Africa, South and Central America, and arid and semi-arid

regions of Australia. Total termite numbers per m^2, for all species in each area, ranged from 12 in a desert grassland steppe and a rain forest in Panama to 4450 in a Trinidad rain forest.

Bodine (1973) used soil cores to measure the density of Gnathamitermes tubiformans in the upper 30 cm of soil in a semi-arid grassland in Texas. From February through November the mean was 4135 termites per m^2, which approached the highest termite density ever recorded (4450/m^2) for all species of termites. From May through July the subsurface density was 3796.7 per m^2 while the surface population numbered 33.3 per m^2 -- only 0.877 percent of the measured population.

Bodine's figures provide a starting point for some speculation about the size of a colony of H. aureus, a figure which has so far defied measurement. Figured on the basis of one instantaneous count of foragers for each of 53 days during one year on the bait sampling grid, the average Heterotermes foraging force was 37,800 per hectare or 3.78 per m^2. Figured on the basis of 40 foraging groups counted during 13 months of circledrat sampling, the average foraging force was estimated at 68,918 per hectare or 6.89 per m^2. If we assume that surface and subsurface proportions for H. aureus and G. tubiformans are the same we can then estimate that the subsurface numbers of H. aureus range from 4.31 to 7.86 x 10^6 per hectare or 431 to 786 per m^2 with a biomass of 1.45 to 2.64 kg per hectare or 0.145 to 0.264 g per m^2.

Further calculation leads us to estimates of the number of individuals per colony. On the bait sampling grid there were an

estimated 181.44 colonies per hectare. Our new figure of 4.31×10^6 termites per hectare divided by colonies per hectare gives us 23,754 termites per colony. On the same basis, the new figure of 7.86×10^6 termites per hectare divided by the circledrat estimate of 160 colonies per hectare, gives 49,125 termites per colony. These figures are wholly speculative and have not in any way been validated by this research.

Wood Available and Termite Numbers

With two exceptions no one has attempted to measure the amount of material available to a species or community of termites. Lee and Wood (1971) measured annual litter fall in a dry sclerophyll forest in Australia and found that, of the total 2300 kg per hectare, 30.4 percent or 700 kg was logs and sticks. The standing crop biomass of litter in this same area was 7338 kg per hectare (Lee and Wood, 1968). Assuming the same percentage of sticks and logs to total litter their study area would have a dead wood standing crop biomass of 2230.75 kg per hectare. Their dry sclerophyll forest is apparently very similar in its standing crop biomass and annual production biomass of dead wood (2230.75 and 700 kg/ha) to that of the desert grassland of the Santa Rita Experimental Range (2127 and 450 kg/ha). A comparison of the impact of Nasutitermes exitiosus, a sound dead-wood feeder in the sclerophyll forest, and that of Heterotermes aureus on the desert grassland will be made in the discussion of simulated wood consumption.

Wood Consumption

The factors affecting wood consumption by termites are numerous and often complexly interrelated. Among the most important of these are wood species and hardness, presence or absence of toxic substances, feeding inhibitors or deterrents, presence or absence of fungi and degree of fungal decay, moisture content of wood and soil, and temperature. Other factors not often mentioned in the literature but nonetheless important are colony nutrition and time of year (Smythe and Esenther, 1973). Becker (1969) has recently reviewed the role of temperature and other variables in connection with laboratory rearing of termites for testing purposes.

Wood consumption is usually measured by the reduction in weight of the test material. It has been expressed in a variety of ways: percent weight loss (Behr, Behr and Wilson, 1972; DaCosta and Gay, 1966) or weight loss of the wood over the consumption period with a given number of termites (Becker, 1962; Smythe, 1972; Smythe and Carter, 1969 and 1970; Smythe and Mauldin, 1972; Smythe, Carter and Baxter, 1971); and weight of wood consumed per unit weight of termite per unit time.

This last measure of wood consumption has been modified by various authors. Gay et al. (1955) used a given live weight of termites (25g) over a long period (4-12 weeks) and reported their total consumption. Becker (1967) used a given number of termites and expressed their consumption as mg wood consumed over the test period per gram live termite. Haverty and Nutting (1974) reported wood

consumption similarly as mg wood consumed per g termite dry weight per hour. A further refinement averages initial and final termite weight and expresses wood consumption as mg wood consumed per gram live termite per day (Hrdý and Zelený, 1967; Bodine, 1973).

This was not used because it assumes the decrease from initial to final weight to be linear. In the H. aureus wood consumption tests 26 percent of the experimental units, which terminated early, were apparently healthy when the entire group suddenly died. To average the termite biomass in this situation would be incorrect because the decrease was definitely not linear.

For modeling purposes a rate in the form of mg wood consumed per gram termite dry weight per hour or day is essential. Measuring consumption as percent of wood removed is not of much ecological value; however, wood weight loss can be converted to a useful rate if termite weight and test duration are known.

Comparing results of these wood consumption studies directly with those of other authors is impossible because they are expressed in so many different forms. Table 14 reduces the results of most of the important studies to a common rate. These range from a low of 2.0 to a high of 90.8 mg consumed per g of termite live weight per day. That is, termites may consume from 0.2 to 9.1 percent of their body weight per day. This is significantly higher than the 1.0 ± 0.4 percent dry body weight consumed per day by soil surface-feeding saprophages in an eastern deciduous forest (McBrayer and Reichle, 1971).

Table 14. Summary of literature reports of wood consumption rate as mg wood consumed/g live termite/day. Consumption rates determined at 26°C unless otherwise noted.

Family and Species	Wood Species	Termite Live wt.	Consumption[9] mg/g/day	Reference
Mastotermitidae				
Mastotermes darwiniensis	*Eucalyptus regnans*	41.67	11.47	Gay, et al., 1955
Kalotermitidae				
Cryptotermes cavifrons	lime and pine	4.10	16.0 a	Hrdý and Zelený, 1967
C. dudleyi	avg of many spp.	5.52	28.6	Becker, 1967
Kalotermes flavicollis	avg of many spp.	12.93	26.8[7]	Becker, 1967
K. flavicollis	avg of many spp.	12.93	64.3[7]	Becker, 1967
K. flavicollis	pine (sap & heart wood)	7.00	24.3	Seifert, 1962
Neotermes castaneus	lime and pine	17.47	31.0 a	Hrdý and Zelený, 1967
N. jouteli[8]	lime and pine	11.36	22.0 a	Hrdý and Zelený, 1967
Paraneotermes simplicicornis	avg of 3 spp.	7.38[10]	45.7	Haverty and Nutting, 1974
Hodotermitidae				
Zootermopsis angusticollis	avg of many spp.	70.70	10.1	Becker, 1967
Rhinotermitidae				
Rhinotermitinae				
Prorhinotermes simplex	lime and pine	3.28	8.0 a	Hrdý and Zelený, 1967

Table 14. Summary of literature reports of wood consumption rate as mg wood consumed/g live termite/day. Consumption rates determined at 26°C unless otherwise noted, continued.

Family and Species	Wood Species	Termite Live wt.	Consumption[9] mg/g/day	Reference
Coptotermitinae				
Coptotermes acinaciformis	*Eucalyptus regnans*	3.64	17.8	Gay, et al., 1955
C. amanii	avg of many spp.	2.76[4]	26.8	Becker, 1967
C. formosanus	*Pinus elliottii* var. *elliottii*	3.79[1]	23.4 b	Smythe and Carter, 1970
C. lacteus	*Eucalyptus regnans*	3.70	12.2	Gay, et al., 1955
Heterotermitinae				
Heterotermes aureus	avg of 4 spp.	1.89	19.0[2]	Haverty and Nutting, 1974
H. aureus	*Cercidium floridum*	1.89	28.8[2]	Haverty and Nutting, 1974
H. indicola	*Pinus sylvestris*	1.89[3]	14.0	Becker, 1962
H. indicola	*Fagus sylvaticus*	1.89[3]	81.2	Becker, 1962
H. indicola	*Pycnanthus angolensis*	1.89[3]	90.8	Becker, 1962
H. indicola	*Nauclea trillesii*	1.89[3]	13.0	Becker, 1962
H. indicola (30° stock)	avg of many spp.	1.89[3]	58.9	Becker, 1967
H. indicola (26° stock)	avg of many spp.	1.89[3]	28.6	Becker, 1967
Reticulitermes flavipes	*Pinus elliottii* var. *elliottii*	2.52[1]	33.2 b	Smythe and Carter, 1970
R. lucifugus santonensis[8] (30° stock)	avg of many spp.	2.76[4]	20.4	Becker, 1967
R. lucifugus santonensis (26° stock)	avg of many spp.	2.76[4]	19.3	Becker, 1967

Table 14. Summary of literature reports of wood consumption rate as mg wood consumed/g live termite/day. Consumption rates determined at 26°C unless otherwise noted, continued.

Family and Species	Wood Species	Termite Live wt.	Consumption[9] mg/g/day	Reference
R. virginicus	*Pinus elliottii* var. *elliottii*	2.45[1]	25.9 a	Smythe, 1972
R. virginicus	*Pinus elliottii* var. *elliottii*	2.45[1]	20.0 b	Smythe and Carter, 1970
Termitidae				
Termitinae				
Gnathamitermes tubiformans	*Buchloe dactyloides* (Buffalo grass)	2.44	23.8 c	Bodine, 1973
Nasutitermitinae				
Nasutitermes costalis	lime and pine	2.09	2.0 a	Hrdý and Zelený, 1967
N. exitiosus	*Eucalyptus regnans*	4.76	12.2	Gay et al., 1955
N. exitiosus	*Eucalyptus obliqua*	5.00	10.6	Lee and Wood, 1971
N. rippertii	lime and pine	5.39	9.0 a	Hrdý and Zelený, 1967

[1] Personal communication from R. V. Smythe.

[2] Consumption rate of mg wood (dry)/g live termite/day determined by dividing rate of mg wood (dry)/g dry termite/day by ratio of termite live wt:dry wt.

[3] Live wt calculated from known dry wt which is the same as *H. aureus*.

Table 14. Summary of literature reports of wood consumption rate as mg wood consumed/g live termite/ day. Consumption rates determined at 26°C unless otherwise noted, continued.

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[4] Estimated live wt is the avg of live wts given for *Reticulitermes* spp. by Collins (1969).

[5] Estimated live wt is the avg of live wts given for *Calotermes* spp. by Collins (1969).

[6] Estimated live wt is the avg of live wt given for *Zootermopsis angusticollis* by Collins (1969).

[7] 26.80 = avg wood consumption, 64.30 = best wood consumption.

[8] *Neotermes jouteli* (as *Kalotermes jouteli*), *Reticulitermes lucifugus santonensis* (as *R. santonensis*).

[9] Consumption rates followed by a letter determined at a temperature other than 26°C: a = 25, b = 26-27, c = 28°C.

[10] Average of all castes.

My own studies and those summarized in Table 14 emphasize the importance of the effects of wood species and temperature on wood consumption. Specific differences in wood hardness have been mentioned by Behr et al. (1972) and in extractives by Carter and Smythe (1972). The fact that H. aureus consumed over twice as much Cercidium floridum as Acacia greggii is difficult to understand, but could be related to either hardness or extractives. However, such results are not uncommon, since Becker (1962) found that wood consumption by H. indicola varied as much as sevenfold (Table 14). These statistically significant differences in the effect of wood species on consumption do not necessarily represent preferences since these were all compulsory feeding experiments. Wood preferences will be discussed below.

Becker (1969) showed that the amount of wood eaten by six species of termites in three families increased linearly to an optimum temperature (30-34°C), then decreased rapidly between 32 and 36°C. Smythe and Williams (1972) and Smythe (1972), working with Reticulitermes flavipes and R. virginicus, reported increased consumption up to 30 or 31.5°C with a rapid decline thereafter. With H. aureus the effect of temperature on consumption was similar to the above examples except that at the higher temperatures consumption decreased gradually or not at all, regardless of the manner of expressing wood consumption. When wood consumption for all wood species was measured as a rate with respect to termite biomass, the data could be fitted to a quadratic curve with optimal consumption occurring at 31.16°C.

Heterotermes aureus and H. indicola are similar in their response to temperature (Becker, 1962 and 1967). H. indicola has a slightly higher optimal consumption temperature (33°C) than H. aureus (31°C) and both survive well between 32 and 36°C. Their survival below 20°C is reduced and this may be due to the selective defaunation of cold sensitive hindgut flagellates as has been demonstrated for Coptotermes formosanus Shiraki (Mannesmann, 1972).

Wood Preference

In essentially a choice situation the frequency of attack on different species of wood in the field has given an ordering of wood species perference. The wood of the chollas, Opuntia spinosior and O. fulgida, has a higher probability of attack than mesquite, catclaw acacia and especially palo verde, Cercidium floridum. The probability of attack of C. floridum by H. aureus, and consequently its preference rating, are extremely low. This is in sharp contrast to its high rate of consumption in laboratory tests. Some woods are definitely not preferred (joints of O. fulgida and O. spinosior, Gutierrezia sarothrae and Ephedra trifurca) although their probabilities of attack are not significantly different from that of C. floridum.

Other workers have used differences in wood consumption rates in compulsory and choice feeding experiments as a measure of wood preference. Smythe and Carter (1970) found preferences the same whether compulsory or choice feeding tests were used. McMahan (1966) determined wood species preference by measuring the quantity of wood removed. This technique would lead to erroneous conclusions with

H. aureus, because Cercidium floridum would have appeared to be the most preferred wood.

In the course of the field work, H. aureus has been recorded as feeding on almost all woods but rarely on grass or dung. This corroborates the finding of Ferrar and Watson (1970), that Australian species of Heterotermes are seldom found in dried dung.

Physical Factors Affecting Foraging

Seasonal fluctuations in termite foraging activity have been reported for several African species (Bodot, 1967b; Bouillon. 1970) and for a temperate rangeland species (Bodine, 1973). Although some authors feel it is difficult to distinguish between endogenous and exogenous control, temperature and moisture (or evaporation) are most often the environmental parameters responsible for these fluctuations.

Bodot (1967b) investigated the seasonal foraging cycles of three species in an African savanna: Trinervitermes trinervius (Rambur), Ancistrotermes cavithorax (Sjöstedt) and Macrotermes natalensis (Haviland). She found these major trends for each species: 1) foraging is continuous throughout the year with seasonal fluctuations in intensity, 2) foraging activity increases during the short rainy season, and 3) foraging decreases at the initiation of the long dry season. The environmental parameters most highly correlated with increased foraging activity differ according to each species' foraging behavior. T. trinervius harvests grass on the open soil surface and displays a negative correlation with mean maximum temperature and

evaporation while having a positive correlation with mean minimum relative humidity. Temperature is limiting at its higher values while humidity is limiting at its lower values. A. cavithorax attacks dead wood and live vegetation by covering them with a shield of soil. Its activity shows no correlation with temperature but is positively correlated with rainfall and negatively with evaporation. With M. natalensis neither rainfall nor relative humidity has any effect on foraging. The key stimulus is increasing temperature, which increases foraging activity.

Bodine (1973) studied the activity of Gnathamitermes tubiformans on a temperate grassland where temperatures vary considerably more than in the tropical savanna. He found that surface foraging activities were most highly correlated with the temperature at 45 cm in the soil. On the basis of an equation containing soil temperature at 45 cm, air temperature, and soil moisture at 45-60 cm, he claimed to account for nearly 100 percent of the variability in explaining numbers of termites at the soil surface. In his regression equation soil temperature has a positive coefficient whereas air temperature and soil moisture have negative coefficients. This implies that increased soil moisture has the effect of reducing foraging populations. This is the only study seen thus far which makes this conclusion. Bouillon (1970) considers moisture to be of the utmost importance in determining diurnal foraging cycles of tropical termites. Any weakness in Bodine's attempt to explain the control of foraging activity is probably due to insufficient data -- a short sampling

period involving only three data points (May through July, 1972) with 40 replications per point.

The results presented in this study agree with the general conclusions of Bodot (1967b) in that 1) foraging was continuous throughout the year, when temperature extremes permitted, 2) foraging was increased during the summer rainy season and 3) foraging was reduced during a long dry period. Although it is possible that these observed seasonal fluctuations were due to endogenous rhythms (Bouillon, 1970), they seem more likely to be under the primary control of temperature and rainfall. This view is supported by highly significant regressions of activity with these two factors.

After an initial screening of temperatures at various locations in, on and above the soil, it was determined by linear correlation and curvilinear regression that the temperature at the roll-soil interface would be the most useful temperature in predicting the number of foragers at the food source. The temperatures in this location are probably not controlling the initiation and cessation of foraging activities; these appear to be temperature extremes measured from the roll-soil interface to 15 cm in the soil (LaFage et al., 1973 and Nutting et al., 1973).

Equation 6 of Table 9 best describes the relationship of foraging intensity with temperature and rainfall. At lower and medium range temperatures foraging numbers increase logarithmically with increasing temperature, but this effect is dampened at higher temperatures. Similar relationships have been found between time and cattle

lactation (Wood, 1967) and time and poultry egg production (McNally, 1971). DeBruyn and DeBruin (1972) reported a quadratic relationship between ground level temperatures and number of Formica polyctena Först on a foraging path. Finnegan (1973) reported an increase in foraging activity with increasing temperature for three species of Formica in Quebec.

Rainfall, with associated increases in soil moisture and humidity and decrease in saturation deficit, accentuated the increase in foraging numbers of H. aureus. In contrast, ants with a more heavily sclerotized cuticle, are less dependent on a low saturation deficit (Nielsen, 1972; Finnegan, 1973) than are termites (Bouillon, 1970; Bodot, 1967b).

Notwithstanding the obvious environmental parameters, internal colony pressures may also affect foraging. Bouillon (1970) found that the seasonal foraging cycle is also related to an annual cycle of the number of individuals in the society, its division into the different castes, and of the rate of its total food consumption, which is continuous throughout the year. Bodot (1967b) found that foraging increased with the appearance of reproductive nymphs in a colony and decreased after the imaginal molt. With H. aureus any influence of colony nutrition or alate production was not obvious. During the period when nymphs were present (late November through early June) foraging was not particularly intense even though temperatures were very favorable to foraging. This may have been a result of an extremely dry winter from January on. The reduction in winter

foraging may also have accounted for a rather poor production of alates during the 1972 flight season (Nutting and Haverty, 1974).

Simulated Wood Consumption

Two of the most important features in the simple wood consumption model are number of foragers visiting the surface per unit time and the species specific wood consumption rates. The number of termite foragers attacking a food source per unit time has been given as the product of two temperature dependent functions: the foraging force above the surface and the rate at which this force is turned over. DeBruyn and DeBruin (1972) use the same type of logic in developing a model to determine the number of Formica polyctena captured in pitfall traps. This number is the product of the two factors: the number of ants present at a given temperature (P_t) and their velocity at this temperature (V_t): $N_t = (P_t)\ (V_t)$.

The estimation made here of annual wood consumption by H. aureus is of a reasonable order of magnitude and considerably less than the annual accumulation. However, certain parameters used in the model are probably contributing to the over- or under-estimation of consumption, and should be refined.

Foraging population estimates are good since they were checked against actual counts, and their relationships with environmental factors are quite good (Table 9). However, the velocity function does not account for worker inefficiency. Social insects spend a good deal of their time idle (Wilson, 1971). These considerations might easily cause over-estimation of forager turnover rate.

Laboratory wood consumption rates are probably lower than the field rates. This is because the termites in the test groups have no nest mates to feed. Since they do not appear to store wood, they consume only what they need for themselves. Therefore, the over-estimation of wood consumption due to an excessive turnover rate tends to balance the under-estimation caused by low consumption rates.

Termites may have a considerable role in the removal and recycling of plant material in an ecosystem. Basson (1972) conservatively estimated that Hodotermes mossambicus removed 274 kg per hectare per year from veld in South Africa. Nel (1970), in a different area, calculated the same species to remove only 14.6 kg per hectare per year or one percent of the total production of dry material. Bodine (1973) estimated that G. tubiformans removed 360 kg of grass per hectare per year or 12 percent of the net primary productivity. Lee and Wood (1971) estimated that Nasutitermes exitiosus, which feeds on sound wood, consumed 116 kg per hectare per year or 16.6 percent of the annual production of wood. The effect of termite grazing can be so great that whole areas are denuded of grass (Coaton, 1951; Watson and Gay, 1970).

The effect of H. aureus on the fallen dead wood on the Santa Rita Experimental Range is comparable to that of N. exitiosus in a dry sclerophyll forest in Australia. Heterotermes removes 78.9 kg per hectare per year, which represents 3.71 percent of the superficial dead wood standing crop biomass and 17.54 percent of the annual dead wood production. Its impact on wood recycling is greatest

in its selective pressures exerted on different species of wood.

Heterotermes aureus is only one of four important soil dwelling termites on the Santa Rita Experimental Range. The other three species appear to have host preferences (Acacia and grasses for example) which complement those of H. aureus.

Other factors which might play an important role in reducing superficial dead wood biomass are fungi and other micro-organisms and sunlight. Under suitable moisture and temperature conditions fungi (Ascomycetes and Fungi Imperfecti) can reduce the weight of wood by 20 percent in 16 weeks (Becker, 1967). Sunlight alone has been shown to reduce the weight of Pinus ponderosa dowels from 0.7 to 1.64 percent per year in northern Idaho, depending on dowel diameter (Campbell, 1952). Since fungal action is heavily dependent on moisture as well as temperature it probably plays a limited role in wood breakdown in this desert grassland. Sunlight might be expected to play a more important role here in reducing dead wood biomass than in northern Idaho.

Heterotermes aureus is one of four abundant subterranean termites on the Santa Rita Experimental Range and it consumes a considerable portion of the dead wood produced annually. It feeds heavily on certain species of wood and complements the food preferences of the other three species. Termite micro-organisms have recently been shown to fix atmospheric nitrogen (Breznak et al., 1973; Benemann, 1973). Along with other termites and fungi, H. aureus functions to

increase fertility of the soil by the addition of available nitrogen compounds synthesized concurrently with the process of cellulose degradation. Therefore, Heterotermes aureus has been shown to be a more important component of the desert grassland ecosystem than previously imagined.

SUMMARY

Field and laboratory experiments were carried out to evaluate the efficiency of Heterotermes aureus (Snyder) as a detritivore in a desert grassland ecosystem. The following parameters were examined: 1) size and dispersion of foraging populations, 2) production and availability of wood, 3) wood consumption rates as a function of temperature and wood species, 4) wood preference and 5) environmental control of termite foraging activity.

Foraging groups or colonies were estimated at 160 and 181 per hectare with an average of 68,918 and 37,800 foraging termites per hectare at any given moment during the year of study. Average colony foraging territory was 13.14 m^2. Foraging groups of termites consisted of 97.2 percent larva-workers, 1.5 percent soldiers and 1.3 percent nymphs, larvae and pre-soldiers. The numbers or biomass of termites was generally not correlated with the amount of wood available.

Standing crop biomass of superficial dead wood on the study site was 2127 kg per hectare. Of this figure five plant species represent 97.6 percent of the biomass. Six plant species account for 96.4 percent of the 450 kg per hectare of superficial dead wood produced annually.

Wood consumption by H. aureus in the laboratory is best described as a linear or quadratic function of temperature, with maximum consumption occurring between 28 and 32°C. A significantly

greater amount of blue palo verde, Cercidium floridum, was consumed than cholla, Opuntia fulgida, mesquite, Prosopis juliflora, and catclaw, Acacia greggii. H. aureus is a general feeder, yet it appears to prefer O. fulgida, P. juliflora, and A. greggii over C. floridum and other less abundant woods. This contrasts with its ability to consume significantly greater amounts of C. floridum in compulsory feeding trials.

Surface foraging occurs throughout the year between 7 and 47°C, extremes measured between the bait-soil interface down to 15 cm in the soil. Foraging intensity increases with increasing temperature, then decreases rather rapidly. Increased soil moisture increases foraging intensity. The number of foragers at a given point in time may be predicted by the equation: $\ln Y = -0.985 - 0.0761 T + 2.928 \ln T + 0.327 \ln R$, where Y = the number of foragers at that time, T = daily mean temperature at the bait-soil interface and R = daily rainfall.

Total foraging density of H. aureus is estimated at 431 to 786 per m^2 with a biomass of 0.145 to 0.264 g per m^2. Average colony size may range from ca. 23,754 to 49,125 individuals.

A simulated wood consumption model predicts that H. aureus foragers made 4.61×10^{10} foraging sorties per hectare per year. In the course of these trips foragers removed surface wood at the rate of 78.9 kg per hectare per year. This represents 3.7 percent of the standing crop biomass and 17.5 percent of the annual production of

superficial dead wood. Therefore, Heterotermes aureus has been shown to be an important component of this desert grassland ecosystem.

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