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1974 PROGRESS REPORT

**DEMOGRAPHY OF TERMITE COLONIES AS RELATED TO
VARIOUS ENVIRONMENTAL FACTORS: POPULATION
DYNAMICS AND ROLE IN THE DETRITUS CYCLE**

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ABSTRACT

Increasing the accuracy in estimating the efficiency of termites as detritivores has been one of our major concerns. To this end we have extended our analyses to include more species of termites, refined a number of estimates and revised the submodel which considers the problem of fallen dead wood consumption by termites on an annual basis. Our estimates of surface dead wood production and standing crop biomass on the Santa Rita site (Tucson Basin) remain at $450 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ and 2127 kg/ha . Instantaneous estimates of mean surface foraging numbers of the five most important subterranean species are 6.89, 0.35, 1.31, 1.51 and $0.12 \text{ termites/m}^2$. Estimated total number for all five species is $1025/\text{m}^2$ with a biomass of 0.414 g/m^2 . Superficial dead wood and termites are not randomly dispersed. The abundance of particular oligophagous termites is correlated with the quantity of highly preferred woods, while there is no correlation between the abundance of polyphagous species and wood species. Each termite species maintains a rather exclusive niche through a characteristic mode of attack on a preferential selection of host woods. *Heterotermes* and *Gnathamitermes* forage throughout the year under a wide range of temperatures, with foraging intensity regulated primarily by temperature and modified by soil moisture. Our revised submodel estimates that *Heterotermes aureus* consumes dead wood in the desert ecosystem at a rate of $78.9 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, 3.7% of the standing crop biomass or 17.5% of the annual production. Using less reliable data for the other species, we estimate that all 10 species of termites known from Santa Rita might consume $413.9 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (92% of the annual production of $450 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and that termites and fungi together might consume $463 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (103% of annual production). Estimates of the amounts of residual detritus and feces delivered to the decomposers are also given. Alate production by five species was measured at Santa Rita during summer flight seasons in 1973 (very dry) at 52,158 alates or 137 g/ha , in 1974 (ca. normal rainfall) at 72,803 alates or 190 g/ha . Both vertebrates and invertebrates prey heavily on these winged forms.

INTRODUCTION

On a continuing basis we have sought to measure the rate of dead wood production and to characterize the desert termite populations and their activities so as to predict the annual rate of wood consumption by these important detritivores. We have also proposed to measure the annual production of termite biomass, as winged forms, which generally ends up as food for a variety of predators.

By 1973, woody litter production at Santa Rita had been determined and a model developed for estimating its consumption by one species of subterranean termite. This year further details of density, dispersion and wood preferences of foraging populations have been worked out so that the impact of four species on woody detritus can now be estimated within a reasonable order of magnitude. Alate production has also been measured during a drought year and a succeeding normal year for several important species.

Plans for 1975 involve continuing laboratory studies on food-energy relationships between a typical dry-wood termite and samples of woody detritus, together with evaluation of the nutritive quality of termites as predator food. Hopefully it will be possible to gain some idea of the proportional amount of woody detritus consumed by termites vs. that removed through microbial decomposition.

OBJECTIVES

No basic changes have been made in the long-term objectives of the whole project. These objectives are to:

1. Determine the colony or foraging group characteristics, dynamics of colony development and alate production, and activity patterns of representative dry-wood and

subterranean termites as functions of biotic and abiotic variables.

2. Assess the role of termites in the detritus cycle.
3. Determine the importance of termites as producers of seasonal swarms of winged forms which serve as food for a variety of predators, both vertebrate and invertebrate.

Supporting objectives have guided the research during 1974 approximately as follows:

1. For purposes of synthesis, data refinement and ordering of research priorities, exercise the computer model, TERMITE, replacing earlier estimates and literature data with new data as they become available. (Accomplishment was limited to correction and some revision of our termite wood-consumption model. Results of a reasonable order of magnitude included here.)
2. Investigate certain food- (wood) energy relationships, with emphasis as follows: a) assemble and summarize supporting literature on nutrient dynamics of termites (nearly completed for inclusion in an IBP Synthesis Volume "Social insects, their significance in ecosystem dynamics"); b) determine rates of wood consumption for additional species of termites as wood consumed per hour per gram dry weight of termite. Make some attempt to assess and improve the realism of laboratory-determined rates with reference to the field situation; c) determine metabolic energy values for one species of dry-wood termite under controlled temperature and RH on a single species of wood; d) determine nitrogen balance for the same species under the same conditions. (These last three subjects are incomplete and continuing.)

3. Continue work on the estimation of alate production per colony and per hectare for some of the important species. (Complete and reported.)
4. Determine correlations between seasonal alate flights and major meteorological variables. (Analyses continuing; progress reported.)
5. Relate geographic distribution of major species to several environmental variables in Arizona. (No further progress here due partly to the death of our collaborator, J. R. Hastings.)
6. For increasing realism of our model, conduct miscellaneous studies to determine parameters such as O₂ consumption rates, forager turnover rates, etc. (Accomplishments confined to determination of host-wood preferences for five more species, estimation of foraging populations for four more species, and in-depth analysis of environmental control of foraging activity for two species.)
7. Continue collection and analysis of data dealing with colony growth rates and accompanying developmental characteristics. (No additional field work was done since data at hand have not yet been analyzed.)

METHODS

DENSITY, DISPERSION AND COMPOSITION OF FORAGING POPULATIONS AND THEIR RELATIONSHIP TO SUPERFICIAL DEAD WOOD

Sampling for superficial dead wood, associated termite activity and foraging group size was done on the limited destructive sampling area of the untreated plot at Santa Rita. From a grid, covering an area of ca. 20 ha which had been used for soil moisture sampling, 50 points were chosen randomly and served as the centers of the 50 "circledrats" (circular quadrats). In the beginning sampling was done both day and night to randomize the times when termite populations were observed. It was soon decided that their foraging activity should be studied separately and intensively; this was done with detailed attention to several environmental variables (see Environmental Control of Foraging Activity). At least two of the termite species studied, *Heterotermes aureus* and *Gnathamitermes perplexus*, were found to forage day and night throughout the year, with temperature governing foraging intensity (Haverty et al. 1974, LaFage 1974). Consequently, circledrats were sampled during favorable environmental conditions with primary attention devoted to dead wood and foraging group size and density.

Using the random points as centers, fifty 50-m² circledrats were "drawn" and sampled between May 3, 1971, and June 7, 1972, according to DSCODE A3UNE02. To determine dead wood production, each point was resampled between May 2, 1972, and June 5, 1973, one year after their initial sampling (A3UNE09). All the dead wood accessible to subterranean termites from the ground within each circle was identified and weighed in pounds and ounces on a hand-held Chatillon® hide scale. These field weights were corrected for moisture content and adhering debris (Nutting et al. 1974, p. 61) before conversion to grams.

When foraging groups were encountered, they were either counted on the spot or the wood containing them was brought to the laboratory and the termites extracted and counted. When clean and healthy termites were brought back to the laboratory, occasional samples were removed and dried to constant weight (nearest 0.1 mg) at 60 C for 24 hr (A3UNE04).

The circledrat method yielded data for determining several types of information: biomass of dead wood of each species/ha available to termites; biomass of dead wood of each species produced annually/ha; numbers and biomass of surface foraging populations of several subterranean termite species/ha; and the relationship between the amount of wood available and the termite numbers and biomass.

The departure of distributions of both wood and termites from a Poisson model was tested by the relationship:

$$\chi^2/(N-1) = (s^2/\bar{x})$$

where s^2 = variance, N = number of samples, \bar{x} = mean, s^2/\bar{x} = coefficient of dispersion.

Values within the 0.95 and 0.05 limits for $\chi^2/N-1$ are considered to represent a random distribution, whereas those greater than the 0.05 limit imply aggregation (Southwood 1966). Relationships between the standing crop of superficial dead wood and termite numbers or biomass were obtained by linear correlation. Correlations for termite numbers and biomass were examined using the average biomass for each caste and the corrected biomass of each wood species for each circledrat.

HOST-WOOD PREFERENCES

Identical procedures for sampling dead wood (A3UNE02) and associated termite activity (A3UNE04) were used here as described in the previous section. Data from the same 50 circledrats were analyzed along with those from 6 circledrats in the chained plot and 13 from the periphery of the entire Santa Rita site. Each piece or group of associated pieces of wood was scored as "positive" (attacked) if termites were present or if there was any evidence of their past activity.

Each termite species attacks wood in a characteristic way and leaves fecal evidence which makes its work readily identifiable. *Heterotermes aureus* generally works inside superficial and partially buried wood. Its tunnels and galleries have a mottled lining of light brown fecal material although areas of active excavation are clean. *Gnathamitermes perplexus* leaves distinguishing light-colored patches on wood in the same situation by scraping off the outer weathered fibers. It seldom deposits feces in its tunnels but it covers exposed surfaces being worked with sheets of soil. Dead grasses, herbaceous material and bovine dung are also eaten by this species but were not included in our study. *Paraneotermes simplicicornis* attacks only buried or partially buried wood, particularly stumps. While it may

work the peripheral parts of hard acacia and mesquite stumps, it more frequently bores central tunnels through dead roots and branches. Its workings are heavily lined with feces and contain dumps of its characteristic conical fecal pellets, their color depending on the color of the wood. The *Amitermes* spp., *A. wheeleri*, *A. minimus* and *A. silvestrianus*, attack wood in similar ways by penetrating superficial or buried wood much as does *H. aureus*. They line their galleries with dark brown to black fecal matter. Unless foraging groups with soldiers were encountered during sampling, the work of the individual species was impossible to distinguish and was simply lumped under the common genus.

Wood preferences were determined by tabulating the number of occurrences of each species of wood in all 69 circledrats. The occurrences were scored according to the number of pieces of each species of wood attacked or not attacked by each termite species. The resulting frequencies were analyzed by chi-square. Probabilities of attack were separated at the $\alpha = .05$ level by a Student-Newman-Keuls' multiple range test with ∞ d.f. To compare wood preferences of all termite species a preference index was established for five dominant wood species by dividing the probability of attack for each wood species by the probability of attack for all woods combined.

ENVIRONMENTAL CONTROL OF FORAGING ACTIVITY --
Heterotermes aureus AND *Gnathamitermes perplexus*

Large quantities of data were stored (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14) as the result of one major effort to study the foraging behavior of subterranean termites on the Santa Rita chained plot between October 15, 1971, and October 13, 1972. The basic approach involved setting out 16 10 x 10-m plots of toilet paper rolls (100 rolls/plot), with rolls on a grid at 1-m intervals. The surface of the area had been raked clear of all dead wood and each roll wrapped with tape to prevent raveling. The two most abundant termites on the site, *H. aureus* and *G. perplexus*, began feeding on the rolls within the first week and continued with vigorous activity throughout the study. Twelve plots were reserved for routine examination with minimum disturbance of the termites (Fig. 1, No. 1-12). A different block of 100 was quickly examined visually at 2-hr intervals, during one 24-hr period, once each week for one year (53 days). Evidence of past termite activity and an estimate of the number of foragers (if present) in each roll (in size classes of 1-5, 6-50, 51-150, 151-250, 251+) were recorded on A3UNE6G and 6H. Pertinent environmental variables were recorded on the remaining DSCODES. Related groups of data have been analyzed in a number of different ways for different purposes in the following paragraphs.

After 53 weeks, 205 rolls of toilet paper were collected from the four undisturbed plots (Fig. 1, no. 13-16). As these rolls were gathered, the number of foragers present was estimated in the usual way and each roll, termites included, was placed in a separate plastic bag. The estimates were later verified in the laboratory by making actual counts of the foragers. There were no significant differences between

field estimates and laboratory counts ($t_{.05} = 0.39$ $df = 58$) of *G. perplexus*. For *H. aureus*, however, 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 estimates.

Data Analysis

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

To illustrate more clearly the relationship between observed foraging intensity of *G. perplexus*, temperature and rainfall, three-dimensional computer graphs were constructed. The 53 weekly estimates of foragers present at the rolls were plotted against daily mean temperature (roll-soil interface) and cumulative weekly rainfall.

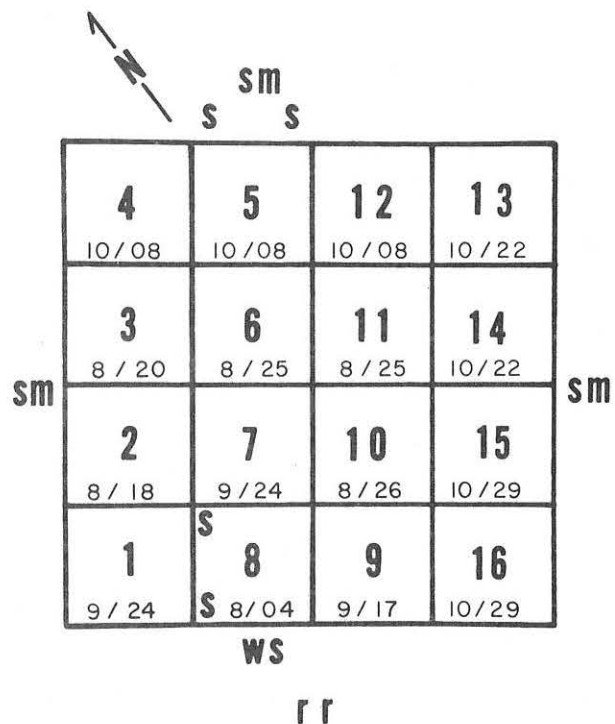


Figure 1. Map of sixteen 10 x 10-m plots for studying the foraging behavior of *Heterotermes aureus* and *Gnathamitermes perplexus* on the chained plot, Santa Rita site. S, soil temperature recording station; sm, soil moisture measurement sites; r, rain gauges; ws, weather station containing hygrothermograph. Large numbers identify individual plots which were ready for use on the dates given in each plot (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

Simple and step-wise regression analyses were used to select the environmental parameters most highly correlated with changes in termite foraging intensity. Several prediction equations were developed and analyzed for biological credibility (see Results).

COLONY DENSITY AND FORAGING TERRITORY -- *Heterotermes aureus*

This study was done on the Santa Rita chained plot and the experimental design is essentially described in the previous section. Detailed observations on the termites foraging there were made during one 24-hr period each week from October 15, 1971, to October 13, 1972 (A3UNE6H). A different subplot of 100 rolls in a block of 12 (Fig. 1) was checked every 2 hr. The fact that no single roll was observed more than once a week allowed termites time to re-establish their roll-soil connections. The four remaining subplots (Fig. 1, No. 13-16) were reserved for studies of soil movement and paper consumption by termites and were examined for activity only once at the end of the year. A weekly record was kept of foraging intensity for each roll of paper. From this, frequency tables of foraging-number size classes were developed (see Environmental Control of Foraging Activity) which allowed calculation of the average number of foragers visiting each roll during the year. The weekly records also provided a basis for observing the lateral spread of foraging territories.

We were able to establish boundaries of what we consider to be foraging territories of individual colonies, but not by the ingenious method of noting aggression (or lack of it) displayed between individuals from different areas as was done by Nel (1968). Rolls attacked on the first week of the study and rolls with large mean weekly counts of termites were considered as colony foci. The lateral spread of territories from these points to new rolls was followed weekly. Isolated rolls or groups of two or three rolls were arbitrarily included with larger aggregations if they were within two rolls of the larger clump and appeared to represent a temporal expansion of the original foci.

Weekly activity records were not available for the four plots reserved for soil studies or the intermediate rows within the study plot, since only end-of-the-year evidence of attack was available for these rolls. Consequently, colony boundaries were empirically determined here on the basis of the relative severity of attack on closely associated rolls (see Figure 9, page 69).

Based on the assumption that each roll subtended 1 m² of territory, the spatial area of each foraging territory was calculated 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*. Areas of colonies on the periphery of the plot were multiplied by two because, on the average, only half of each such colony would fall within the plot. In determining densities of colonies, colonies completely within the plot were counted as whole colonies but, according to the preceding assumption, those divided

by plot boundaries were counted as half colonies.

Only one other subterranean termite, *G. perplexus*, was abundant on the study plot. However, its large, open and relatively clean cavities were easily distinguished from the narrow, deeply penetrating and heavily spotted galleries of *H. aureus*. The fact that *Gnathamitermes* attacked 96% of the toilet paper rolls, including 53% of those attacked by *Heterotermes*, suggests that it may have influenced the foraging patterns of *Heterotermes*. We have chosen to defer any consideration of interspecific competition pending completion of our analysis of the foraging populations of *Gnathamitermes*.

ALATE PRODUCTION

Winged dispersal forms of several species were caught in ultraviolet light traps set up inside two 12 x 12 x 8-ft cages on the toilet paper plot at Santa Rita during the flight season from July 2 to September 3. Further details were given by Nutting et al. (1974) while termite and associated rainfall data have been stored in A3UNE20 and dry weights in A3UNE04.

PHENOLOGY OF DISPERSAL FLIGHTS -- *Heterotermes aureus*

Studies on the seasonal dispersal flights are in the analytical stage, but have reached a point where progress can be illustrated with some descriptive information on a major subterranean species. Detailed records on the flights of eight species at one urban Tucson locality have been accumulated since 1961. Among other items these include date, time and number of individuals in each flight (A3UNE22), air temperature, rainfall, RH and evaporation, time of sunrise and sunset (A3UNE21) and some biological information. Observations have been made within a radius of ca. 50 m from two white lights so that estimates of number of alates/flight is admittedly only a crude, relative measure of flight size. No realistic measure of production/unit area could be based on these figures.

Boyer's (1973) heat-sum approach for studying pollen-shedding phenology has been taken as a possible method for describing the conditions which trigger these seasonal flights. We have focused on the period from the presumed beginning of alate development to the peak of the following flight season (date of largest flight). Our first objective has been to find the best combination of starting date and base developmental temperature which would provide the heat sum most closely predicting the peak flight date. Degree-days were calculated by estimating the area under a sine curve passing through daily maxima and minima (Arnold 1960), with Baskerville and Emin's (1969) method being used when the minimum fell below the developmental threshold.

In an initial screening, daily air temperatures were processed by computer to provide degree-day heat sums through the peak flight date for all combinations of 18 starting dates (ca 10-day increments from October 1 to

March 21) and five base temperatures (40, 45, 50, 55 and 60 F). Means and coefficients of variation were obtained for each of the ninety 12-year groups. A low coefficient of variation was used to measure variability in comparing combinations of base temperatures and starting dates. A second round of calculations was made when screening results showed that starting dates might better be shifted to August 1 to December 21, and base temperatures to 32, 34, 36 and 38 F.

MODELING WOOD CONSUMPTION --
Heterotermes aureus

We have described (Nutting et al. 1974) a submodel, EATIT, developed to answer the question, "How much wood can *Heterotermes aureus* remove from the ecosystem per hectare per year?" During 1974 EATIT was revised and the estimation of certain parameters improved. Temperature-dependent functions of termite foraging intensity (A3UNE6H) and wood consumption (A3UNE17) are still most critical. To reduce computer time the model is now designed to run on daily mean temperatures (food-soil interface; A3UNE07) and daily rainfall (A3UNE08) for a period of one year. It also uses data from A3UNE02, 04 and 09.

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

1. For each day of the year, 24 hourly temperatures and daily rainfall are read in and a daily mean temperature calculated. It was assumed that the termites forage every day of the year provided the mean temperature does not fall below 4.0 C, since this is the lowest daily mean temperature at which *H. aureus* has been observed foraging.

2. Temperature and rainfall values are entered into the equation:

$$\ln Y = -0.985 - 0.0761 (\text{Temp}) + 2.928 (\log_e \text{Temp}) + 0.327 (\log_e \text{Rain})$$

to determine Y, the mean number of foragers above the surface per 100 m² at any point in time during the day (Haverty et al. 1974). At temperatures below 4.0 C, the number of foragers is automatically assigned a value of 0. Since these data come from a study area of only 0.01 ha (LaFage et al. 1973, Nutting et al. 1973), the number of foragers observed must be multiplied by 100 to provide an estimated foraging force/ha.

3. 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 are very large. That is, there will always be an ample subsurface force to replace those foraging above. This assumption necessitated the establish-

ment of a forager "turnover rate" based on the speed at which termites travel as a function of temperature. Skaife (1961) measured the speed (in cm/min) of *Amitermes hastatus* (Haviland) between 10-30 C. On the assumption that *H. aureus* moves at the same speed, these data have been used to develop the following equation to calculate the distance a forager can travel in one day:

$$\text{Speed (cm/day)} = (-1.47 + (1.62 \times \text{Temp})) \times 60 \times 24.$$

To complete one circuit from the underground forager pool (estimated at 2 cm below the soil surface) to the food source (here we have used the height of a toilet paper roll; LaFage et al. 1973) and back to the pool, a termite must travel a maximum distance of 26.9 cm. Thus the number of foraging roundtrips per unit time, or turnover rate, may be expressed as follows:

$$\text{Turnovers/day} = \text{Speed (cm/day)} / \text{Maximum distance (cm)}.$$

4. If number of turnovers per day is multiplied by number of foragers observed at some instant during the day, the product represents the total force visiting the food source during that day.

5. Forager biomass must next be calculated from data on size and caste composition of foraging groups. Proportional caste composition and corresponding individual caste biomass of *H. aureus* foraging groups are given in Table 1. The foraging biomass is obtained by summing the products of the numbers of each caste times the average biomass per individual. Numbers were converted to biomass because wood consumption rates have been determined as a function of termite biomass (Haverty and Nutting 1974), not numbers of termites.

6. 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 (Haverty and Nutting 1974) and regressed to yield consumption equations for each of 11 species or

Table 1. Caste composition and individual caste biomass of an average *Heterotermes aureus* foraging group on the Santa Rita site. Data based on counts and measurements of 40 foraging groups (A3UNE02, 04)

| Caste | Percent of group | Individual biomass, mg ¹ |
|--------------|------------------|-------------------------------------|
| Larva | 0.1 | 0.26 |
| Larva-worker | 97.2 | 0.34 |
| Soldier | 1.6 | 0.47 |
| Nymph | 1.1 | 1.05 |

¹Dried to constant weight at 60C.

Table 2. Equations for consumption (mg wood/g termite biomass/day) of ten species or categories of wood by *Heterotermes aureus* as a function of temperature (X) (A3UNE17)

| Wood species | Consumption rate mg wood/g termite biomass/day |
|--|---|
| <i>Acacia greggii</i> ¹ | 70.32 |
| <i>Cercidium floridum</i> | $-137.90 + 20.45x - 0.338x^2$ |
| <i>Prosopis juliflora</i> | $-13.66 + 3.48x$ |
| <i>Opuntia fulgida</i> , <i>Opuntia spinosior</i> ² | $-310.15 + 27.96x - 0.462x^2$ |
| <i>Celtis pallida</i> , <i>Ephedra trifurca</i> , <i>Gutierrezia sarothrae</i> , <i>Opuntia engelmannii</i> , <i>O. fulgida</i> and <i>O. spinosior</i> joints, Other woods ³ | $-165.38 + 20.45x - 0.338x^2$ |

¹No significant regression obtainable; therefore, consumption rate is mean of 6 rates determined between 16-36C.

²Because of the similarity between species, *spinosior* was assigned the same consumption rate as that determined for *fulgida*.

³Specific consumption rates for these 6 categories of wood were not determined. Rate estimated by combining data for 4 wood species tested between 16-36C.

categories of wood (Table 2). At some temperatures above 4 C it is possible to obtain negative consumption values with the regression equations. This is, of course, biologically impossible; therefore, if the consumption equation yields a negative value, a consumption rate of zero is assumed. Since termites preferentially divide their foraging attention toward different types of wood (Table 3) it follows that foraging biomass must also be partitioned into percentages of the total which will process each of the 11 species or categories of wood in the system. Thus the amount of each wood species consumed is the product of a particular consumption rate times its assigned termite biomass.

7. 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

DENSITY, DISPERSION AND COMPOSITION OF FORAGING POPULATIONS AND THEIR RELATIONSHIP TO SUPERFICIAL DEAD WOOD

Fallen Dead Wood Available to Termites and Annual Dead Wood Production

Correcting field weights of all superficial dead wood, we estimate the standing crop biomass at Santa Rita to be 2127 kg/ha (Table 4). Five dominant plant species (*Acacia greggii*, *Prosopis velutina*, *Opuntia fulgida*, *Opuntia spinosior* and *Cercidium floridum*) account for 97.6% of the biomass. The coefficients of dispersion for all of the above dominant species are beyond the 0.05 critical limit for

Table 3. Proportion of termite biomass assigned to each species or category of wood, Santa Rita site (A3UNE02, 04)

| Wood species or category | Proportion ¹ |
|--|-------------------------|
| <i>Acacia greggii</i> | .173 |
| <i>Celtis pallida</i> | .061 |
| <i>Cercidium floridum</i> | .017 |
| <i>Ephedra trifurca</i> | .038 |
| <i>Gutierrezia sarothrae</i> | .006 |
| <i>Opuntia engelmannii</i> | .017 |
| <i>O. fulgida</i> | .179 |
| <i>O. spinosior</i> | .355 |
| <i>O. fulgida</i> and <i>O. spinosior</i> , joints | .012 |
| <i>Prosopis juliflora</i> | .133 |
| Other woods | .009 |
| Total | 1.0 |

¹The proportion is the ratio of the number of units of each species or category of wood attacked by *H. aureus* to all units attacked by it.

Table 4. Biomass of superficial dead wood standing crop and dead wood produced annually on the natural plot, Santa Rita site, based on fifty 50-m² circledrats (A3UNE02, 09)

| Wood species | Standing Crop | | | Annual Production | | |
|------------------------------|----------------------------------|---------------|--------------|----------------------------------|---------------|--------------|
| | \bar{x} wt/ circle- drat | s^2/\bar{x} | Est kg/ha | \bar{x} wt/ circle- drat | s^2/\bar{x} | Est kg/ha |
| <i>Acacia greggii</i> | 3.162 | 20.916 | 632 | 0.158 | 1.658 | 32 |
| <i>Prosopis juliflora</i> | 1.801 | 12.647 | 360 | 0.796 | 14.668 | 159 |
| <i>Opuntia fulgida</i> | 1.766 | 8.841 | 353 | 0.415 | 9.894 | 83 |
| <i>Opuntia spinosior</i> | 1.562 | 2.256 | 312 | 0.074 | 1.014 | 15 |
| <i>Opuntia</i> spp. joints | 1.405 | 4.898 | 281 | 0.274 | 0.923 | 55 |
| <i>Cercidium floridum</i> | 0.688 | 18.480 | 138 | 0.352 | 8.651 | 70 |
| <i>Celtis pallida</i> | 0.087 | 3.034 | 17 | 0.003 | 0.062 | 1 |
| <i>Opuntia engelmannii</i> | 0.051 | 0.608 | 10 | 0.102 | 2.529 | 20 |
| <i>Ephedra trifurca</i> | 0.041 | 0.390 | 8 | 0.023 | 0.087 | 5 |
| <i>Gutierrezia sarothrae</i> | 0.040 | 1.125 | 8 | 0.045 | 0.333 | 9 |
| Other woods | 0.034 | 0.294 | 7 | 0.007 | 0.068 | 1 |
| Total | 10.636 | 8.688 | 2127 | 2.249 | 7.839 | 450 |

Table 5. Mean biomass of castes of each of five termite species based on samples from foraging groups on the natural plot, Santa Rita site (A3UNE04)

| Caste | <i>H. aureus</i> | | <i>G. perplexus</i> | | <i>P. simplicicornis</i> | | <i>A. wheeleri</i> | | <i>A. minimus</i> | |
|---------------|------------------|---|---------------------|---|--------------------------------------|--|--------------------|---|-------------------|---|
| | # indiv. weighed | \bar{x} biomass/indiv., mg ^a | # indiv. weighed | \bar{x} biomass/indiv., mg ^a | # indiv. weighed | \bar{x} biomass/indiv., mg ^a | # indiv. weighed | \bar{x} biomass/indiv., mg ^a | # indiv. weighed | \bar{x} biomass/indiv., mg ^a |
| Larva | 50 | 0.2640 | | | 356 | 1.0815 | | | | |
| Larva-worker | 11,100 | 0.3408 | | | | | | | | |
| Worker | | | 594 | 0.6455 | | | 727 | 0.4497 | 483 | 0.2756 |
| Pseudergate | | | | | 314 | 2.3497 | | | | |
| Soldier | 200 | 0.4675 | 29 | 0.6000 | 141 | 4.0624 | 43 | 0.4163 | 63 | 0.2825 |
| White Soldier | 29 | 0.3862 | | | | | | | | |
| Nymph | 311 | 1.0540 | | | 463 ^b 494 ^c | 1.9769 ^b 3.2372 ^c | | | | |

^aBiomass determined by oven-drying at 60°C for 24 hr.

^bNymphs with short wing buds.

^cNymphs with long, overlapping wing pads.

$\chi^2/N-1$ (= 1.354), indicating a nonrandom dispersion of the standing crop biomass.

Biomass of all superficial dead wood produced annually is estimated at 450 kg/ha (Table 4). This estimate does not allow for dead wood produced and consumed by termites during the year. Although we did not measure wood consumption, very few termites were collected in re-sampling and hence, the wood consumed was probably minimal. Six plant species (the above plus *Opuntia engelmannii* Salm-Dyck) account for 96.4% 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 of *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% of the annual dead wood production of *C. floridum*. As with standing crop, the coefficients of dispersion indicate a nonrandom pattern in four of the six dominant species. *Opuntia* spp. joints and *O. spinosior* are exceptional since they appear to display a random dispersion.

Foraging Group Characteristics

Estimates of numbers of termites and termite biomass/ha are based on foraging groups collected while sampling superficial dead wood. Selected samples of clean termites were taken to determine mean biomass (milligrams) for each caste (Table 5). The mean numbers of individuals and

Table 6. Mean number and biomass of four species of subterranean termites in each of fifty 50-m² circledrats sampled on the natural plot, Santa Rita site (A3UNE02, 04)

| | Numbers | | Biomass (mg) ^a | |
|-------------------------------------|-----------|----------------------------|---------------------------|----------------------------|
| | \bar{x} | s ² / \bar{x} | \bar{x} | s ² / \bar{x} |
| <i>Heterotermes aureus</i> | 344.58 | 1599.84 | 120.74 | 542.05 |
| <i>Gnathamitermes perplexus</i> | 17.32 | 395.90 | 11.16 | 255.53 |
| <i>Paraneotermes simplicicornis</i> | 65.44 | 1723.71 | 163.44 | 4546.46 |
| <i>Amitermes</i> spp. ^b | 81.58 | 1636.14 | 35.59 | 752.59 |
| All termites | 508.20 | 1379.16 | 330.93 | 2422.92 |

^aBiomass determined by summing weight of each caste (Table 2) times the number of each caste.

^b*Amitermes* spp. includes 10 groups of *A. wheeleri*, 1 of *A. silvestrianus*, and 2 of *A. minimus*.

biomass of each species per circledrat are given in Table 6. A greater number of *H. aureus* foragers was found than of all other species combined. With only 12.9% of the mean number for all termites, *P. simplicicornis* accounted for just under 50% of the total mean biomass, due to its much greater individual biomass (Table 5). The coefficients of dispersion of numbers and biomass for each and all termite species are beyond the critical χ^2 level ($\alpha = .05$), indicating a clumped rather than random distribution.

Table 7. Average composition, density and biomass of foraging groups of five species of termites collected in 50-m² circledrats on the natural plot, Santa Rita site (A3UNE02, 04)

| | <i>H. aureus</i> | <i>G. perplexus</i> | <i>P. simplicicornis</i> | <i>A. wheeleri</i> | <i>A. minimus</i> |
|---|------------------|---------------------|--|--------------------|-------------------|
| Avg. groups/circledrat (50-m ²) | 0.80 | 0.30 | 0.22 | 0.22 | 0.04 |
| Avg. group composition: | | | | | |
| Larvae | 0.40 (0.1%) | | 36.00 (12.1%) | | |
| Larva-workers | 418.80 (97.2%) | | | | |
| Workers | | 56.40 (97.8%) | | 338.45 (98.6%) | 151.00 (99.0%) |
| Pseudergates | | | 56.36 (19.0%) | | |
| Soldiers | 6.28 (1.5%) | 1.33 (2.2%) | 29.55 (9.9%) | 4.64 (1.4%) | 1.50 (1.0%) |
| White soldiers | 0.53 (0.1%) | | 0.36 (0.1%) | | |
| Nymphs | 4.73 (1.1%) | | 92.18 (31.0%) ^b 83.00 (27.7%) ^c | | |
| Total | 430.74 | 57.73 | 237.45 | 343.09 | 152.5 |
| Avg. group weight, mg ^a | 150.96 | 37.21 | 742.33 | 154.13 | 42.04 |
| Est. foraging groups/ha | 160 | 60 | 44 | 44 | 8 |
| Est. foraging termites/ha | 68,918 | 3,464 | 13,088 | 15,096 | 1,220 |
| Est. foraging biomass/ha, g | 24.15 | 2.23 | 32.69 | 6.78 | 0.34 |

^aBiomass figures based on Table 5.

^bNymphs with short wing buds.

^cNymphs with long, overlapping wing pads.

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/ha (Table 7). Average group size was 430.74. Larva workers (undifferentiated larvae of at least the third instar) comprised 97.2% of the foraging termites collected, soldiers 1.5%, reproductive nymphs 1.1% and white soldiers and larvae 0.1% each. Biomass figures of individual castes (Table 5) permit calculation of an average group weight of 150.96 mg. With 160 foraging groups/ha it is estimated that there are 68,918 foragers/ha with a biomass of 24.154 g. Similar data for *G. perplexus*, *P. simplicicornis*, *A. wheeleri* and *A. minimus* are presented in Table 7. The foraging biomass figures must represent only a small portion of the total colony biomass since they represent an instantaneous sample of only a fraction of the total foraging force (Bodine 1973).

Relationship Between Wood Biomass and Termite Numbers and Biomass

One of the major questions which arises in a study of this nature asks, "Does a relationship exist between the number of termites in an area and the amount of wood available?" A test for such a possibility was made by linear correlation, even though the distributions of termites and wood do not meet the necessary requirements of normality. Therefore, statistically significant correlation coefficients (*r*) do not necessarily indicate a significant correlation at a particular probability level, but are used here only to suggest a strong possibility of such a relationship.

Apparently significant relationships exist between standing crop biomass of various categories of superficial dead wood and numbers of *H. aureus*, *P. simplicicornis*, all termites and biomass of all termites (Table 8). Numbers of *H. aureus* appear highly correlated with standing crop biomass of *Opuntia spinosior*. *Paraneotermes* numbers are highly correlated with both standing crop biomass of *Acacia greggii* and total dead wood, apparently because *A. greggii* standing crop is highly correlated with total dead wood standing crop (*r* = .646). Numbers of all termites show a relationship with *O. spinosior* (Table 8), probably due to the dominance of *H. aureus* in the mean number of all termites observed per circle (Table 6). Biomass of all termite species is influenced greatly by *P. simplicicornis* (Table 6) and, as a result, a significant relationship is indicated between biomass of all termite species and *A. greggii* and total dead wood biomass (Table 8). Neither *Gnathamitermes* nor *Amitermes* shows any indication of a significant relationship with any category of superficial dead wood.

HOST-WOOD PREFERENCES

The following nine species were encountered most often as superficial dead wood at Santa Rita: catclaw acacia, *Acacia greggii* Gray; desert hackberry, *Celtis pallida* Torr.; blue paloverde, *Cercidium floridum* Benth.; joint-fir, *Ephedra trifurca* Torr.; snakeweed, *Gutierrezia sarothrae* (Pursh) Britt. and Rusby; prickly pear, *Opuntia engelmannii* Salm-Dyck; jumping cholla, *Opuntia fulgida* Engelm.; cane cholla *Opuntia spinosior* (Engelm. and

Table 8. Matrix of correlation coefficients (r) for 12 categories of standing crop biomass of superficial dead wood, and associated numbers and biomass of four species of subterranean termites in each of fifty 50-m² circledrats sampled on the natural plot, Santa Rita site (A3UNE02, 04)

| Woods | Termites | | | | | Biomass of all termites |
|--|-----------------------|--------------------------|-------------------------------|----------------------------|-------------------|-------------------------|
| | # of <i>H. aureus</i> | # of <i>G. perplexus</i> | # of <i>P. simplicicornis</i> | # of <i>Amitermes</i> spp. | # of all termites | |
| <i>Acacia greggii</i> | -.112 | -.041 | .686** | .119 | .223 | .644** |
| <i>Celtis pallida</i> | -.065 | -.036 | -.034 | -.039 | -.091 | -.059 |
| <i>Cercidium floridum</i> | -.065 | -.029 | -.037 | -.028 | -.088 | -.061 |
| <i>Ephedra trifurca</i> | -.083 | -.053 | -.065 | .024 | -.094 | -.090 |
| <i>Gutierrezia sarothrae</i> | .090 | -.040 | -.037 | -.043 | .042 | -.020 |
| <i>Opuntia engelmannii</i> | -.120 | -.062 | -.047 | .205 | -.042 | -.043 |
| <i>Opuntia fulgida</i> | .017 | -.092 | -.034 | .092 | -.032 | -.022 |
| <i>Opuntia spinosior</i> | .393** | -.046 | -.096 | -.014 | .299* | .012 |
| <i>O. spinosior</i> & <i>O. fulgida</i> joints | -.209 | -.061 | -.063 | -.087 | -.254 | -.147 |
| <i>Prosopis juliflora</i> | -.119 | -.019 | -.004 | -.072 | -.140 | -.047 |
| Other woods | .018 | -.030 | .208 | -.037 | .080 | .198 |
| Total of all woods | -.156 | -.124 | .513** | .066 | .084 | .449** |

* Correlation coefficients significant at the $\alpha = 0.05$ level.

** Correlation coefficients significant at the $\alpha = 0.01$ level.

Bigel.) Toumey; velvet mesquite, *Prosopis velutina* (Woot.) Sarg. Species found less frequently and lumped together as "other woods" are as follows: *Aloysia wrightii* (Gray) Heller; *Echinocereus fendleri* (Engelm.) Rümpler; *Encelia frutescens* Gray; *Ferocactus wislizenii* (Engelm.) Britt. and Rose; and a few small unidentified woody perennials.

Table 9 lists total number of observations, ratio of number of attacks to nonattacks and probability of attack on nine species of wood for each of the four termite species. Probabilities of being attacked are used here as a measure of wood preference. The χ^2 values for wood preference are significant at the $\alpha = .005$ level for each termite species.

Heterotermes aureus and *Gnathamitermes perplexus* are general feeders, even though they show distinct preferences for certain species of wood. With one exception (*H. aureus* and cane cholla joints), both species attacked every species and type of wood which they encountered (Table 9). *Paraneotermes simplicicornis* and *Amitermes* spp., however, are specialized feeders in that they attacked only certain plant species, completely avoiding or rarely attacking some of the dominant plants (Table 9).

Desert hackberry is the wood most preferred by *H. aureus* -- even more so than the two cholla species, although not significantly so ($\alpha = .05$). However, it is relatively uncommon in terms of the total standing crop biomass (0.8% of superficial dead wood (Table 4). The wood of chollas and catclaw acacia is significantly preferred over mesquite and blue paloverde, while the least preferred wood types are cholla joints.

Gnathamitermes prefers cholla joints to all other types of woody plant material. Apart from these joints it is a rather general feeder, showing a significant preference only for cholla wood (both species) and mesquite over catclaw acacia and desert hackberry.

Our results indicate that *P. simplicicornis* prefers catclaw acacia to all other species of wood. This may be somewhat misleading, for it is nearly always found in stumps or large branches with a considerable underground volume. The counts reported here include superficial as well as partially buried wood. In this area catclaw acacia has a multiple-trunked habit which favors the production of a large amount of partly buried dead wood which is apparently very attractive to *Paraneotermes*. We believe that, if we had sampled only dead stumps to the exclusion of all other superficial dead wood, the incidence of attack upon mesquite and catclaw acacia would be very high and would be much higher on jumping cholla than the reported 0.041. In other studies in this area we have observed *P. simplicicornis* attacking stumps of cane cholla and prickly pear.

Since the foraging groups of *Amitermes* were relatively uncommon and often unidentifiable as to species, they were necessarily lumped. With the exception of snake weed, the *Amitermes* spp. tend to concentrate their efforts on the woody, leguminous species; catclaw acacia, blue paloverde and mesquite. Catclaw acacia is the most preferred wood, its probability of attack being significantly different from that of the wood and joints of chollas, prickly pear, joint-fir and desert hackberry.

ENVIRONMENTAL CONTROL OF FORAGING ACTIVITY -- *Heterotermes aureus* AND *Gnathamitermes perplexus*

Seasonal Trends in Foraging

These two species foraged at the toilet paper rolls day and night during most of the year of study. Figures 2 and 3 are plots of the total number of foragers observed at the rolls during the fifty-three 24-hr checks from October 15, 1971, to October 13, 1972. The mean daily temperature at the roll-soil interface for each observation period and the cumulative rainfall for the week preceding each period are included for reference.

Gnathamitermes perplexus—Foraging by this species was most intense from mid- to late October 1971. Moderate daily mean temperatures (18-25 C) combined with heavy rainfall for the week prior to the checks (>4.0 cm), may have caused the high activity levels during this period.

Table 9. Number of observations, number of attacks and non-attacks, and probability of attack by termites on all items of nine species of wood in sixty-nine 50-m² circledrats, Santa Rita site (A3UNE02)

| Wood species | Total observations | No. attacked/no. not attacked, probability of being attacked ¹ | | | |
|---|--------------------|---|---------------------|--------------------------|-----------------------|
| | | <i>H. aureus</i> | <i>G. perplexus</i> | <i>P. simplicicornis</i> | <i>Amitermes</i> spp. |
| <i>Acacia greggii</i> | 113 | 60/53 .531bc | 25/88 .221c | 15/98 .133a | 18/95 .159a |
| <i>Celtis pallida</i> | 27 | 21/6 .778a | 4/23 .148c | 0/27 .000b | 0/27 .000b |
| <i>Cercidium floridum</i> | 21 | 6/15 .286de | 10/11 .476bc | 0/21 .000b | 3/18 .143ab |
| <i>Ephedra trifurca</i> | 34 | 13/21 .382cd | 13/21 .382bc | 0/34 .000b | 0/34 .000b |
| <i>Gutierrezia sarothrae</i> | 18 | 2/16 .111def | 6/12 .333bc | 0/18 .000b | 2/16 .111ab |
| <i>Opuntia engelmannii</i> | 17 | 6/11 .353cde | 7/10 .412bc | 0/17 .000b | 0/17 .000b |
| <i>O. fulgida</i> , wood | 97 | 62/35 .639ab | 51/46 .526b | 4/93 .041b | 2/95 .021b |
| <i>O. fulgida</i> , joints | 46 | 4/42 .087ef | 44/2 .957a | 0/46 .000b | 0/46 .000b |
| <i>O. spinosior</i> , wood | 186 | 123/63 .661ab | 118/68 .634b | 0/186 .000b | 4/182 .022b |
| <i>O. spinosior</i> , joints | 20 | 0/20 .000f | 17/3 .850a | 0/20 .000b | 0/20 .000b |
| <i>Prosopis juliflora</i> var. <i>velutina</i> | 135 | 46/89 .341de | 76/59 .563b | 1/134 .007b | 8/127 .059ab |
| Other woods | 18 | 3/15 .167def | 7/11 .389bc | 0/18 .000b | 1/17 .056ab |
| Totals | 732 | 346/386 .473 | 378/354 .516 | 20/712 .027 | 38/694 .052 |

¹Probabilities of being attacked within each termite species followed by the same letter are not significantly different at the $\alpha = .05$ level by Student-Newman-Keul's multiple range test with ∞ d.f.

Although moderate to heavy rain fell throughout December 1971, low temperatures (<9.0 C) apparently led to depressed foraging activity. No foragers were observed on four days during the study (December 10, December 17, December 31 and January 7, when the mean temperatures were below 8.8 C). Although little rain fell from January 1, 1972, to May 30, 1972, gradually increasing temperatures may have been the reason for increasing activity (Fig. 2). In 1972 the summer monsoon began during June and continued through the termination of the experiment in mid-October. Foraging was intense throughout this period (Fig. 3). Figures 4a and 4b are equivalent three-dimensional computer plots viewed from two different angles with foraging intensity of *G. perplexus* plotted against cumulative weekly rainfall and daily mean temperature at the roll-soil interface. Although some activity occurred in the absence of rainfall (Fig. 4a), intense foraging occurred only at combinations of moderate to high temperatures and measurable rainfall (Figure 4b).

Heterotermes aureus—On only two days were no foragers of this species observed (December 17, 1971, and January 7, 1972, when the mean temperatures were 4.8 and 9.9 C). However, foragers were observed on one 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 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. In the spring and fall, foraging intensity was moderately higher than in the winter months. During the summer it was high but erratic.

The number of foragers generally increased with increasing temperature. From October through December when the temperature (at the roll-soil interface) 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 C (June 29-July 14, July 27-August 4, August 17-25, 1972), even with precipitation, foraging numbers dropped sharply.

Environmental Factors Affecting Foraging

No foraging activity was observed when the daily mean temperature (roll-soil interface) fell below 8.8 C for *G. perplexus* and 4.0 C for *H. aureus*, even though substantial rain fell at and below this temperature. The daily mean temperature at the roll-soil interface, however, was not a reliable parameter for identifying the temperature range within which *G. perplexus* foraged because differences between daily maximum and minimum temperatures at this level varied considerably during the year.

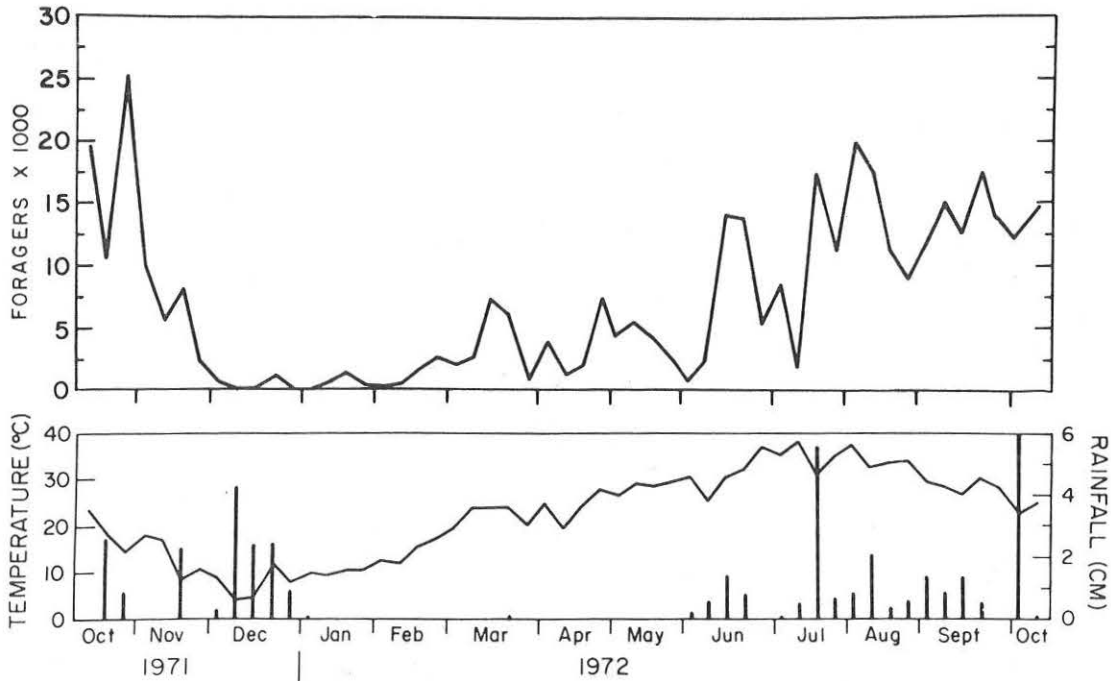


Figure 2. Seasonal foraging trends of *Gnathamitermes perplexus* at toilet paper rolls on the Santa Rita site from October 15, 1971, to October 13, 1972. Foraging numbers are totals observed at 1200 rolls during 24-hr observation periods. Temperature is a daily mean at the roll-soil interface while rainfall is a total for the week prior to the 24-hr observation period (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

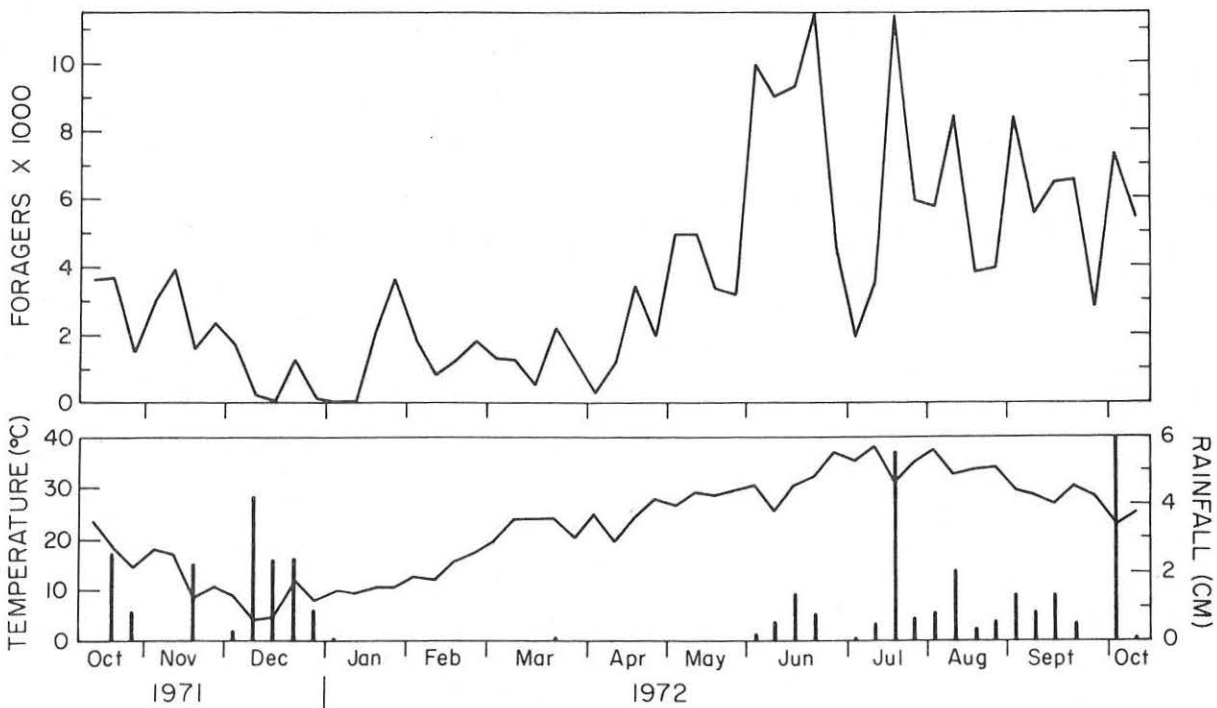


Figure 3. Seasonal foraging trends of *Heterotermes aureus* at toilet paper rolls on the Santa Rita site from October 15, 1971, to October 13, 1972. Foraging numbers are totals observed at 1200 rolls during 24-hr observation periods. Temperature is a daily mean at the roll-soil interface while rainfall is a total for the week prior to the 24-hr observation period (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

Two observations led to the selection of another environmental variable for identifying the temperature limits of this termite. First, *G. perplexus* constructs extensive foraging galleries within the upper 15 cm of soil. Second, the exact depth within this 15-cm layer where the highest or

lowest temperature occurred, shifted vertically during a 24-hr observation period. During the afternoon it was found at or near the surface. After sunset, however, surface temperatures were often much lower than those 3-5 cm below the surface. During the early morning hours prior to sunrise, the highest temperature had migrated to the 15-cm level and the coldest to the surface. The termites therefore, must pass through a migrating temperature barrier found at varying depths within the upper 15 cm, depending on the time of day.

Since temperature data had been recorded for surface, under a roll, 1-, 3-, 5-, 10- and 15-cm levels, the upper and lower temperatures which limit foraging were identified by searching this series for maximum and minimum temperatures at each of the activity checks (total -- 504). In this manner it was concluded that *G. perplexus* foraged whenever temperature extremes within this series were in the range, 9-49 C, while the range for *H. aureus* was 7.6-47 C. Laboratory studies by Collins et al. (1973) have demonstrated that temperatures of 49 and 47 C are not too high for *G. perplexus* and *H. aureus*.

The relationship between foraging intensity (number of foragers per unit area) and environmental parameters (recorded prior to the bihourly checks) was examined from the viewpoint of constructing prediction equations. Preliminary scattergrams of foraging intensity vs. single environmental parameters indicated that these relationships would be best represented by curvilinear functions. The data were subsequently fitted to four such functions (Dixon 1973). Given the proper coefficients, each equation allowed for a decrease in foraging activity at high levels of the independent variables. The equations tested were

$$Y = b_0 + b_1X + b_2X^2$$

$$\ln Y = b_0 + b_1X + b_2X^2$$

$$\ln Y = b_0 + b_1X + b_2/X$$

$$\ln Y = b_0 + b_1X + b_2 \ln X$$

where Y = the number of foragers at the surface and X = the environmental parameter. These simple regression analyses showed that changes in several environmental variables were equally correlated with changes in foraging intensity. Among these variables were temperature at 3 cm, under a roll (roll-soil interface), and the highest or lowest temperature in the series from under the roll to 15 cm. The temperature at the roll-soil interface was chosen for future equation building because it was available as a continuous recording for the 53-week study and was easier to monitor than the others.

It was obvious, however, that temperature alone did not account for the total variation in foraging activity. Throughout the study soil moisture had appeared to have a positive modifying effect on foraging intensity whenever soil temperatures were elevated. Although soil moisture records

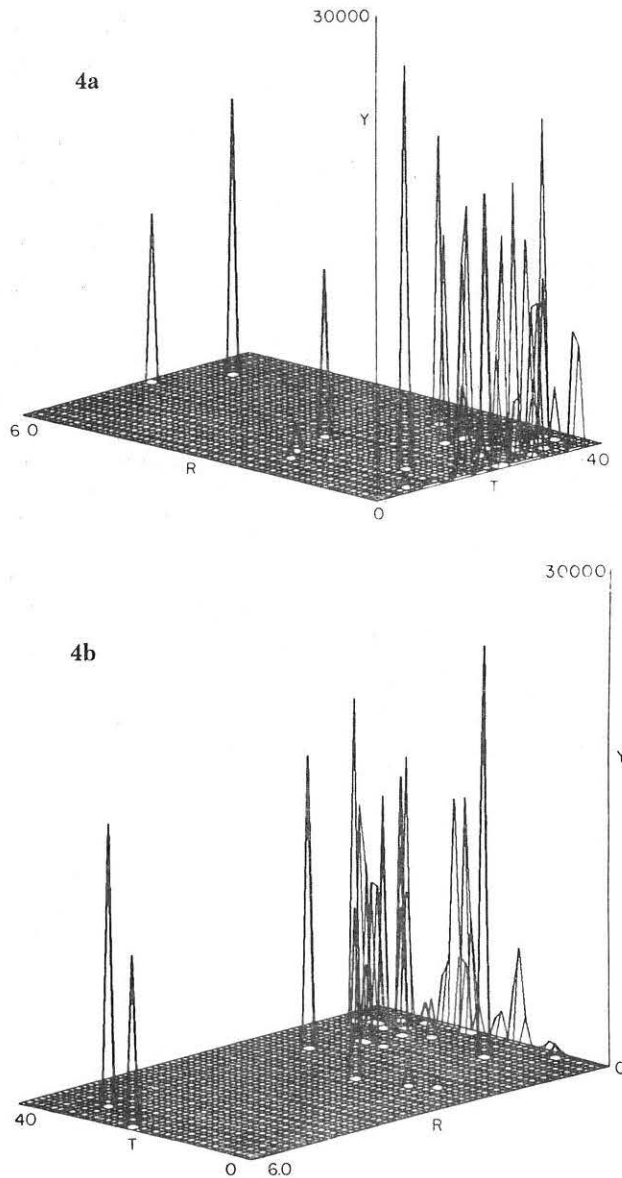


Figure 4. Foraging activity of *Gnathamitermes perplexus* (Y) plotted against temperature (T) (0-40 C) at the roll-soil interface and cumulative rainfall (R) (0-6.0 cm) for the week prior to each activity check. Individual activity estimates (Y) were based on the total number of foragers observed at 1200 toilet paper rolls during one 24-hr observation period (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14). (a) View from an angle which illustrates foraging intensity at low rainfall levels. (b) View from an angle which illustrates foraging intensity at combinations of measurable rainfall and varying temperature.

were available for only six months, cumulative weekly rainfall was highly correlated with soil moisture ($r = 0.83$, $N = 328$). Thus, rainfall was selected as a second variable to be employed in constructing prediction equations for termite foraging intensity.

Equation development—The relationship between foraging intensity, daily mean temperature at the roll-soil interface, and daily rainfall was studied using a step-wise multiple linear regression analysis (Dixon 1973). The set of variables giving the best prediction equation for foraging intensity (number of termites at 100 rolls) was found using the following procedure. Independent variables were transgenerated to \log_e , reciprocal and square. The dependent variable (foraging intensity) was treated linearly and logarithmically. The step-wise procedure added independent variables to the multiple regression equation only if they caused a significant reduction in the error sum of squares. At each step the next variable added to the equation was the one which made the greatest reduction in the error sum of squares (Dixon 1973). The program option of forcing certain independent variables into the equation was chosen. Eight prediction equations were constructed for each species using this method. Although the step-wise procedure was allowed to continue for five steps during construction of the eight equations, none of the final equations contained more than four independent variables. The eight final equations for *G. perplexus* and *H. aureus* appear in Tables 10 and 11.

Because all eight equations have similar R^2 's, two additional criteria were used to choose the best prediction equation. The statistic " C_p " was calculated for each equation according to the following formula (Gorman and Toman 1966):

$$C_p = (RSS_p / \sigma^2) - (N - 2p)$$

where RSS_p = residual sum of squares for the equation; N = number of observations (53); σ^2 = the estimate of variance based on the error mean square with all possible independent variables included in the equation. With this statistic regression equations can be compared with respect to bias and random error (Gorman and Toman 1966). When C_p 's calculated for a number of regression equations with similar R^2 's are plotted against p , the equations with low bias will have C_p 's that fall near or below the line, $C_p = p$. Those equations for which the C_p 's fall above the line will possess substantial bias. Stated differently, all equations may be discarded in which the ratio $C_p:p > 1.0$. Equations 3, 6, 7 and 8 (Table 10) and equations 2, 4 and 7 (Table 11) were eliminated because they possessed substantial bias in estimating error. The remaining equations were examined visually for biological plausibility and the best overall equation for each species was chosen. For *G. perplexus* only the four biologically sound functions were plotted using three-dimensional computer graphing methods. Each was plotted (Figs. 5-8c) with temperature (roll-soil interface) varying from 0-40 C and daily rainfall varying from 0-6.0 cm. Intensity, measured as number of foragers at 100 toilet paper rolls, constitutes the vertical axis for each graph. Equations 1, 2 and 4 (Figs. 5, 6 and 7) were eliminated because foraging intensity rose continuously within the temperature range plotted. Field observations had confirmed that foraging intensity decreased rapidly at very high daily mean temperatures. Equation 5 demonstrated this trend clearly and was selected as the best equation for predicting termite foraging intensity. Additional factors which favored equation 5 were a high R^2 , a favorable $C_p:p$ ratio (0.98) and an inherent biological plausibility.

Table 10. Equations predicting the number of *Gnathamitermes perplexus* foragers at 100 toilet paper rolls (Y) as a function of daily mean temperature at the roll-soil interface (T) and daily rainfall (R) (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14)

| Equation | p^a | C_p^a | R^{2b} |
|---|-------|---------|----------|
| 1. $Y = -1742.31 - 29.17 T - 20.78 R + 1044.87 \ln T + 214.16 \ln R$ | 5 | 4.44 | .50 |
| 2. $Y = -1795.69 - 30.55 T + 1070.36 \ln T + 212.63 \ln R - 3.24 R^2$ | 5 | 4.40 | .51 |
| 3. $Y = -925.34 - 23.21 R + 550.36 \ln T + 197.22 \ln R$ | 4 | 4.11 | .49 |
| 4. $Y = -992.32 + 559.26 \ln T + 172.70 \ln R$ | 3 | 2.38 | .49 |
| 5. $\ln Y = 2.39 + 0.31 T - 0.11 R - 0.01 T^2 + 0.54 \ln R$ | 5 | 4.92 | .70 |
| 6. $\ln Y = 2.18 + 0.31 T - 0.01 T^2 + 0.43 R$ | 4 | 4.56 | .69 |
| 7. $\ln Y = 1.23 - 0.08 R + 1.65 \ln T + 0.48 \ln R$ | 4 | 9.12 | .66 |
| 8. $\ln Y = 1.00 + 1.68 \ln T + 0.40 \ln R$ | 3 | 8.04 | .65 |

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

^bCoefficient of determination.

Table 11. 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 ^{2b} |
|---|----------------|-----------------------------|-----------------|
| 1. $Y = 275.278 + 8.010 T - 2090.073/T + 291.816 R - 2.515/R$ | 5 | 3.107 | .60 |
| 2. $Y = 116.850 + 16.323 T + 68.772 \ln R$ | 3 | 6.100 | .53 |
| 3. $Y = -541.332 + 291.913 \ln T + 274.360 R - 2.467/R$ | 4 | 1.578 | .59 |
| 4. $Y = -365.958 + 292.365 \ln T + 78.870 \ln R$ | 3 | 3.688 | .56 |
| 5. $\ln Y = 6.235 + 0.0147 T = 17.567/T + 0.647 R - 0.0143/R$ | 5 | 4.285 | .61 |
| 6. $\ln Y = -0.985 - 0.0761 T + 2.928 \ln T + 0.327 \ln R$ | 4 | 2.656 | .61 |
| 7. $\ln Y = 0.784 + 1.580 \ln T + 0.420 R - 0.0126/R$ | 4 | 4.926 | .59 |
| 8. $\ln Y = 1.039 + 1.643 \ln T + 0.282 \ln R$ | 3 | 0.656 | .59 |

^a p = number of constants in an equation, $C_p = \frac{RSS_p}{\hat{\sigma}^2} - (N-2p)$ where RSS_p = 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 possible variables in the equation (Gorman and Toman, 1966).

^b Coefficient of determination

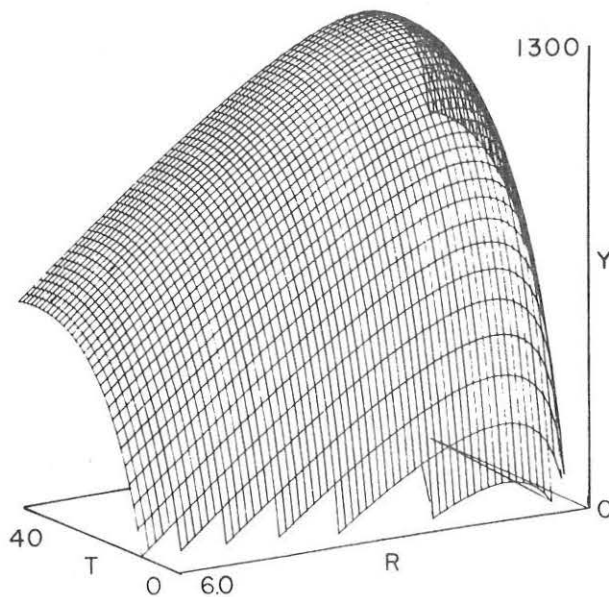


Figure 5. Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $Y = -1742.31 - 29.17 T - 20.78 R + 1044.87 \ln T + 214.16 \ln R$. Y = foraging intensity (0-1300 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40 C) at the roll-soil interface, R = daily rainfall (0-6.0 cm) (A3UNE6G, 6H, 07, 08, 09, 11, 12, 13, 14).

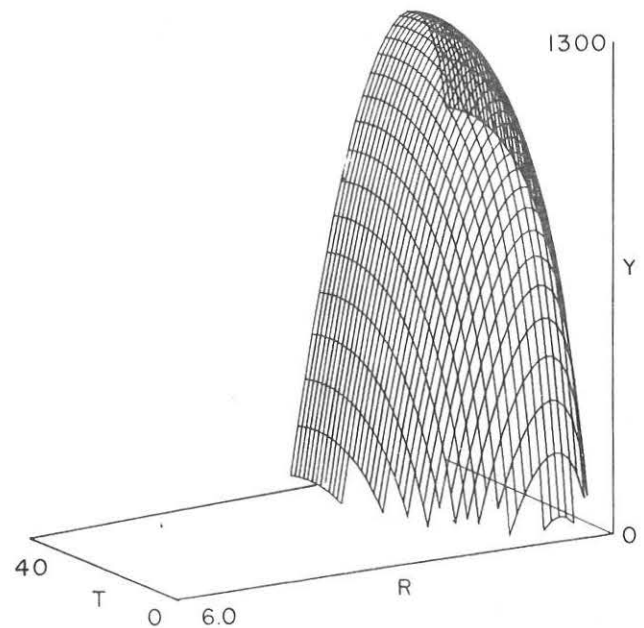


Figure 6. Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $Y = -1795.69 - 30.55 T + 1070.36 \ln T + 212.63 \ln R - 3.24 R^2$. Y = foraging intensity (0-1300 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40 C) at the roll-soil interface, R = daily rainfall (0-6.0 cm) (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

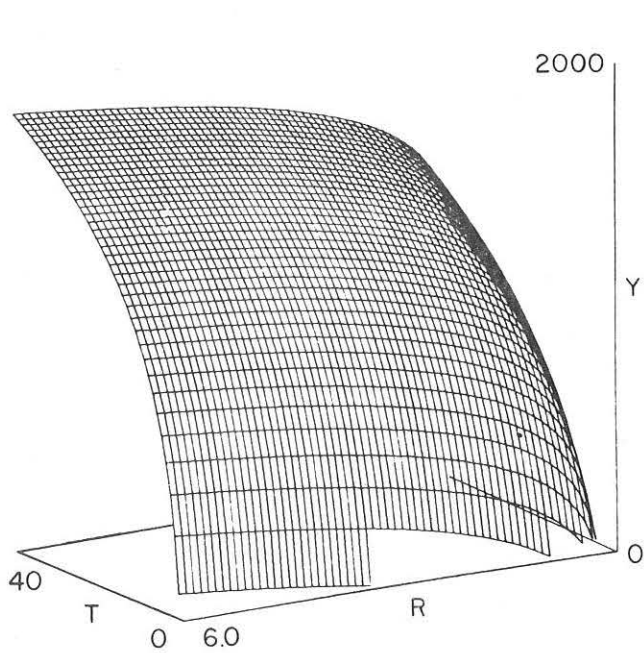


Figure 7. Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $Y = -992.32 + 559.26 \ln T + 172.70 \ln R$. Y = foraging intensity (0-2000 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40 C) at the roll-soil interface, R = daily rainfall (0-6.0 cm) (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

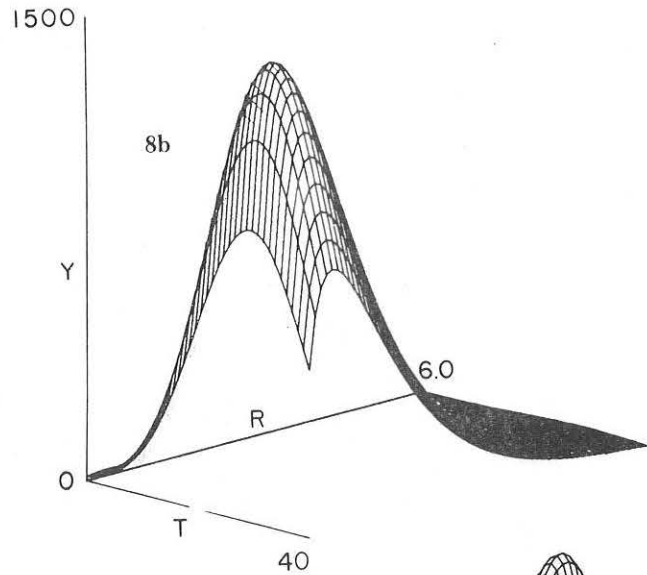
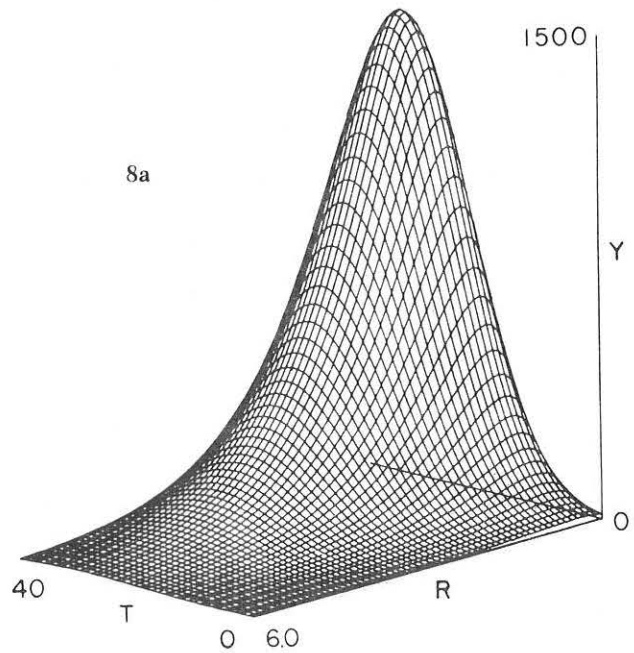
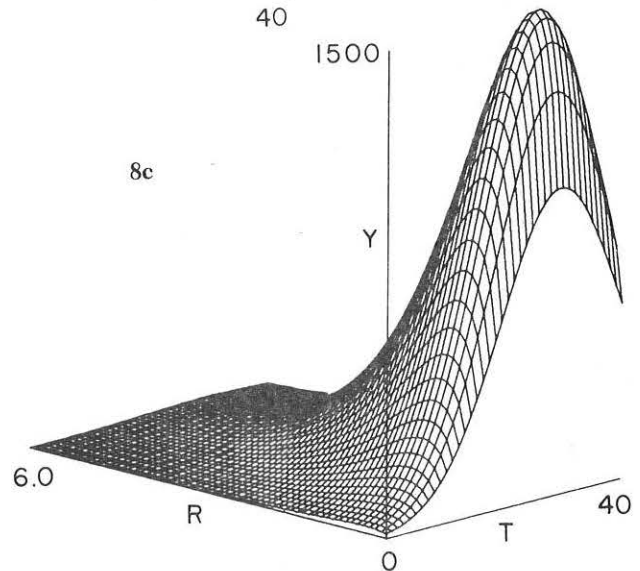


Figure 8. Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $\ln Y = 2.39 + 0.31 T - 0.11 R - 0.01 T^2 + 0.54 \ln R$. Y = foraging intensity (0-1500 termites) at 100 rolls of toilet paper, T + R as in Figure 7 (A3UNE6G, 6H, 07, 08, 11, 12, 13, 14).

(a) View from an angle which illustrates foraging intensity as a function of 1) high rainfall and varying temperature and 2) varying rainfall and low temperature.

(b) View from an angle which illustrates foraging intensity as a function of 1) low rainfall and varying temperature and 2) low rainfall and varying temperature.

(c) View from an angle which illustrates foraging intensity as a function of 1) varying rainfall and low temperature and 2) low rainfall and varying temperature.



Equation 5 (Fig. 8a) shows that foraging intensity is curtailed at low temperatures regardless of rainfall amounts. As stated earlier, this occurred during the winter rainy period of 1971. Figures 8b and 8c show that foraging intensity began to rise quickly as temperatures rose. This effect was positively modified by increasing rainfall; however, larger amounts of rain definitely suppressed activity regardless of temperature (Figs. 8a and 8c). The only area of the response surface not substantiated by actual field observations occurred where very high temperatures (> 35.0 C) and rainfall (> 3.0 cm) occurred simultaneously (Fig. 8b). This is reasonable because rainfall always reduced soil temperatures. Termite activity might be expected to decline at this combination of temperature and rainfall based on the work of Collins et al. (1973). They postulated that *G. perplexus* could withstand high external temperature best when the surrounding atmosphere contained little moisture, allowing for cooling by evaporation. The response surface predicted by equation 5 would tend to support their view.

For *H. aureus*, equation 8 (Table 11) was eliminated because it does not allow for a decrease in activity once temperature passes an optimum. Equation 6 is chosen as the best because of its high multiple regression coefficient, only three independent variables and a low $C_p:p$ ratio indicating a random estimate of error.

COLONY DENSITY AND FORAGING TERRITORY --
Heterotermes aureus

The average number of *H. aureus* foragers visiting each roll of paper/check on the 12 subplots is shown in Figure 9 while Figure 10 gives the number of weeks that each roll was part of an active foraging territory. Rolls on the four adjacent subplots and in the rows interspersed among them are identified as being attacked (+) sometime during the year or not (-). We do not know whether there were correlations between colony foci and existing dead wood since none of these items was located on our grid maps. This information thus provided the basis for our delineation of probable colony boundaries shown in Figures 9 and 10. It is entirely possible, however, that our groupings represent foraging areas or subcolonies of a much larger colony.

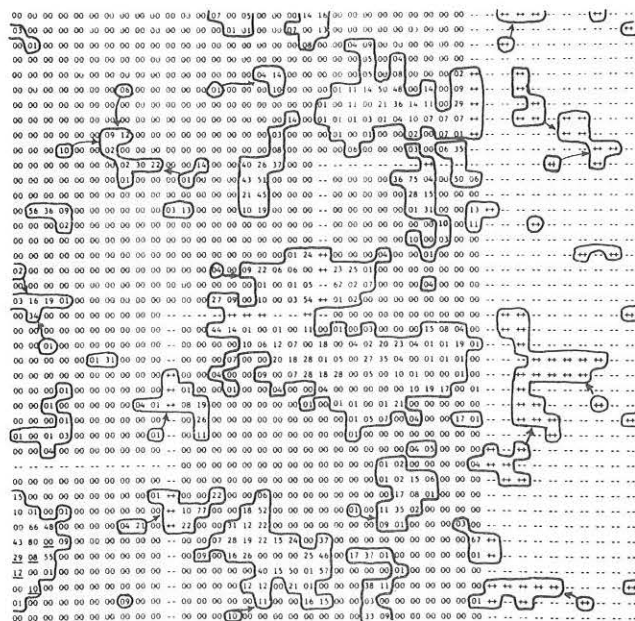


Figure 9. Foraging territory pattern and distribution for individual colonies of *Heterotermes aureus* on bait sampling grid of toilet paper rolls, Santa Rita site. Numerals represent the average number of *H. aureus* foragers observed per roll per weekly check. Underlined numerals are 100 plus the number shown. Pairs of pluses and minuses represent presence or absence of attack upon individual rolls by *H. aureus* as determined at the end of the 53-week study period (A3UNE6H).

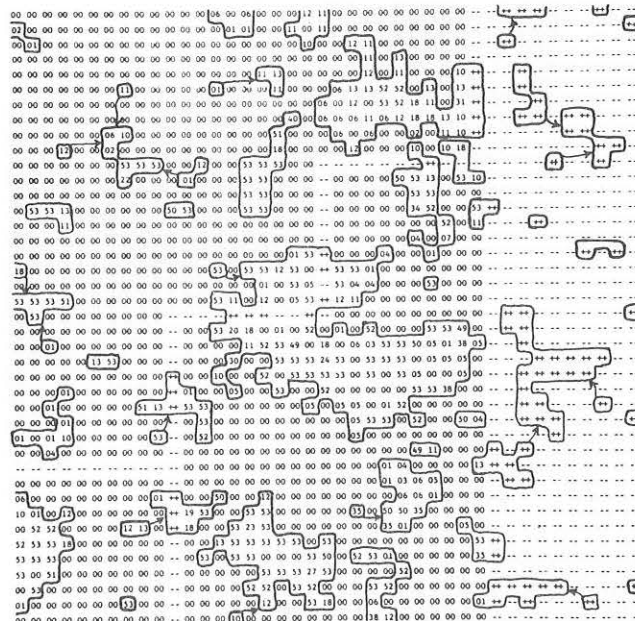


Figure 10. Foraging territory pattern and distribution for individual colonies of *Heterotermes aureus* on bait sampling grid, Santa Rita site. Numerals represent the numbers of weeks for which each roll was part of an active foraging territory. Pairs of pluses and minuses represent presence or absence of attack upon individual rolls by *H. aureus* as determined at the end of the 53-week study period (A3UNE6H).

Heterotermes attacked 383 (22.8%) of the rolls of paper. The distribution of the 26 complete and 12 partial (one-half) colony territories is outlined in Figures 9 and 10. The area of a colony averaged 12.5 m² and occasionally included a few unattacked rolls. Extrapolation on the basis of 32 colonies on the study plot gives a density of 190.4 colonies/ha.

ALATE PRODUCTION

Alate production and biomass estimates of five species from two years of field trapping at Santa Rita appear in Table 12. The corrections for the proportion of the total area occupied by *Heterotermes* remain the same as in Nutting et al. (1974, p. 68). The appearance of the flights in relation to rainfall is shown in Table 13 and considered in the Discussion.

PHENOLOGY OF DISPERSAL FLIGHTS --
Heterotermes aureus

Reduction of data from Tucson is providing flight schedules for each species as illustrated by that for *Heterotermes* (Table 14). The extreme limits of its flight season range from June 8 to October 4 (mean limits, July 11-September 1). The season ranges from 9-100 days long with a mean duration of 51.6 ± 27.1 (± S.D.). The peak flight date (day of largest flight) occurs between July 8 and August 13, with the mean at July 26 ± 10.7 days.

Table 12. Estimated numbers and biomass of termite alates trapped during the 1973 and 1974 flight seasons, Santa Rita site (A3UNE04, 20)

| Termite | 1973 | | 1974 | |
|-------------------------------------|---|--------------------|---------------------|--------------------|
| | Est. No. Alates/ha. | Biomass, g/ha | Est. No. Alates/ha | Biomass, g/ha |
| Subterranean | | | | |
| <i>Amitermes pallidus</i> | 748 ¹ | 0.98 | 1,495 ¹ | 1.96 |
| <i>Gnathamitermes perplexus</i> | 12,707 ² | 44.27 | 15,324 ² | 53.39 |
| <i>Heterotermes aureus</i> | 3,197 ² (13,455 ¹) | 3.28 | 3,286 ² | 3.37 |
| Dry-Wood | | | | |
| <i>Incisitermes banksi</i> | 14,202 ¹ | 35.36 ³ | 26,536 ¹ | 66.07 ³ |
| <i>Paraneotermes simplicicornis</i> | 21,304 ¹ | 53.11 | 26,162 ¹ | 65.22 |
| TOTALS | 52,158 | 137.00 | 72,803 | 190.01 |
| Rainfall (mm) ⁴ | 78.5 | | 166.0 | |

¹ Estimates uncorrected for proportion of total area occupied or foraged by colonies (probably high).

² Estimates corrected for proportion of total area occupied or foraged by colonies.

³ Dry weight of similar *Paraneotermes* alate used for biomass estimate.

⁴ July-Aug. average ca. 200 mm.

Table 13. Rainfall and numbers of termite alates trapped during collection intervals, 1973 and 1974 flight seasons, Santa Rita site (A3UNE20)

| | | 1973 | | | | 1974 | | | | | |
|---------------------|------------------------|---------------------|---------------------|---------------------|---------------------|-------------------------------------|------------------|--------|--------|----|---|
| Collection Interval | Rain for Interval (mm) | Alates collected | | | Collection Interval | Rain for Interval (mm) ¹ | Alates collected | | | | |
| | | Gnaper ² | Hetaur ² | Parsim ² | | | Gnaper | Hetaur | Parsim | | |
| 07 | 03/04 | 0 | 0 | 0 | 07 | 02/04 | 3.8 | 0 | 0 | 1 | |
| | 05/08 | 19.8 | 0 | 0 | 17 | 05/07 | 78.1 | 31 | 16 | 57 | |
| | 09/11 | 0 | 0 | 0 | 1 | 08/10 | 0 | 4 | 7 | 9 | |
| | 12/15 | 18.3 | 18 | 7 | 10 | 11/14 | 3.7 | 1 | 0 | 3 | |
| | 16/19 | 0 | 1 | 7 | 25 | 15/17 | 7.2 | 4 | 6 | 0 | |
| | 20/22 | 0 | 0 | 0 | 0 | 18/21 | 12.7 | 0 | 1 | 0 | |
| | 23/26 | 0 | 0 | 0 | 0 | 22/25 | 8.1 | 1 | 2 | 0 | |
| | 27/29 | 18.8 | 15 | 16 | 0 | 26/28 | 10.7 | 0 | 0 | 0 | |
| | 07/08 | 30/02 | 0 | 0 | 0 | 4 | 29/31 | 1.0 | 0 | 3 | 0 |
| | | 03/05 | 0 | 0 | 0 | 0 | 08 | 01/04 | 27.2 | 0 | 2 |
| 06/09 | | 0 | 0 | 0 | 0 | 05/07 | 3.8 | 0 | 0 | 0 | |
| 10/12 | | 2.2 | 0 | 0 | 0 | 08/11 | 0 | 0 | 0 | 0 | |
| 13/16 | | 0 | 0 | 0 | 0 | 12/14 | 0 | 0 | 0 | 0 | |
| 17/19 | | 3.9 | 0 | 0 | 0 | 15/18 | 0 | 0 | 0 | 0 | |
| 20/22 | | 0 | 0 | 6 | 0 | 19/22 | 2.0 | 0 | 0 | 0 | |
| 23/26 | | 7.6 | 0 | 0 | 0 | 23/27 | 0 | 0 | 0 | 0 | |
| 27/30 | | 0 | 0 | 0 | 0 | 08/09 | 28/02 | 4.3 | 0 | 0 | 0 |
| 08/09 | | 31/03 | 7.9 | 0 | 0 | 0 | | | | | |

¹ 3.6 mm of rain fell before 1974 collections began.

² Termite species: Gnaper, *Gnathamitermes perplexus*; Hetaur, *Heterotermes aureus*; Parsim, *Paraneotermes simplicicornis*

Table 14. Twelve-year summary of flight data for *Heterotermes aureus* in Tucson, Arizona (A3UNE22)

| Year | Flight Season, Julian Dates | Duration of Flight Season, Days | Largest Flight, Julian date | No. Flights, days | Total Alates | Avg. No. Alates/Flight, \pm S.D. |
|------|-----------------------------|---------------------------------|-----------------------------|-------------------|-----------------|------------------------------------|
| 1961 | 202-235 | 33 | 204 | 9 | 92 | 10.2 \pm 12.8 |
| 1962 | 184-271 | 87 | 209 | 16 | 599 | 37.4 \pm 76.2 |
| 1963 | 213-248 | 35 | 214 | 12 | 470 | 39.2 \pm 84.9 |
| 1965 | 191-255 | 64 | 198 | 15 | 716 | 47.7 \pm 86.0 |
| 1966 | 206-215 | 9 | 206 | 4 | 35 ¹ | 17.5 \pm 17.7 ¹ |
| 1967 | 177-277 | 100 | 198 | 11 | 518 | 47.1 \pm 94.6 |
| 1968 | 203-234 | 31 | 212 | 8 | 332 | 41.5 \pm 50.1 |
| 1969 | 197-231 | 34 | 225 | 12 | 80 ¹ | 8.0 \pm 5.7 ¹ |
| 1970 | 202-249 | 47 | 201 | 3 | 306 | 102.0 \pm 171.5 |
| 1971 | 186-234 | 48 | 223 | 7 | 118 | 16.9 \pm 34.6 |
| 1972 | 160-245 | 85 | 199 | 12 | 245 | 20.4 \pm 28.8 |
| 1973 | 189-235 | 46 | 189 | 4 | 68 | 17.0 \pm 25.3 |

¹No quantitative information available for two flights this year.

Heterotermes averages 9.4 \pm 4.3 flights/season (range 3-16). The number of alates observed at this single location averaged 31.7 (8-102) individuals/flight or 298.3 \pm 231.9 (35-599) per season.

Phenological analyses involving heat sums between the estimated beginning of alate development and peak flight data have not as yet produced very realistic results. Because the flights of *Heterotermes* and several other subterranean species appear to be closely associated with rainfall it will probably be more profitable to search for significant relationships between flight and accompanying meteorological events.

MODELING WOOD CONSUMPTION -- *Heterotermes aureus*

The model predicts 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. Foragers were thus able to make 4.61 x 10¹⁰ visits to the surface/ha during the year of simulation. It calculates that this species removed superficial dead wood at the rate of 78.9 kg·ha⁻¹·yr⁻¹. This represents 3.7% of the standing crop biomass and 17.5% of the annual production of superficial dead wood on our research area (2127 and 450 kg·ha⁻¹·yr⁻¹, respectively (Table 4). The simulated, annual consumption of individual wood species is presented in Table 15. *H. aureus* fed upon eleven categories of wood, four species of which account for 80.61% of all wood consumed in our simulation (kg·ha⁻¹·yr⁻¹): *Opuntia spinosior* (26.0), *Acacia greggii* (13.3), *O. fulgida* (13.1) and *Prosopis velutina* (11.2).

Our model also emphasizes *Heterotermes*' role in selectively removing wood from the ecosystem. Two (*O. spinosior* and *O. fulgida*) of the five dominant wood species

Table 15. Simulated annual consumption of 12 categories of wood by *Heterotermes aureus*, and percentage of dead wood standing crop biomass consumed (No DSCODE)

| Wood species | Annual consumption (kg/ha/yr) | % annual consumption of standing crop |
|---|-------------------------------|---------------------------------------|
| <i>Acacia greggii</i> | 13.3 | 2.1 |
| <i>Celtis pallida</i> | 5.6 | 32.8 |
| <i>Cercidium floridum</i> | 2.3 | 1.7 |
| <i>Ephedra trifurca</i> | 3.5 | 43.1 |
| <i>Gutierrezia sarothrae</i> | 0.5 | 6.6 |
| <i>Opuntia engelmannii</i> | 1.6 | 15.9 |
| <i>Opuntia fulgida</i> | 13.1 | 3.7 |
| <i>Opuntia spinosior</i> | 26.0 | 8.3 |
| <i>O. fulgida</i> and <i>spinosior</i> , joints | 1.1 | 0.4 |
| <i>Prosopis juliflora</i> | 11.2 | 3.1 |
| Other woods | 0.8 | 11.4 |
| All woods, average | 78.9 | 3.7 |

Table 16. Wood preference indices (probability of attack for each wood species divided by probability of attack for all woods combined) of four termite species for five species of wood (A3UNE02)

| Wood species | <i>Heterotermes aureus</i> | <i>Gnathamitermes perplexus</i> | <i>Paraneotermes simplicicornis</i> | <i>Amitermes</i> spp. |
|--|----------------------------|---------------------------------|-------------------------------------|-----------------------|
| <i>Acacia greggii</i> | 1.12 | 0.43 | 4.93 | 3.06 |
| <i>Cercidium floridum</i> | 0.61 | 0.92 | 0.00 | 2.75 |
| <i>Opuntia fulgida</i> | 1.35 | 1.02 | 1.52 | 0.40 |
| <i>O. fulgida</i> , joints | 0.18 | 1.86 | 0.00 | 0.00 |
| <i>Opuntia spinosior</i> | 1.40 | 1.23 | 0.00 | 0.42 |
| <i>O. spinosior</i> , joints | 0.00 | 1.65 | 0.00 | 0.00 |
| <i>Prosopis juliflora</i> var. <i>velutina</i> | 0.72 | 1.09 | 0.26 | 1.14 |

(plus *Cercidium floridum*) are consumed by *H. aureus* at a rate equal to or greater than that of the overall average (Table 15). Although substantial quantities of *A. greggii* and *P. velutina* are consumed, this is only a small proportion of the standing crop of each species (2.10 and 3.11%, respectively; Table 4). The larger portion of the latter two wood species is probably consumed by other soil-dwelling termites, *Gnathamitermes perplexus* (Banks), *Paraneotermes simplicicornis* (Banks) and *Amitermes* spp., which allocate a substantial portion of their foraging activities to these two woods (Table 16).

Of the remaining, less abundant, species of wood, *H. aureus* appears to exert extreme pressure on both *Celtis pallida* and *Ephedra trifurca*. Since *Celtis* is highly preferred and attacked almost exclusively by *H. aureus*, one would expect a heavy impact on this species. *Ephedra*, on

the other hand, is less preferred but attacked as often by *G. perplexus* as by *H. aureus* (Table 9). It is curious then, that the model predicts such a high annual consumption of this wood. The average, temperature-dependent consumption rate of *E. trifurca* may be much too high.

DISCUSSION

Improving our estimation of the effectiveness of termites as detritivores has been one of our major concerns. To this end we have extended some analyses to include more species of termites, refined a number of estimates and revised our wood-consumption model. The resulting, updated figure for wood consumption by all subterranean termites at Santa Rita is included here for the record. Since a number of subjects bearing on this problem can now be referred to manuscripts or publications, they will be considered only briefly below.

Caste proportions in termite colonies or foraging groups are known to vary with the time of day, season, species and colony size or age, with the most dramatic manifestations being associated with flights (Bodot 1969 and 1970, Sands 1965, Bouillon 1964, Noirot 1969, Nutting 1970). Knowledge of caste composition is necessary for converting termite numbers to an accurate biomass figure. With some species, especially those with a high percentage of one caste, numbers and biomass are highly correlated. But with others such as *P. simplicicornis* with several castes of unequal biomass, caste composition is critical for calculating biomass.

Subterranean termites are not usually randomly dispersed in the soil because of their aggregations into colonies and foraging parties (Sands 1972). Our results support Sands' view that termite distributions are best described by the negative binomial (Table 6). Therefore, we must accept sample population values with great variability for extrapolating to larger unit areas.

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 semiarid regions of Australia. Total termite numbers/m², 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 estimate the density of *Gnathamitermes tubiformans* in the upper 30 cm of soil in a semiarid grassland in Texas. From February through November the mean was 4135 termites/m², which approached the highest termite density ever recorded (4450/m²) for all species of termites in an area (Lee and Wood 1971). From May through July the subsurface density was 3796.7/m², with a surface density of 33.3/m² -- only 0.877% of the measured population.

Rocky soil influenced our decision to sample surface foraging groups rather than subsurface numbers. It is unlikely that absolute colony sizes can be determined practically, i.e., by digging, for one or more of the species we have studied, and there from total termite numbers per unit area. It may therefore be of some value to speculate on the size of subsurface numbers of *H. aureus*, *G. perplexus*, *A. wheeleri* and *A. minimus*, based on Bodine's (1973) subsurface:surface proportions (114:1) of *G. tubiformans*. From extensive field experience with *P. simplicicornis* we feel that the ratio would be much lower, ca. 10:1 for this species. On the basis of the foraging groups collected during 13 months of circledrat sampling, we estimate the average surface foraging force for *H. aureus* to be 6.89; *G. perplexus*, 0.35; *P. simplicicornis*, 1.31; *A. wheeleri*, 1.51; and *A. minimus*, 0.12 termites/m². Using Bodine's subsurface:surface proportion, we estimate the numbers of these species of termites to be 786, 40, 13, 172 and 14 termites/m², or a total of 1025 termites/m². Similarly for biomass, the figures would be 0.275, 0.025, 0.033, 0.077 and 0.004 g/m², or a total of 0.414 g/m². Even though two uncommon or cryptic subterranean species are not included in this estimate, total termite density is higher than any cited by Lee and Wood (1971) for arid or semiarid situations. However, it is still less than one fourth of Bodine's figure for *G. tubiformans* in west Texas.

As far as we are aware, only two efforts have been made 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/ha, 30.4% or 700 kg was logs and sticks. The standing crop biomass of litter in this same area was 7338 kg/ha (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 2231 kg/ha. Their dry sclerophyll forest is thus apparently very similar in its standing crop biomass and annual production biomass of dead wood (2231 and 700 kg/ha) to that of the desert grassland of the Santa Rita Experimental Range (2127 and 450 kg/ha). Additional similarities occur in that the most common termite, *Nasutitermes exitiosus* (Hill), is present in numbers (600/m²) comparable to *H. aureus* (786/m²).

Generally, factors such as climate, vegetation and soil interact in their effects on the distribution and abundance of termites so that it is often not possible to determine whether or not one is dominant. Within a small geographical area, climate is sufficiently equitable that only soils and vegetation interact to affect termite abundance and dispersion. The major interactions are shade or plant cover, water holding capacity of soil with a particular vegetation complex, and variety and quantity of food plants (Lee and Wood 1971).

We have felt that standing crop of superficial dead wood must be a key factor in determining the abundance of many of the termites on our study area. As our results indicate, the

abundance of only two of the five termite species appears to be correlated with superficial dead wood biomass; *H. aureus* with *O. spinosior* and *P. simplicicornis* with *A. greggii*. These plant species are also among their preferred hosts (see Host-wood Preferences). *Gnathamitermes* is a general feeder and, as a result, shows no such relationship with dead wood biomass. The fact that the *Amitermes* spp. have a definite preference for *A. greggii* probably explains the high correlation coefficient (Table 8) with dead wood of that plant. In summary, the dispersion of both the surface foraging populations of five species of subterranean termites and the standing crop biomass of their food material is not random in this desert grassland ecosystem. The abundance of the termites appears to be correlated with dead wood standing crop of a particular plant species only in those termites which show strong feeding preferences.

We have chosen to use frequency of attack on wood species present in the field, or an essentially free choice situation, as a measure of termite wood preference. Others have determined preferences in both free choice and compulsory laboratory feeding experiments. Sands (1961) has shown that *Trinervitermes* spp., if given an option of many grasses, will harvest those of preferred species and fragment size. These preferences allow the coexistence in one area of five species of *Trinervitermes*, provided a suitable mosaic of conditions is met. Nel et al. (1970) found that *Hodotermes mossambicus* (Hagen) preferred certain grasses when given a choice between a control and test species. By measuring wood consumption and survival, Smythe and Carter (1970) found the preferences of *Coptotermes formosanus* Shiraki, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) to be similar whether compulsory or choice feeding tests were used. McMahan (1966) determined preferences of *Cryptotermes brevis* (Walker) by measuring the quantity of wood consumed in a free choice test.

Our studies demonstrate that if the wood consumption technique is used, especially in a compulsory test, it might easily lead to erroneous conclusions about wood preference. *H. aureus* scored a higher probability of attack (resulting in a higher preference rating) on the wood of the chollas and on catclaw acacia than on mesquite and especially blue paloverde. Its probability of attack on blue paloverde, and the resulting preference rating, are extremely low. This contrasts sharply with its high rate of consumption of paloverde in compulsory laboratory tests (Haverty and Nutting 1974). If wood consumption in compulsory feeding tests had been used as a measure of preference, blue paloverde would have been ranked significantly more preferred than cholla, mesquite and catclaw acacia.

Table 16 gives the preference index for each termite species on the five dominant species of wood. The wood of the chollas is worked preferentially by three species; however, their modes of attack render their workings mutually exclusive; *G. perplexus* attacks only weathered surfaces, seldom penetrating sound wood. The fallen joints of cholla are almost exclusively attacked by *G. perplexus*. *P.*

simplicicornis utilizes only the stumps and larger roots of jumping cholla while *H. aureus* attacks stumps, trunks, branches and fragments of both chollas, essentially whatever is not occupied by the others or by ants.

Mesquite is a preferred host of *G. perplexus* and *Amitermes* spp. Both attack superficial and partially buried pieces in different ways. Although the data do not show it, large buried mesquite stumps are almost exclusively attacked by *P. simplicicornis*. *Amitermes* spp. concentrate more effort on paloverde than do the other termites. In contrast three termite taxa (*H. aureus*, *P. simplicicornis* and *Amitermes* spp.), each with similar modes of attack, concentrate an above-average amount of attention on catclaw acacia. All combinations of pairs of the three species have been found on catclaw acacia but never all three at once. In terms of mass of dead wood, this species is the most abundant on our research site (Table 4). The wood is not evenly distributed but occurs as large concentrations in the form of partially buried limbs under trees or as isolated dead trees. Such a concentration of wood, perhaps in different states of decay, may account for these three species exploiting the same food source.

In the lower elevations of this shrub-invaded, desert grassland, five plant species (Table 4) account for 97.6% of the standing crop biomass of superficial dead wood. The four major termite species here do not appear to compete heavily for these food sources, but maintain mutually exclusive niches through distinctive modes of attack and specific wood preferences.

Although it is possible that seasonal fluctuations in numbers of foraging *Heterotermes* and *Gnathamitermes* were influenced by endogenous rhythms (Bouillon 1970), our data strongly indicate that temperature and rainfall are the primary controlling factors. DeBruyn and DeBruyn (1972) reported a quadratic relationship between ground-level temperatures and numbers of *Formica polyctena* Först workers on a foraging path. Finnegan (1973) reported an increase in foraging activity with increasing temperature for three species of *Formica* in Quebec. At lower and medium range temperatures foraging numbers of both species increase logarithmically with increasing temperature, but this effect is dampened at higher temperatures. Rainfall, with associated increases in soil moisture and humidity, and a corresponding decrease in saturation deficit, also accentuated the increase in foraging numbers of both species. In contrast, ants, which have a more heavily sclerotized cuticle, are less dependent on a low saturation deficit (Finnegan 1973, Nielsen 1972) than are termites (Bodot 1967, Bouillon 1970).

Notwithstanding these obvious environmental parameters, internal colony pressures may also affect foraging. Bouillon (1970) reported that the seasonal foraging cycle is also related to an annual cycle of the number of individuals in the colony, variable caste composition and nutritional status of the colony. Bodot (1967) found that foraging

increased with the appearance of reproductive nymphs in a colony and decreased after the appearance of winged reproductives. With either *Heterotermes* or *Gnathamitermes* no such influence of colony nutrition or alate production was obvious. When nymphs of *Heterotermes* were present, from late November to early June, foraging was not particularly intense even though temperatures were very favorable.

In the Sonoran Desert, both species forage throughout the year under a wide range of temperatures. While foraging intensity is regulated primarily by temperature, its effect is modified by soil moisture. Equations describing this relationship will be coupled with temperature-dependent wood-consumption rates to estimate the quantity of wood processed by these termites in the desert.

When compared with the few other species that have been studied, the average foraging territory of the *Heterotermes* colony is very small (12.5 m²), although colony density is correspondingly high (190.4/ha). Nel (1968) observed the foraging behavior of 16 colonies of the harvester, *Hodotermes mossambicus* on a 2980-m² plot. Of these, 13 were wholly within the area and three were bisected by its borders. Nel determined the mean territory of 12 colonies to be 92.1 m², while calculations comparable to ours give 48.7 colonies/ha. Other literature reports of colony density are for mound-building species (Lee and Wood 1971). Greaves (1962) reported that foraging galleries of *Coptotermes acinaciformis* (Froggatt) radiated from the mound to a maximum of 47.5 m and those of *C. brunneus* Gray to 45.7 m. Colonies of both *C. acinaciformis* and *C. brunneus* were spaced consistently at 90 m apart, each apparently controlling an area of at least 8210 m².

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 et al. 1965, Elton 1932, Nel 1968, and Wilson et al. 1971). The colony territories of *H. aureus* do not appear to overlap and neutral zones occur between most of them. In some cases, however, their boundaries are tangential, expanding until apparently halted by contact with neighboring colonies (Fig. 10). Since foraging is dynamic, territories on our study plot probably expanded to exploit the new, uniformly distributed food source. Whether or not discrete boundaries are maintained by intraspecific aggressive behavior as Nel (1968) reported is not known.

In many habitats, including the Santa Rita Experimental Range, there seems to be much unexploited food for termites. Emerson (1955) has observed this in many parts of the world and has postulated that competition for colonizing and nesting sites is greater than for nutritive resources. Wilson (1971) has also noted that the intrinsic rate of population increase for termites is low. Therefore, it is doubtful that the addition of rolls of paper at the rate of 1769 kg/ha accounted for any increase in termite numbers, and hence an expansion of territory. In fact, the amount of paper was less than the original standing crop biomass of

superficial dead wood (2127 kg/ha; Table 4). The territorial expansion we observed appears more likely to have been the result of a general increase in foraging activity. Most rolls were attacked during the first five weeks of the study, from October 15 to November 12 (roll values 49-53; Fig. 10), and during the last 18 weeks, from June 8 to October 13 (roll values 1-18; Fig. 10). This coincides with periods of high foraging activity for this species (Fig. 3).

The number of individuals in a colony of an entirely subterranean species has never been reported; therefore, we feel that it should be profitable to speculate on average colony size based on the data presented here. During our study we observed an average of 3.78 foragers per roll/weekly check (Fig. 9). Bodine (1973) used soil cores to estimate the density of *Gnathamitermes tubiformans* in the upper 30 cm of soil in a semiarid grassland in Texas. From May through July he observed that the subsurface density was 3797 termites/m², with a surface density of 33.3/m². If we assume that *H. aureus* has the same subsurface:surface proportions (114:1) as *G. tubiformans*, the total density of *H. aureus* would be 4.31×10^6 termites/ha. Dividing the total number of termites by 190.4 colonies/ha, we get an estimated, 22,632 termites/colony. This estimate is highly speculative but, in the absence of others for comparison, we feel not at all unreasonable.

We are convinced that long-term use of similar bait-sampling grids, local environmental conditions permitting, should reveal much information on the characteristics and behavior of subterranean termite populations around the world. It should be particularly useful, especially when combined with other methods such as core-sampling or some variation of the mark-recapture technique.

The 1973 and 1974 flight seasons were very different with respect to rainfall (Table 12). In 1974 (July 2 to September 3) the site received 166.0 mm of rain compared with 78.0 mm in 1973 (July 1 to September 3). However, total numbers of alates of *H. aureus* and *G. perplexus*, both of which appear to be dependent on summer rainfall (Nutting 1969), differ very little from one season to the next. Although our analysis of environmental parameters affecting termite flights has only begun, this suggests that the total number of alates which emerge is not dependent upon, or correlated with, the amount of rain occurring during the flight season.

On the other hand, individual flights do appear to be associated with, or triggered by rainfall. Table 13 presents the collection records for 3- or 4-day intervals during both flight seasons. Flights of *G. perplexus* and *H. aureus* in general occur with, or shortly after, rains greater than 3.0 mm. *Paraneotermes* flights appear here to be associated with storms of greater than 18 mm, and several flights occurred in 1974 after an extremely large storm (78.1 mm) although its season is known to begin well in advance of the summer rains (Nutting 1966). The cue which triggers their flight activity is unknown, but it is certainly not rainfall acting alone since flights of all three species are sometimes

staged on rainless evenings. Flight cues may also include one or more of the following: changing light intensity or barometric pressure, atmospheric electricity and increases in soil moisture (Nutting 1969).

Wood or food consumption by termites may be measured directly by weight difference of food offered for a given period of time (Nutting et al. 1973, see below). However, if direct measurement is not practical, indirect estimates of consumption can be derived through two types of simulation. The first requires a detailed knowledge of the species energy budget and population parameters (Josens 1973). If maintenance and production energy requirements are known for a population of a certain size, it should be possible to predict, a posteriori, the amount of food it would need to consume in order to meet its energy requirements under given environmental conditions (Hadley 1972). The second approach requires a knowledge of population parameters and behavioral responses under known environmental conditions. Wood consumption is predicted, a priori, by coupling population numbers or foraging sorties with temperature-dependent, species-specific food consumption rates as we have done here.

We have determined the number of termite foragers attacking a food source per unit time as the product of two temperature-dependent functions: the size of the surface foraging force and the rate at which it turns over. DeBruyn and DeBruin (1972) have used the same type of logic in developing a model to determine the number of *Formica polyctena* Först captured in pitfall traps (N_t). This number is the product of two factors: $N_t = (P_t)(V_t)$ where P_t is the number of ants present at a given temperature and V_t is their velocity at this temperature.

We have assigned *H. aureus* foraging biomass proportionately among the wood species (or categories) on the basis of carefully determined preferences (Table 3). The resulting partitioned foraging biomasses are then coupled with specific, temperature-dependent wood consumption rates which were determined in laboratory tests (Haverty and Nutting 1974). In his simulation of ant food consumption, Baroni-Urbani (1972) assigned all foragers of a particular species to the most preferred food. If this food was being utilized by another ant species or otherwise not available, foragers were then assigned the next most preferred food and so on. However, we do not believe that this is a realistic way to assign termite foragers among wood species (food). Long-term simulation over large areas requires a model to describe and utilize average behavior (Watt 1962). Even though *H. aureus* prefers certain woods it does utilize almost all sources of woody plant material.

Direct measurement of paper (essentially pure cellulose) consumption by *H. aureus* in the field was shown to be at least $19.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and possibly as much as $33.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Nutting et al. 1973). Our simulation estimates of annual wood consumption by *H. aureus* ($78.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) are, therefore, of a reasonable order of magnitude and considerably less than (17.5% of) the annual accumulation

($450 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Table 4). Certain parameters used in the model are undoubtedly contributing to the over- or underestimation of consumption, and should be refined.

We believe our foraging population figures are good since our periodic visual estimates were verified against actual counts, and the relationships between foraging intensity and environmental factors are quite good ($R^2 = .612$, $\alpha < .01$; Table 9). However, forager speed may be excessive since it was determined for horizontal and not vertical movement, and does not allow for any inefficiency. Many students of social insects have noted that these insects spend a good deal of their time idle (Wilson 1971). Such considerations might easily cause overestimation of the forager turnover rate.

Wood consumption rates determined in the laboratory are probably lower than they would be in the field. This is because termites in laboratory test groups have relatively few nest mates to feed and, since they do not appear to store wood, they consume only what they need for themselves. Therefore, in our model, any overestimating of wood consumption due to an excessive turnover rate might tend to balance the underestimation caused by low consumption rates.

Termites may have a considerable role in the removal and recycling of plant material in an ecosystem. The effect of termite grazing can be so great that whole areas are denuded of grass (Coaton 1951, Watson and Gay 1970). Basson (1972) conservatively estimated that *Hodotermes mossambicus* (Hagen) removed $274 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ from veld in South Africa. Nel (1970), in a different area, calculated the same species to remove only $14.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ or 1% of the total production of dry material. Bodine (1973) estimated that *Gnathamitermes tubiformans* (Buckley) removed 360 kg of grass per ha/yr from rangeland or 12% of the net primary productivity. Lee and Wood (1971) estimated that *Nasutitermes exitiosus* (Hill), which feeds on sound wood, consumed $116 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ or 16.6% of the annual production of superficial dead wood ($700 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) in a dry sclerophyll forest in Australia. Both Bodine (1973) and Lee and Wood (1971) used consumption rates determined at one temperature to predict annual consumption of grass or wood.

Our simulated estimate of the effect of *H. aureus* on the fallen dead wood in a desert grassland is comparable to that of *N. exitiosus* in Australia. Each species apparently processed an almost equivalent proportion (17.5 and 16.6%, respectively) of the annual accumulation of fallen sticks and logs. The impact of *Heterotermes* on wood removal is greatest in its selective pressures exerted on certain species of wood, notably *Opuntia spinosior* and *O. fulgida*.

In conclusion, Table 17 presents a breakdown of our current best estimates of dead wood consumption by all 10 species of termites known from the Santa Rita site. It should be noted that the estimate for *Heterotermes* is the only one

Table 17. Best estimates of dead wood consumption by the ten species of termites known from the Santa Rita site (A3UNE02, 04, 6G, 6H, 07, 08, 09, 17)

| Termite | Feeds on Detritus Class ¹ | Consumes kg/ha/yr | Residual, Partially macerated material | Feces, kg/ha/yr ² |
|-------------------------------------|--------------------------------------|-------------------|--|------------------------------|
| <i>Heterotermes aureus</i> | 1,3 | 78.9 | Trivial? | 31.8 |
| <i>Gnathamitermes perplexus</i> | 1,2,3,4 | ca. 240 | Trivial? | 96.8 |
| <i>Paraneotermes simplicicornis</i> | 1,3 | ca. 45 | Very little? | 18.1 |
| <i>Amitermes wheeleri</i> | 1,3,4 | ca. 25 | Trivial? | 10.1 |
| 6 others ³ | 1,2,3,4 | ca. 25 | Very little? | 10.1 |
| Fungi | | 49.1 | | |
| Total | 1,2,3,4 | 463 ⁴ | Trivial? | 166.9 |

¹ Detritus classes: 1, Dead wood; 2, Leaf and plant reproductive material; 3, Dead roots; 4, Dead animal material and dung.

² Calculated from regression of wood consumption on fecal material production for small colonies of *Marginitermes hubbardi*: $Y = 70.77 + 2.48X$ (Nutting, 1973, p. 12).

³ Four subterranean species: *Amitermes emersoni*, *A. minimus*, *A. silvestrianus*, *Tenurotermes tenuirostris*; 2 dry-wood species: *Incisitermes banksi*, *Pterotermes occidentis*.

⁴ Represents 103% of dead wood production of 450 kg/ha/yr.

based on reasonably good, temperature-dependent functions of foraging intensity and wood consumption. Our "best guesses" for the other nine species vary in reliability since they are based on fairly good population data for three other subterranean species (*Gnathamitermes perplexus*, *Paraneotermes simplicicornis*, *Amitermes wheeleri*) and one dry-wood species (*Pterotermes occidentis*), but essentially no population information for three other subterranean (*A. emersoni*, *A. minimus*, *A. silvestrianus*) and one dry-wood species (*Incisitermes banksi*) which are rare and poorly known. The wood-consumption rates determined for *Heterotermes* have been used in our consumption estimates for these nine other species. We have estimated that fungi might conceivably remove about 10.9% of the annual dead wood production (Nutting et al. 1974). Total consumption of dead wood detritus at Santa Rita is thus estimated at $413.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ by the termites (92% of the annual production of $450 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) and at $463 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ by termites and fungi together (103% of annual production). Table 17 also includes estimates of the amounts of residual detrital material and feces delivered by the termites to the decomposition processes.

EXPECTATIONS

Our research plans for 1975 appear in approximate priority below. Only items 3 and 6 are completely new. We will continue to devote a considerable amount of time in preparing data for publication.

1. Determine rates of wood consumption for a dry-wood termite, *Marginitermes hubbardi*, in terms of milligrams of wood consumer per hr/g-dry weight of termite at various temperatures on several wood species.
2. Determine metabolic energy values for *M. hubbardi* using the same environmental parameters as in number 1.
3. Determine major nutrient constituents in wood used for consumption trials in number 1.
4. Determine nitrogen balance for *M. hubbardi* under similar conditions.
5. Determine the amino acid and lipid composition of several termite species with primary emphasis on alates to assess the nutritional suitability of termites as prey.
6. Exclude termites and/or other soil organisms from wood samples by appropriate chemical treatment to furnish preliminary data concerning arthropod-micro-organism interactions.

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