ENVIRONMENTAL FACTORS CONTROLLING THE FORAGING BEHAVIOR OF A DESERT SUBTERRANEAN TERMITE, *GNATHAMITERMES PERPLEXUS* (BANKS)

by

Jeffery Paul La Fage

A Thesis Submitted to the Faculty of the

DEPARTMENT OF ENTOMOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

MASTER OF SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 7 4

STATEMENT BY AUTHOR

This thesis has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Jeffery Paul La Fage

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

William L. Nutting
WILLIAM L. NUTTING
Professor of Entomology

September 18, 1974
Date

ACKNOWLEDGMENTS

My sincere gratitude is extended to Dr. William L. Nutting for his continued advice and patience throughout the preparation of this thesis. I am also indebted to Dr. Larry Crowder and Dr. Gordon Waller for reviewing this manuscript and for serving on my graduate committee. For their helpful suggestions concerning statistical analyses, I am indebted to Dr. James Gebert and Dr. Robert Kuehl. Appreciation is also extended to Mr. Mike Topliff of the University of Arizona Computer Center for his patient assistance in computer graphing.

For their assistance in gathering field data, I am grateful to my wife, Wendy, Dr. W. L. Nutting, Dr. Michael I. Haverty, Marsha Haverty, Mrs. Ruth Nutting, Jeff Nutting, Gardner Nutting, Don Chandler, Dr. Margaret Collins, and Dr. Richard V. Carr. For their help in processing field data, appreciation is extended to Ms. Verne King, Dr. C. Romesburg, Dr. Kim Bridges, and Dr. Mark Westoby.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--*Continued*

LIST OF TABLES

ABSTRACT

Toilet paper rolls, set out at 1-m intervals in a block of 16 10 x 10-m plots, provided the basis for a year-long study of daily and seasonal variations in the foraging behavior of the subterranean termite, *Gnathamitermes perplexus* (Banks) (Termitidae: Amitermitinae). Maximum foraging density and dry-weight biomass were estimated at 705,200 foragers/ha and 451.2 g/ha respectively. Foraging activity was limited by upper soil temperatures (0-15 cm) within the range 9-49°C. Periodic rises in soil moisture resulting from rainfall modified foraging intensity. *G. perplexus* foraged at nearly 100 per cent of the toilet paper rolls on the study site. The number of foragers observed at the surface at a given point in time can be predicted by the equation, $\ln Y = 2.39 + 0.31\ T - 0.11\ R - 0.01\ T^2 + 0.54 \ln R$, where Y = the number of termites at 100 rolls of toilet paper, T = the daily mean temperature at the roll-soil interface, and R = daily rainfall.

INTRODUCTION

Subterranean termites are among the most abundant but cryptic of animals, a factor making behavioral studies very difficult. Consequently, little is known of their foraging behavior or general activity patterns. Previous studies dealing with the diurnal or seasonal dynamics of foraging have been primarily restricted to harvesters which forage in the open (Bodot 1967, Bouillon 1970) or mound builders which construct above-ground structures (Bodot 1967, Bouillon and Lekie 1964, Sands 1961). This concentration of effort on the harvester and mound-building species has created the impression that they are more important ecologically than the more cryptic, totally subterranean species (Sands 1972). Although the density of a totally subterranean termite population has never been estimated reliably (Lee and Wood 1971), it is probable that these species are at least as numerous and ecologically significant as the harvesters or mound builders (Sands 1972).

The genus Gnathamitermes includes four species which are found in the semi-arid to arid regions of the southwestern United States and northern Mexico (Weesner 1970). All four species construct protective shelters of soil particles over food substrates (Light 1934, Weesner 1970) (Figure 1). Within these shelters they often entirely

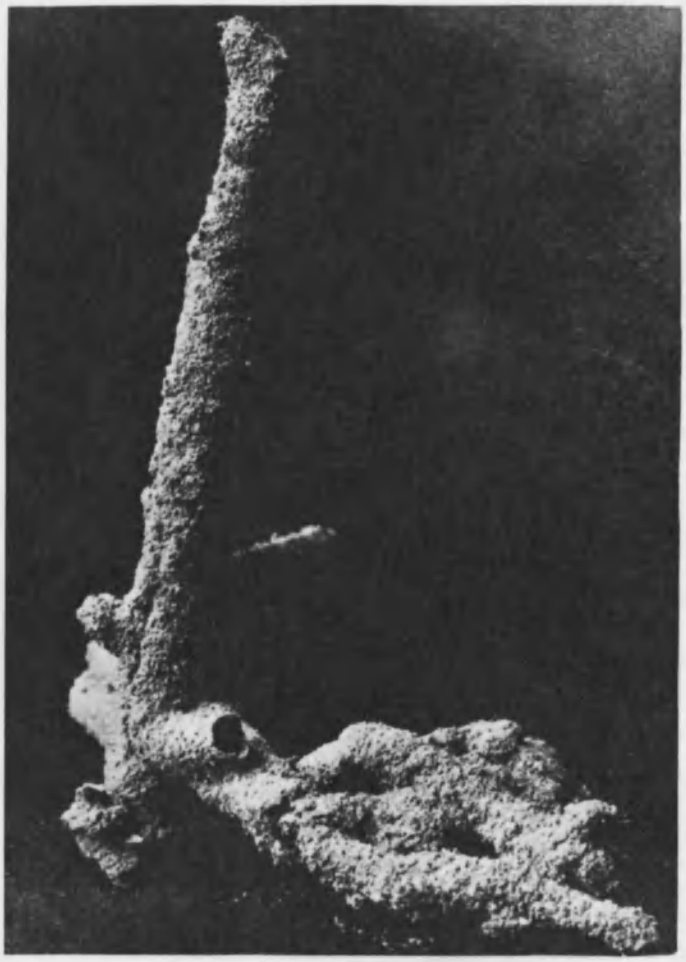


Figure 1. Earthen shelters built by <u>Gnathamitermes</u> sp. in California -- The hollow tubes were left after the plant was consumed. X 0.92. (From Light, Randall, and White, 1930.)

consume the plant material leaving nothing but the hollow tubes. From larger or woody materials only the outer weathered layer is removed.

G. perplexus (Banks) is found throughout Arizona, southern California, southern Nevada, far-western Texas, and northern Mexico (Weesner 1970). It normally does not attack agricultural crops or structures and thus is not considered an economic pest. It is probable, moreover, that this termite is an important and highly beneficial detritivore in the Sonoran Desert. In this area, where earthworms are apparently absent (Nutting, Haverty, and La Fage 1973), *G. perplexus* may be an important factor in aerating the upper soil horizon. Recent data (Nutting et al. 1973) demonstrate that this termite moves considerable quantities of soil to the surface annually. Furthermore, like all termites, it is active in the gradual breakdown and recycling of dead organic materials.

This study was undertaken with the objective of determining some of the environmental factors which regulate the foraging behavior of *G. perplexus*.

MATERIALS AND METHODS

Site Description

The study site was located 40 km south of Tucson, Arizona, on the Santa Rita Experimental Range, at 950 m elevation. The United States Forest Service has made this study area available to the United States International Biological Program, Desert Biome on a continuing basis since 1970. The average annual rainfall of 33 cm occurs equally divided between the winter and summer rainy seasons. Air temperatures typically range from near 40°C in mid-summer to a few degrees below 0°C during winter months. The difference between maximum and minimum daily air temperatures varied from 6-24°C during the study period (Figure 2).

The area is a shrub-invaded, grassland ecotone, characterized by scattered trees, shrubs, and cacti. The predominant trees are mesquite [*Prosopis juliflora* var. *velutina* (Woot.) Sarg.] and blue palo verde (*Cercidium floridum* Benth.). The shrub layer is made up mainly of burrow weed [*Aplopappus tenuisectus* (Green) Blake], and the dominant cacti are the chollas [*Opuntia fulgida* Engel. and *O. spinosior* (Engel. and Bigel.) Toumey]. The perennial grasses, which constitute an important part of the diet of *G. perplexus*, are scattered along water courses and beneath the crowns of trees and shrubs. The five species which

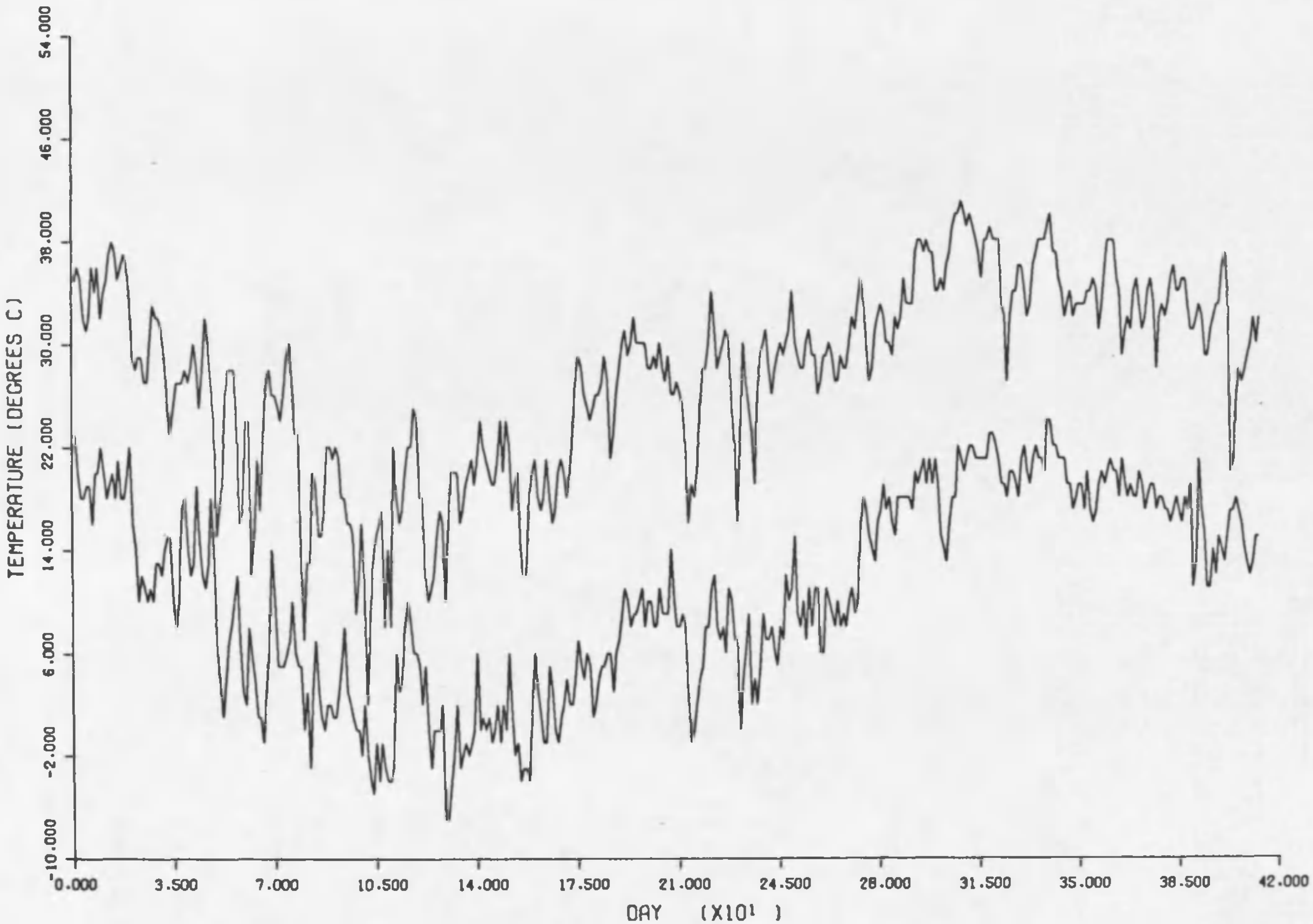


Figure 2. Daily maximum and minimum air temperatures from August 29, 1971 to October 13, 1972 (day 0-420) on the Santa Rita Experimental Range, Pima County, Arizona -- Temperatures were recorded with a hygrothermograph located at the south edge of the bait-sampling grids used to monitor the foraging behavior of Gnathamitermes perplexus.

dominate on the study site are, spider grass (*Aristida ternipes* Cav.), Santa Rita threeawn [*A. glabrata* (Vasey) Hitchc.], *A. hamulosa* Henr., Rothrock gramma (*Bouteloua rothrockii* Vasey), and Arizona cotton grass [*Trichachne californica* (Benth.) Chase].

Sampling Methods

A modification of the bait-sampling technique (Sands 1972) was used to determine the physical factors which are most important in regulating the foraging behavior of *G. perplexus*. Bait materials were placed on grids located on the limited destructive sampling area of the chained plot. This area was selected because it had been cleared of all large shrubs and trees 18 months earlier. Before placing bait on the grids all remaining large debris was removed from an area 40 x 40 m which was then raked to eliminate most of the smaller bits of dead wood and grass. Although some debris remained, little potential food was present which might have drawn termites away from the baits. Litter which accumulated during the duration of the study (53 weeks) was neither removed nor quantified. The 40 x 40-m area was subsequently divided into 16 contiguous study plots, each 10 x 10 m.

Two types of bait were tested during August, 1971, for attractiveness to termites and ease of inspection. The most important quality required of a potential bait was that it could be observed quickly without destroying either termites or the structural integrity of the bait.

The first bait tested consisted of birch tongue depressors. Two hundred depressors were driven half their length into the soil at 1-m intervals on two 10 x 10-m grids. Although moderately attractive to the termites, the tongue depressors were difficult to inspect because most of the termites present were either left in the soil or crushed during the process.

The second material consisted of fir blocks (8.5 x 10.0 x 4.0 cm) cut from ordinary 2 x 4's which had been previously kiln dried commercially. Two hundred of these fir blocks were placed on grids similar to those used for the tongue depressors. After several weeks on the soil surface, few blocks had been attacked by termites. Neither tongue depressors nor fir blocks were acceptable, therefore, as bait for the experiment.

The third type of bait tested was toilet paper (Forest Park®, 650 sheet rolls, 11.43 x 11.43 cm, single ply, white, unscented) wrapped with tape to prevent raveling. This bait proved to be very attractive to two subterranean termites, _Heterotermes aureus_ (Snyder) and _G. perplexus_, and had the advantage, furthermore, of not attracting any other termites. _G. perplexus_ attacked the toilet paper rolls in a manner easily distinguished from that of _H. aureus_. _G. perplexus_ foraged over a large area of the bottom of the roll and packed its excavations with soil (Figure 3). H. aureus drove narrow galleries farther into the roll causing the bottom surface to appear as if it had been drilled (Figure 4).

One hundred rolls of toilet paper were placed on each of the 16 contiguous 10 x 10-m grids at 1-m intervals (Figures 5 and 6). Because it took several hours to set out a single 10 x 10-m plot of toilet paper, several weeks were required to establish all the plots used for the study. Figure 7 is a map of the study area including dates on which individual plots were completed. The 12 plots used to monitor termite foraging activity were completed during the period, August 14, 1971 to October 8, 1971. The four remaining plots (no. 13-16, Figure 7) located on the western edge of the study area, were completed by October 29, 1971. These plots were used for a separate study (Nutting et al. 1973) concerning the vertical movement of soil and nutrients by subterranean termites. In conjunction with this study they provided a means of checking the accuracy of forager estimates at the roll-soil interface and for estimating the quantity of toilet paper consumed during one year.

Observations on the toilet paper rolls were made during one 24-hr period each week from October 15, 1971 to October 13, 1972 (53 weekly checks). Every two hours during these 24-hr periods a different study plot (100 rolls) was checked for the presence of termites. The order in which

Figure 3. Toilet paper roll attacked by Gnathamitermes perplexus, X 0.83.

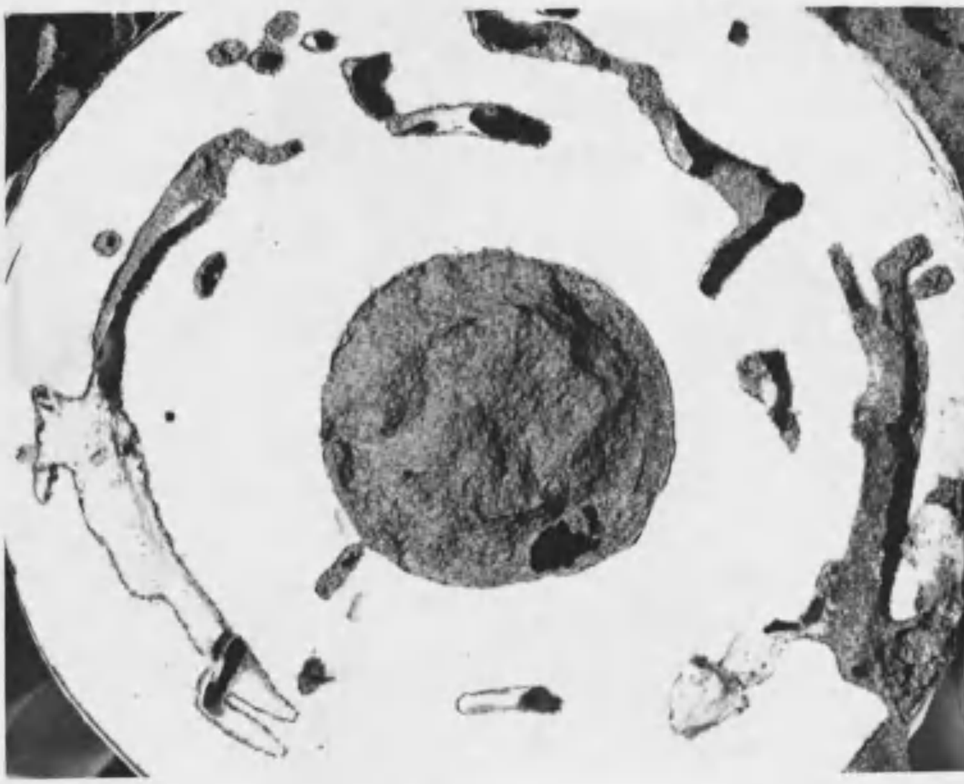


Figure 4. Toilet paper roll attacked by Heterotermes aureus, X 1.15.

Figure 5. Area for studying foraging behavior of Gnathamitermes perplexus on the Santa Rita Experimental Range, Pima County, Arizona -- The lighter area in the foreground was cleared to remove large standing vegetation. Toilet paper rolls for attracting G. perplexus were placed at 1-m intervals on 16 contiguous study plots.

Figure 6. Aerial view of the 40 x 40-m area used to monitor the foraging behavior of Gnathamitermes perplexus.

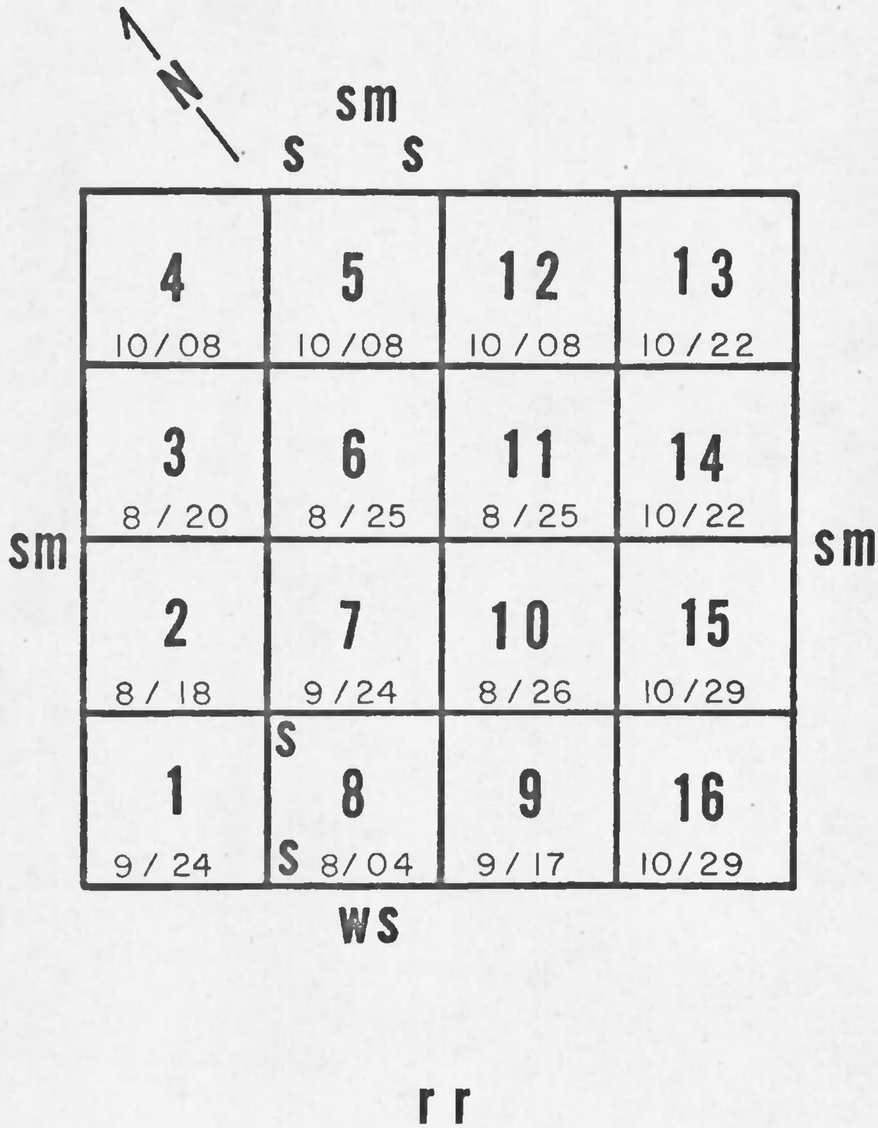


Figure 7. Map of 16 10 x 10-m plots for studying Gnathamitermes perplexus foraging behavior on the Santa Rita Experimental Range, Pima County, Arizona -- S = soil temperature recording station, SM = soil moisture measurement sites, r = location of rain guage, WS = location of weather station containing a hygro-thermograph. Large numbers in the center of each plot are those used to identify plots. The individual study plots were ready for use on the dates which appear below the plot numbers.

the 12 plots were checked was randomly selected. Thus, no single roll was observed more than once a week.

Checking for termite foraging activity involved a quick examination of each roll, notation of the species and approximate number present, or if none were there, any evidence of past activity. Five categories were used to describe the number of foragers observed at a roll: few, 1-5; medium small, 6-50; medium, 51-150; medium large, 151-250; and large, >250. The median values for each category (few, 2.5; medium small, 27.5; medium, 100.0; medium large, 200.0; large, 500.0) were used as the estimates of foragers at a particular roll. In this manner, 100 rolls could be checked in about 30 minutes.

Environmental Measurements

Prior to each bi-hourly check several environmental parameters were measured. Soil temperature at 1, 3, 5, 10, and 15 cm beneath the soil surface and temperature under and in a roll of toilet paper were measured using copper-constantan thermocouples and a Leeds and Northrop, single-range potentiometer. Several additional sub-surface soil temperatures at depths to 125 cm were similarly recorded. The locations of four soil-temperature recording locations are shown on Figure 7. A weather station which contained a hygro-thermograph (Bendix, model 594) is also noted on Figure 7. Soil surface temperatures were recorded at two locations prior to each check using surface thermometers (Pacific Transducer Corp. Instruments, model 310 C).

Cumulative weekly rainfall was measured with two plastic wedge-shaped collector gauges. Soil moisture (at three locations and soil depths of 1-15, 15-30, 30-60, and 60-90 cm) was measured gravimetrically. In addition to air temperature and relative humidity, continuous recordings of temperatures at the roll-soil interface and soil at 5 cm were made with recording thermometers (Auto-lite, model 100).

After 53 weeks, 205 rolls of toilet paper were collected from the four undisturbed plots (no. 13-16, Figure 7). As these rolls were gathered, the number of foragers present was estimated in the usual way. Each roll was placed in a separate plastic bag with all of the termites present. The estimates were later verified in the laboratory by making actual counts of the foragers present. There were no significant differences between field estimates and laboratory counts ($t_{.05} = 0.39$ df = 58).

Data Analysis

Seasonal trends in foraging 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, 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.

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 AND DISCUSSION).

RESULTS AND DISCUSSION

Seasonal Trends in Foraging

G. perplexus foraged at the toilet paper rolls day and night during most of the year. Figure 8 is a plot of the total number of foragers observed at the rolls during the 53 24-hr checks from October 15, 1971 to October 13, 1972. Foraging 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. Although moderate to heavy rain fell throughout December, 1971, low temperatures (<9.0°C) apparently led to depressed foraging activity. No termites were observed foraging on four days during the study (December 10, December 17, December 31, and January 7). Although little rain fell from January 1, 1972 to May 30, 1972, gradually increasing temperatures may have been the reason for increasing activity (Figure 8). 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. Figures 9a and 9b are equivalent three-dimensional computer plots viewed from two different angles with termite foraging intensity plotted against cumulative weekly rainfall and daily mean temperature at the

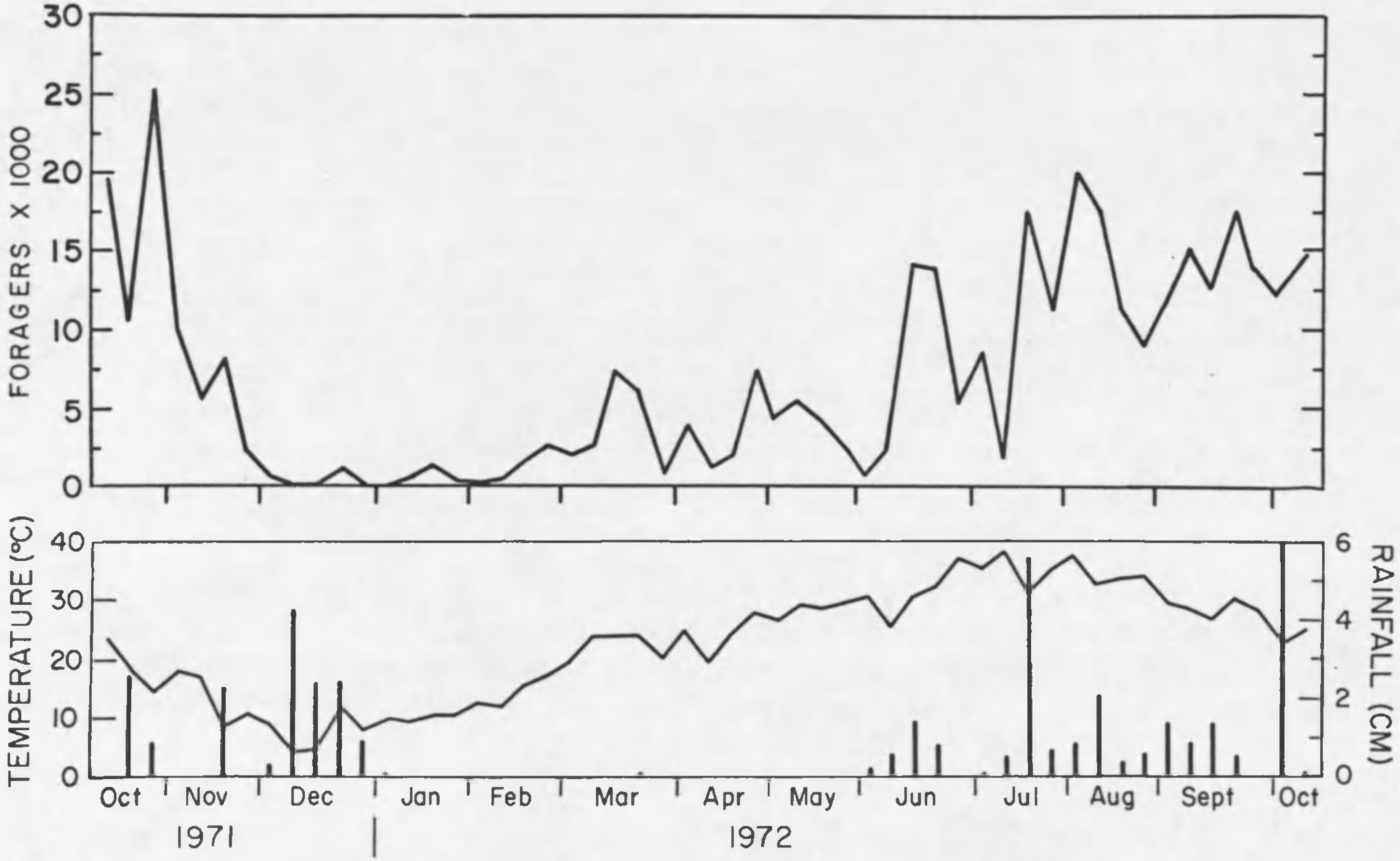
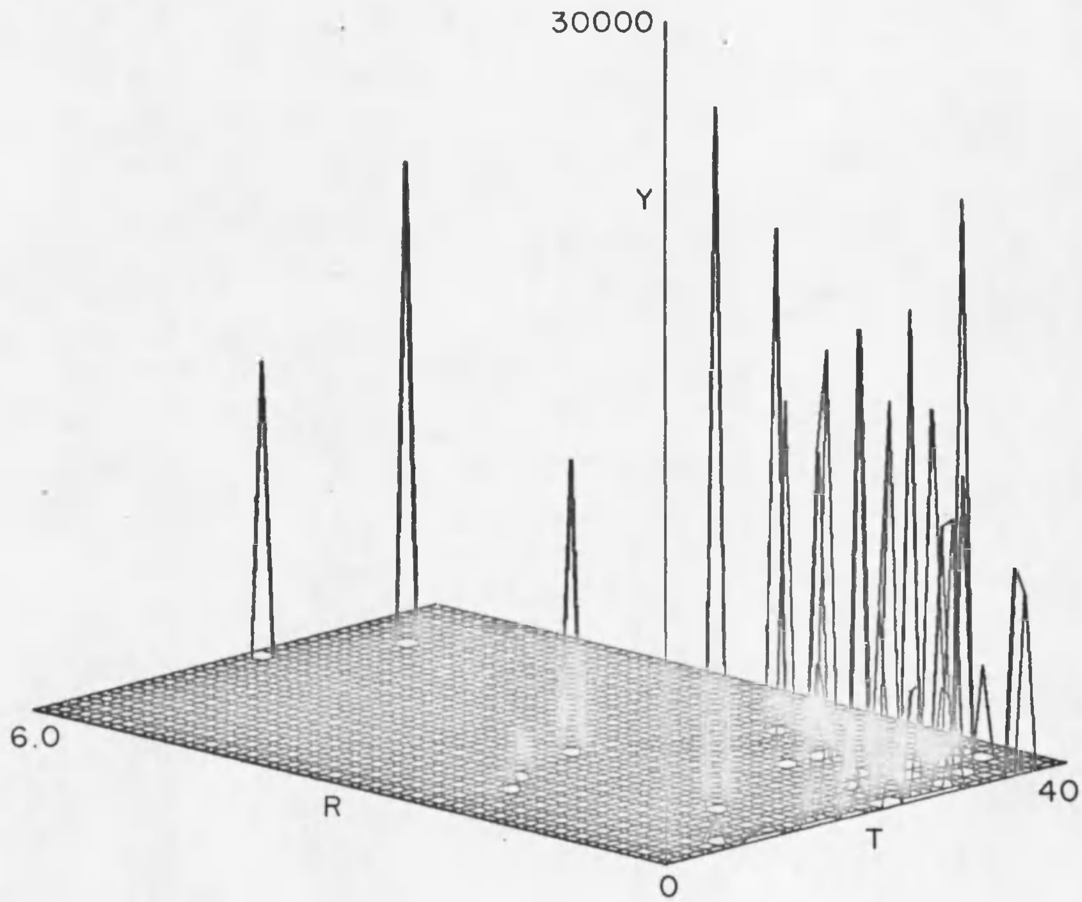
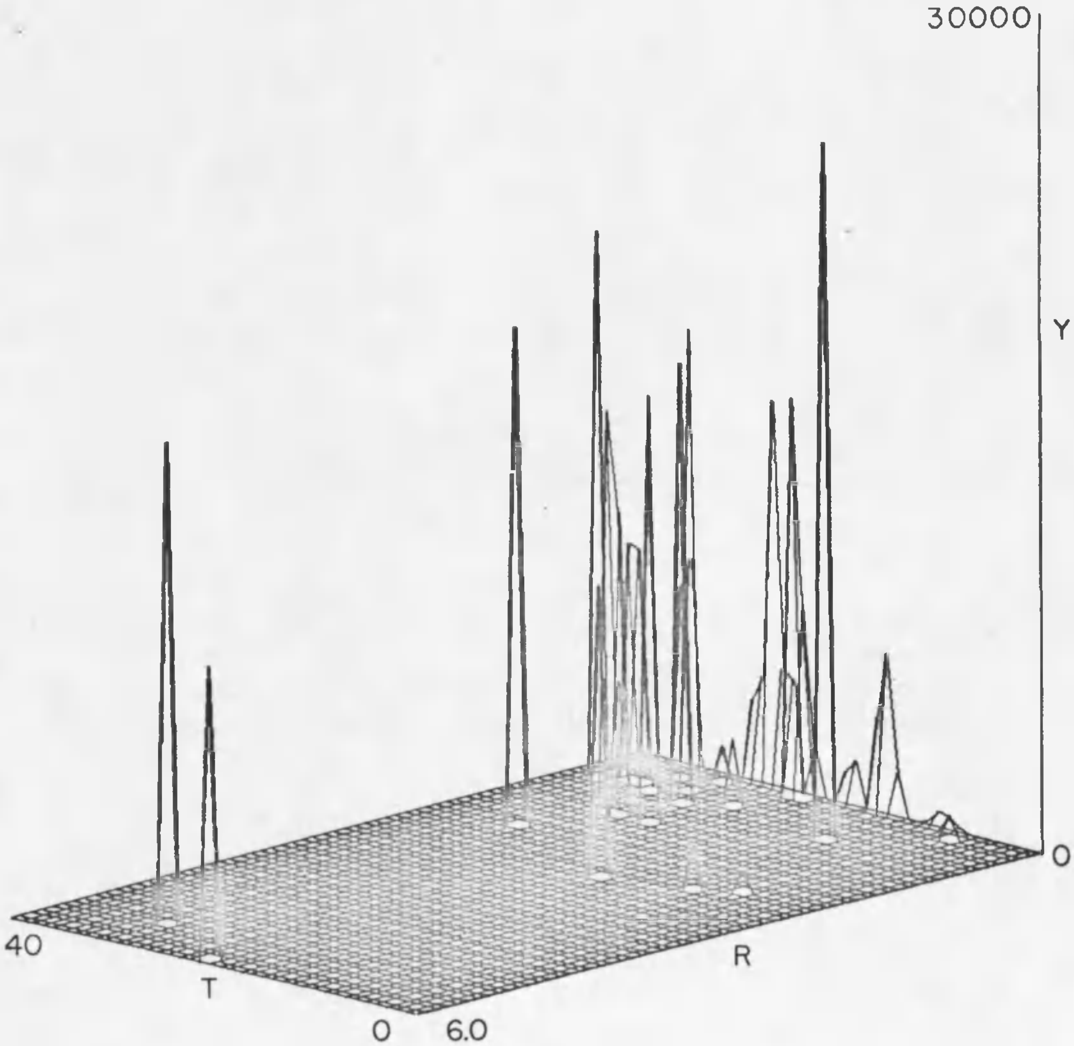


Figure 8. Seasonal foraging trends of Gnathamitermes perplexus at toilet paper rolls on the Santa Rita Experimental Range, Pima County, Arizona, from 10/15/71 to 10/13/72 -- Foraging numbers are totals observed at 1200 rolls during 24-hr observation periods. Temperature is a daily mean at the roll-soil interface while rainfall is a total for the week prior to the 24-hr observation period.



(a) View from an angle which illustrates foraging intensity at low rainfall levels.

Figure 9. 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 activity checks -- Individual activity estimates (Y) were based on the total number of foragers observed at 1200 toilet paper rolls during one 24-hr observation period.



(b) View from an angle which illustrates foraging intensity at combinations of measurable rainfall and varying temperature.

Figure 9.--Continued

roll-soil interface. Although some activity occurred in the absence of rainfall (Figure 9a), intense foraging occurred only at combinations of moderate to high temperatures and measurable rainfall (Figure 9b).

Environmental Factors Affecting Foraging

No foraging activity was observed when the daily mean temperature fell below 8.8°C 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.

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. Laboratory studies by Collins et al. (1973) have demonstrated that 49°C is not too high a temperature for *G. perplexus*.

The relationship between foraging intensity (number of foragers per unit area) and environmental parameters recorded prior to the bi-hourly 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:

1. $Y = b_o + b_1 X + b_2 X^2$
2. $\ln Y = b_o + b_1 X + b_2 X^2$

3. $\ln Y = b_o + b_1X + b_2/X$

4. $\ln Y = b_o + b_1X + b_2\ln X$

where, Y = the number of G. perplexus 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 continuous recordings 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 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 trans-generated 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 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 appear in Table 1.

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

Table 1. 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).

Equation	p[a]	C_p[a]	R^2[b]
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, $C_p = \frac{RSS_p}{\hat{\sigma}^2} - (N-2)$ 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.

equation according to the following formula (Gorman and Toman, 1966):

$$C_p = \frac{RSS_p}{\hat{\sigma}^2} - (N-2p)$$

where: RSS_p = Residual sum of squares for the equation.

N = Number of observations (53).

$\hat{\sigma}^2$ = 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 1) were eliminated because they possessed substantial bias in estimating error. The remaining equations (1, 2, 4, and 5, Table 1) were examined visually for biological plausibility and the best overall equation was chosen. Each of the four functions was plotted using three-dimensional computer graphing methods. Each was plotted (Figures 10-13c) 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 (Figures 10, 11, and 12) 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. Equation 5 (Figure 13a) 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 13b and 13c 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 (Figures 13a and 13c). 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 (Figure 13b). This is reasonable because rainfall always reduces 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.

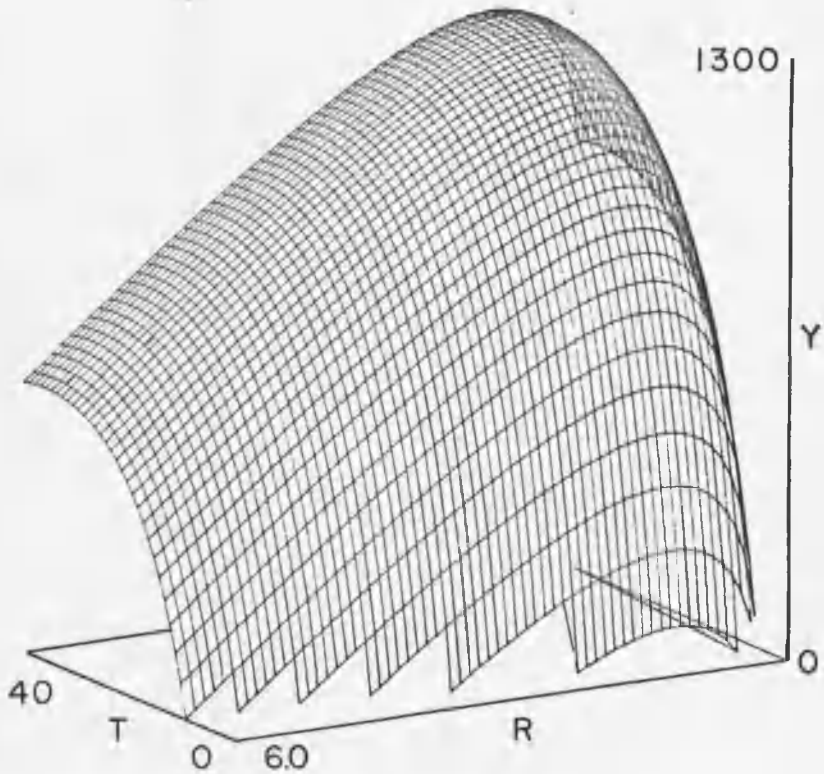


Figure 10. Foraging intensity of Gnathamitermes perplexus predicted by the equation, $Y = -1742.31 - 29.17\ T - 20.78\ R + 1044.87 \ln T + 214.16 \ln R$ -- Y = foraging intensity (0-1300 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40°C) at the roll-soil interface, R = daily rainfall (0-6.0 cm).

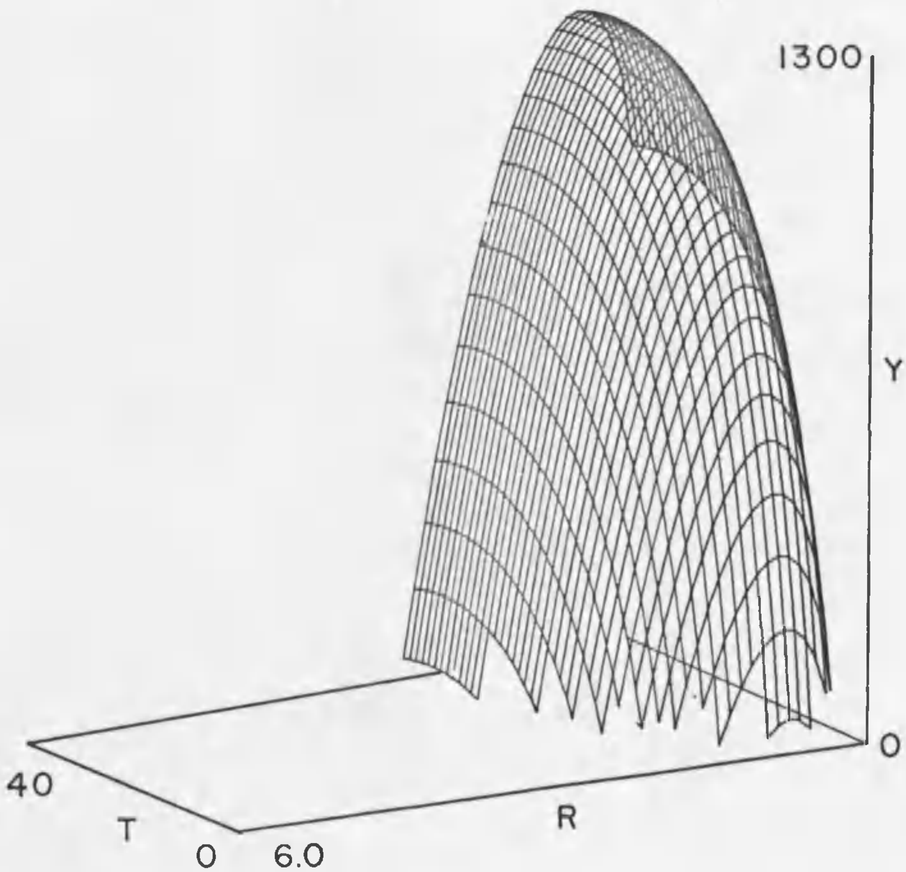


Figure 11. Foraging intensity of Gnathamitermes perplexus predicted by the equation, $Y = -1795.69 - 30.55\ T + 1070.36 \ln T + 212.63 \ln R - 3.24\ R^2$ -- Y = foraging intensity (0-1300 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40°C) at the roll-soil interface, R = daily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

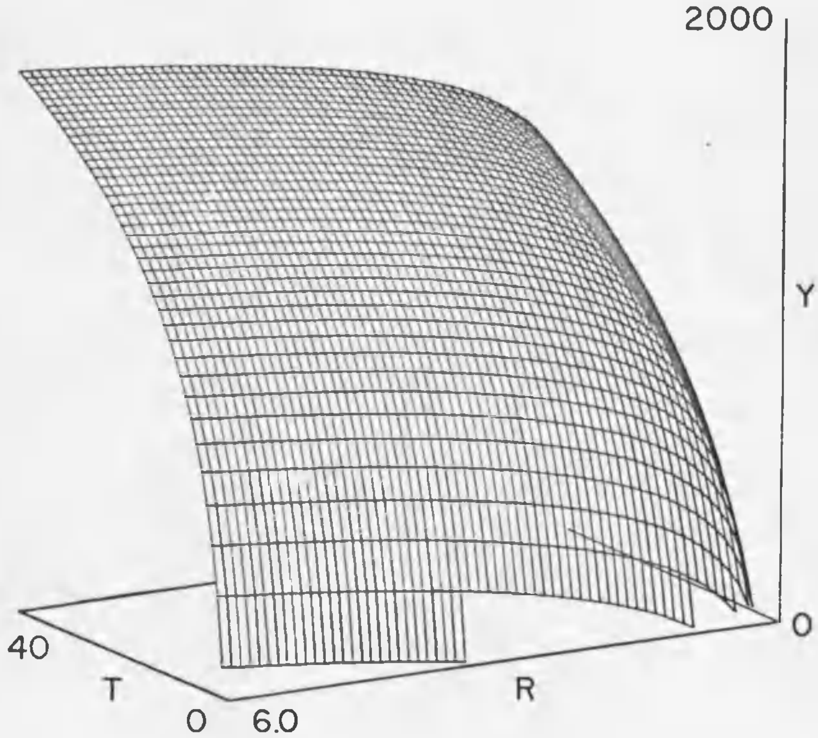
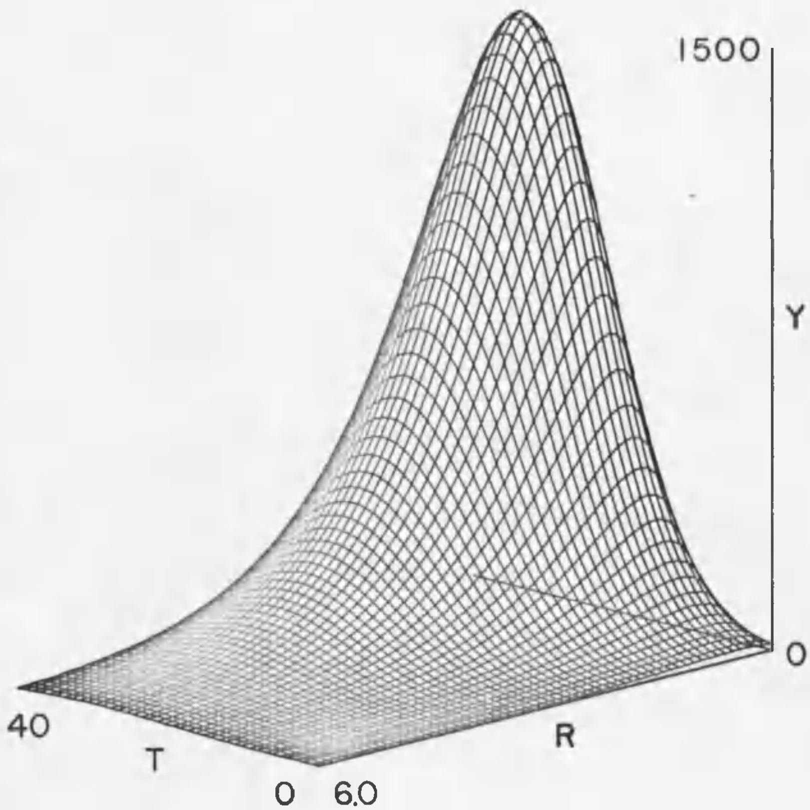
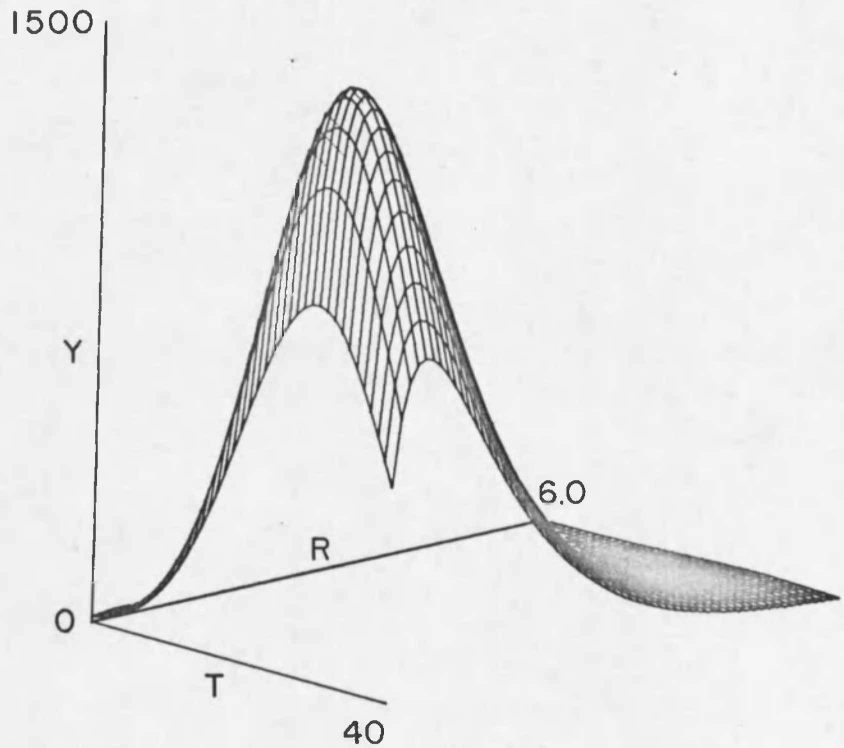


Figure 12. Foraging intensity of Gnathamitermes perplexus predicted by the equation, $Y = -992.32 + 559.26 \ln T + 172.70 \ln R$ -- Y = foraging intensity (0-2000 termites) at 100 rolls of toilet paper, T = daily mean temperature (0-40°C) at the roll-soil interface, R = daily rainfall (0-610 cm).



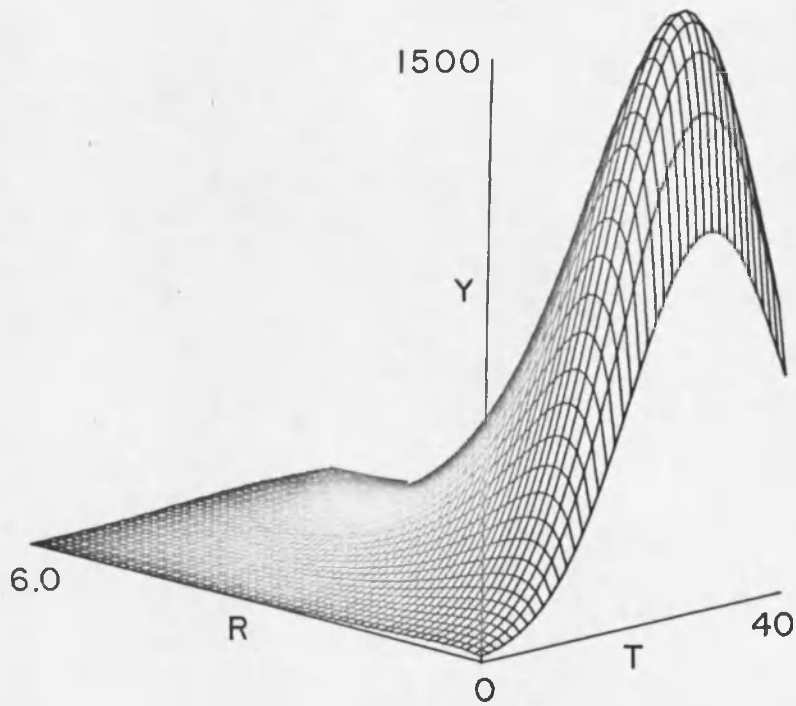
(a) View from an angle which illustrates foraging intensity as a function of (1) high rainfall and varying temperature, (2) varying rainfall and low temperature.

Figure 13. 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 = daily mean temperature (0-40°C) at the roll-soil interface, and R = daily rainfall (0-6.0 cm).



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

Figure 13.--Continued Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $\ln Y = 2.39 + 0.31\ T - 0.11\ R - 0.01\ T^2 + 0.54 \ln R$.



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

Figure 13.--Continued Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $\ln Y = 2.39 + 0.31\ T - 0.11\ R - 0.01\ T^2 + 0.54 \ln R$.

perplexus could withstand high external temperatures 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.

Bodine (1973) found that, in western Texas, changes in the seasonal and diurnal foraging activity patterns of G. tubiformans (Buckley) were highly correlated ($R > 0.99$) with soil temperature at 45 cm, air temperature, and soil moisture at 45-60 cm. G. perplexus showed no dependence whatsoever on any of these variables. Temperatures and soil moisture closer to the surface were clearly more important. In Bodine's (1973) regression equation soil moisture had a negative coefficient suggesting that increases in soil moisture were associated with decreases in foraging intensity. This response to increases in soil moisture was very different from that of G. perplexus (Figures 13a and 13c).

Bouillon (1970) concluded that the seasonal foraging cycles of subterranean and harvester termites are related to many factors including climatic conditions, seasonal abundance of nutrients, colony density, caste composition, and rate of food consumption. He goes on to suggest that seasonal variations in foraging activity tend to be most noticeable in temperate regions. The seasonal foraging pattern of G. perplexus (Figure 8) supports this statement. In South Africa, the diurnal and seasonal foraging patterns of Hodotermes mossambicus (Hagen) appear to be controlled largely by soil surface temperature (Wood, in press). In Australia Nasutitermes exitiosus (Hill) constructs subterranean foraging galleries and ceases to forage when air temperature approaches 0°C (Wood, in press).

Bodot (1967) studied the seasonal foraging patterns of three African termites in a tropical savanna and concluded that foraging occurred throughout the year whenever climatic conditions permitted, that rainfall caused increased foraging intensity, and that foraging activity declined during the dry season. Among the specific climatic factors which she found to influence foraging were soil temperature, relative humidity, and rainfall. It seems likely that the factors which regulate seasonal patterns are considerably more numerous than those which regulate diurnal patterns. The latter appear to be primarily related to climatic factors which in turn are closely correlated with the termite's behavior. Thus, harvesters are more sensitive to changes in light intensity, soil surface temperature, and relative humidity (Bouillon, 1970) than the more cryptic, totally subterranean species. The latter species, including G. perplexus, are far more dependent on changes in temperature and soil moisture below the surface.

The seasonal supply of dead organic materials on the Santa Rita study site appeared to vary little throughout the experiment with the exception that a rather large input of dead grasses occurred during late fall, 1971. It is unlikely that nutrient availability affected the foraging patterns of _G. perplexus_ on the study site. It was not possible to determine whether changes in caste composition or colony density exerted any influence on foraging as no nest was ever found. Changes in the caste composition of foraging groups seen at the surface were not evident. It was also impossible to determine if internal rhythms affected foraging. It is probable, however, that these and other unrecognized factors accounted for the rather low coefficients of determination (R^2's) associated with the final eight prediction equations.

Equation 5 predicts only the number of foragers which might be seen at 100 rolls of toilet paper spaced at 1-m intervals at an instant in time. No information was obtained from monitoring the rolls as to the length of time an individual forager spends at the surface or the quantity of toilet paper it removes during that period. An estimate of toilet paper consumption, based on 205 rolls gathered from plots 13-16 at the end of the study, showed that _G. perplexus_ removed more than 100 kg/ha/yr. _G. perplexus_ was the most numerous termite found on the 16 study plots. Extrapolating from the data on 12 plots during periods of intense foraging activity, maximum foraging density of _G. perplexus_ was estimated at 700,200 foragers/ha (451.2 g/ha, dry-weight). Its ability to forage within a wide range of temperatures and its large populations suggest that it is an important detritivore in some areas of the Sonoran Desert.

SUMMARY

This study was undertaken to determine some of the environmental parameters which are related to the foraging behavior of Gnathamitermes perplexus on the Santa Rita Experimental Range. A modified bait-sampling technique, using toilet paper rolls as a food source, was developed to monitor the diurnal and seasonal trends in foraging. Regression analyses revealed that the time engaged in foraging was controlled by soil temperatures (measured as extremes from the roll-soil interface to 15 cm). Soil moisture, resulting from rainfall, modified foraging intensity. The number of foragers at a point in time at 100 rolls of toilet paper, may be predicted by the equation, $\ln Y = 2.39 + 0.31\ T - 0.11\ R - 0.01\ T^2 + 0.54 \ln R$, where Y = the number of foragers, T = daily mean temperature at the roll-soil interface, and R = daily rainfall.

Extrapolating from the data on 12 plots during periods of intense foraging activity, it was estimated that the maximum foraging density for G. perplexus was 700,200 foragers/ha (451.2 g/ha, dry-weight). During the year of study G. perplexus attacked nearly 100 per cent of the 1200 rolls used to monitor termite activity. It was concluded that its foraging activities are regulated primarily by temperature and secondarily by soil moisture resulting from

rainfall. The data suggest that *G. perplexus* is an important detritivore in the Sonoran Desert.

REFERENCES

Bodine, M. C. 1973. The impact of the termite Gnathamitermes tubiformans on rangeland herbage dynamics. M.S. Thesis. Texas Tech. Univ., Lubbock, Texas. 39 pp.

Bodot, P. 1967. Cycles saisonniers d'activité collective des termites des savanes de basse Côte-d'Ivoire. Insectes Sociaux 14:359-388.

Bouillon, A. 1970. Termites of the Ethiopian region, p. 153-280, In K. Krishna and F. Weesner (Eds.), Biology of Termites, Vol. 2, Academic Press, New York.

Bouillon, A., and R. Lekie. 1964. Populations, rythme d/activité diurne et cycle de croissance du nid de Cubitermes sankurensis. Wasmann (Isoptéra, Termitinae), p. 197-213, In A. Bouillon (Ed.), Études sur les Termites Africains, Masson, Paris.

Collins, M. S., M. I. Haverty, J. P. La Fage, and W. L. Nutting. 1973. High-temperature tolerance in two species of subterranean termites from the Sonoran Desert in Arizona. Environ. Entomol. 2:1122-1123.

Dixon, W. J. (Ed.). 1973. Biomedical Computer Programs, Univ. Calif. Press, Los Angeles. 773 pp.

Gorman, J. W., and R. J. Toman. 1966. Selection of variables for fitting equations to data. Technometrics 8:27-51.

Lee, K. E., and T. G. Wood. 1971. Termites and Soils. Academic Press, New York. 251 pp.

Light, S. F. 1934. The desert termites of the genus Amitermes, p. 199-209, In C. A. Kofoid (Ed.), Termites and Termite Control, Univ. Calif. Press, Berkeley.

Light, S. F., M. Randall, and F. G. White. 1930. Termites and termite damage with preliminary recommendations for prevention and control. Univ. Calif. Agr. Exp. Stn., Circ. 318:1-64.

Nutting, W. L., M. I. Haverty, and J. P. La Fage. 1973. Foraging behaviour of two species of subterranean termites in the Sonoran Desert of Arizona. Proc. 7th Internat. Congr., Internat. Union for the Study of Social Insects, London, September 10-15, 1973, p. 298-301.

Sands, W. A. 1961. Foraging behaviour and feeding habits in five species of Trinervitermes in West Africa. Entomologia exp. appl. 4:277-288.

Sands, W. A. 1972. Problems in attempting to sample tropical subterranean termite populations. Ekol. Polska 20:23-31.

Weesner, F. 1970. Termites of the Nearctic Region, p. 477-525, In K. Krishna and F. Weesner (Eds.), Biology of Termites, Vol. 2, Academic Press, New York.

Wood, T. G. In Press. The food and feeding habits of termites. In M. V. Brian (Ed.), Synthesis Volume on Ants and Termites, Int. Biol. Programme, Cambridge Univ. Press, Cambridge.