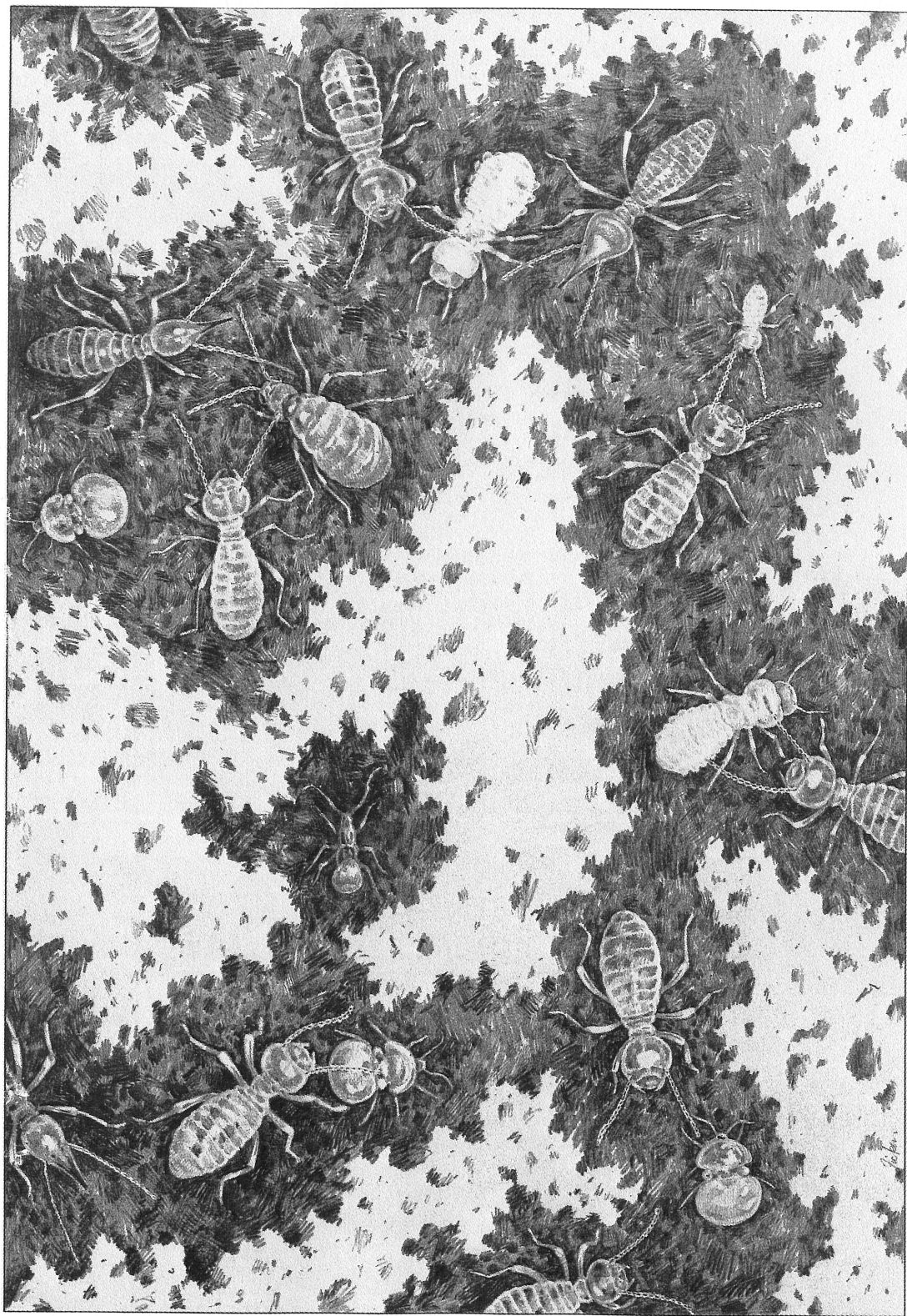




Environmental Factors Correlated With
The Foraging Behavior
Of a Desert Subterranean Termite,
Gnathamitermes perplexus (Banks)^{1, 2},
(Isoptera: Termitidae)

by

J. P. La Fage, M. I. Haverty³ and W. L. Nutting⁴

ABSTRACT

Toilet paper rolls, set out at 1-m intervals in a block of 16 10X10-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. Foraging activity was limited by upper level (0-15 cm) soil temperatures within the range 9-49°C. Periodic rises in soil moisture resulting from rainfall increased foraging intensity. G. perplexus foraged at nearly 100 percent 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 expressed by the equation, in $Y = 2.39 + 0.31 T - 0.11 R - 0.01 T^2 + 0.54 \ln R$, 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.

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²Portion of a thesis submitted by the first author in partial fulfillment of the requirements for the Master of Science degree in the Graduate College, University of Arizona.

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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. 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).

G. perplexus (Banks) is found throughout southwestern Arizona, southern California, southern Nevada, far-western Texas, and northern Mexico (Weesner 1970). It normally does not attack crops or structures and thus is not considered a pest species. 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 LaFage 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 of G. perplexus.

MATERIALS AND METHODS

Site Description

The study site is 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 yearly rainfall which averages 33 cm is about 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 to 24°C during the study period.

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 burro-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 dominate on the study site are spider grass (Aristida ternipes Cav.), Santa Rita threeawn (A. glabrata (Vasey) Hitch.), A. hamulosa Henr.), Rothrock grama (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 closely correlated with the foraging behavior of G. perplexus. Bait units were placed on grids located in an area which 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 40X40 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 40X40-m area was subsequently divided into 16 contiguous study plots, each 10X10 m.

The bait used for the study 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 (Fig. 1). H. aureus drove narrow galleries farther into the roll causing the bottom surface to appear as if it had been drilled (Fig. 2).

One hundred rolls of toilet paper were placed on each of the 16 contiguous 10X10-m grids at 1-m intervals (Figure 3). Because it took several hours to set out a single 10X10-m plot of toilet paper, several weeks were required to establish all the plots used for the study. Figure 4 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) 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 the 12 plots were checked was randomly selected. No single roll was observed more than once a week.



Fig. 1. Toilet paper roll attacked by *Gnathamitermes perplexus*.

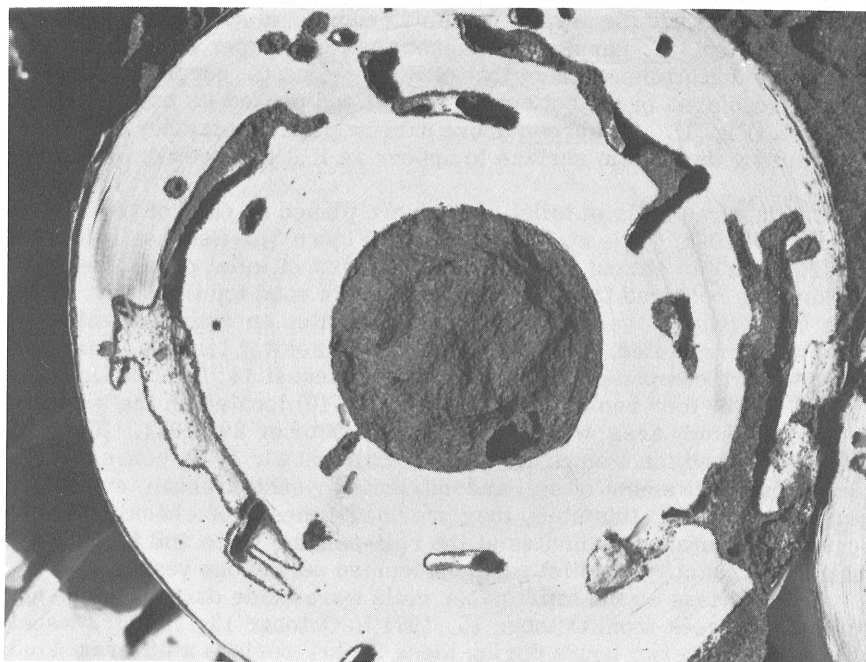


Fig. 2. Toilet paper roll attacked by *Heterotermes aureus*.



Fig. 3. Aerial view of the 40x40-m area used to monitor the foraging behavior of Gnathatermes perplexus.

Checking for termite foraging actively 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

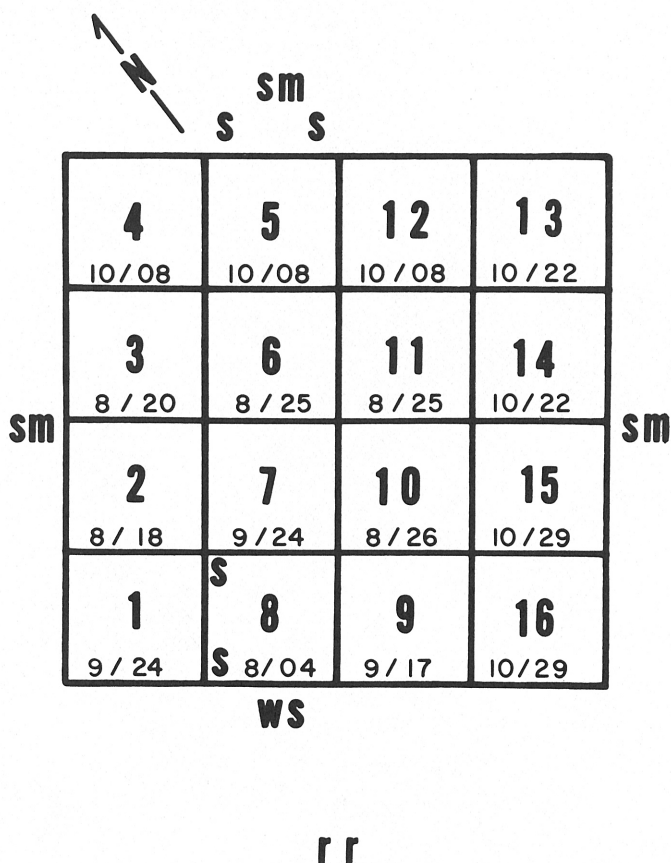


Fig. 4. Map of 16 10 x 10-m plots for studying *Gnathamitermes perplexus* foraging behavior on the Santa Rita Experimental Range, Pima County, Arizona. S = soil temperature recording station, SM = soil moisture measurement sites, r = location of rain gauge, WS = location of weather station containing a hygrothermograph. 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.

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 Northrup single-range potentiometer. Several additional sub-surface soil temperatures at depths to 125 cm were similarly recorded. The location of four soil-temperature recording locations are shown

on Figure 4. A weather station which contained a hygrothermograph (Bendix, model 594) is also noted on Figure 3. 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 4). 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 observations 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 5 is a plot of the numbers 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 (4.0 cm) for the week prior to the checks, may have caused the high activity levels during that 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 stimulated increasing activity (Fig. 5). 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 6a and 6b 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 roll-soil interface. Although some activity occurred in the absence of rainfall (Figure 5), intense foraging occurred only at combinations of moderate to high temperatures and measurable rainfall.

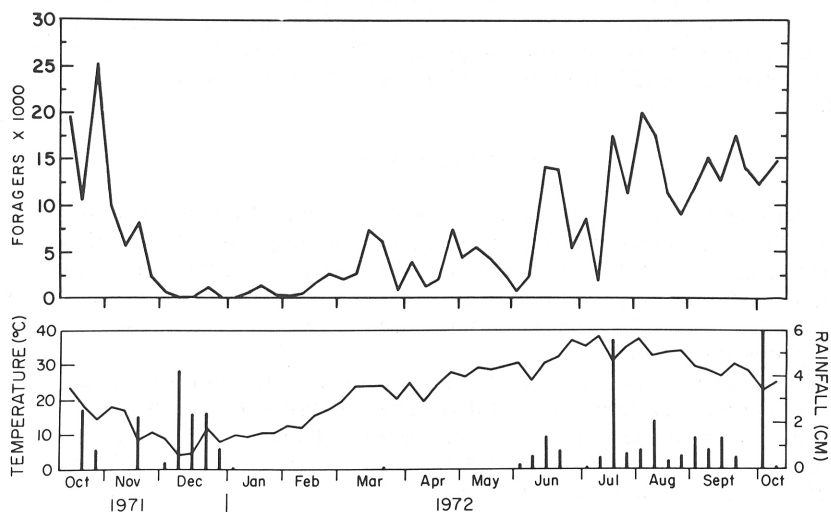


Fig. 5. Seasonal foraging trends of *Gnathamitermes perplexus* at toilet paper rolls on the Santa Rita Experimental Range, Pima County, Arizona, from 10/15/71 to 10/13/72. Foraging numbers are totals observed at 1200 rolls during 24 hour observation periods. Temperature is a daily mean at the roll-soil interface while rainfall is a total for the week prior to the 24 hour observation period.

Environmental Factors Affecting Foraging

No foraging activity was observed when the daily mean temperature at the roll-soil interface fell below 8.8°C even though substantial rain fell at and below this temperature. This temperature, 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 the highest temperature was found at or near the surface; however, after sunset surface temperatures were often much lower than those 3-5 cm below the surface. During the early morning hours before 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 conditions recorded prior to the two hour 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:

$$1. \quad Y = b_0 + b_1X + b_2X^2$$

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

$$3. \quad \ln Y = b_0 + b_1X + b_2/X$$

$$4. \quad \ln Y = b_0 + b_1X + b_2 \ln X$$

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 stepwise 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 by 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 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.

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*	Cp*	R ² †
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

*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). †Coefficient of determination

Because all eight equations have similar R²'s, two additional criteria were used to choose the best prediction equation. The statistic "Cp" was calculated for each 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.

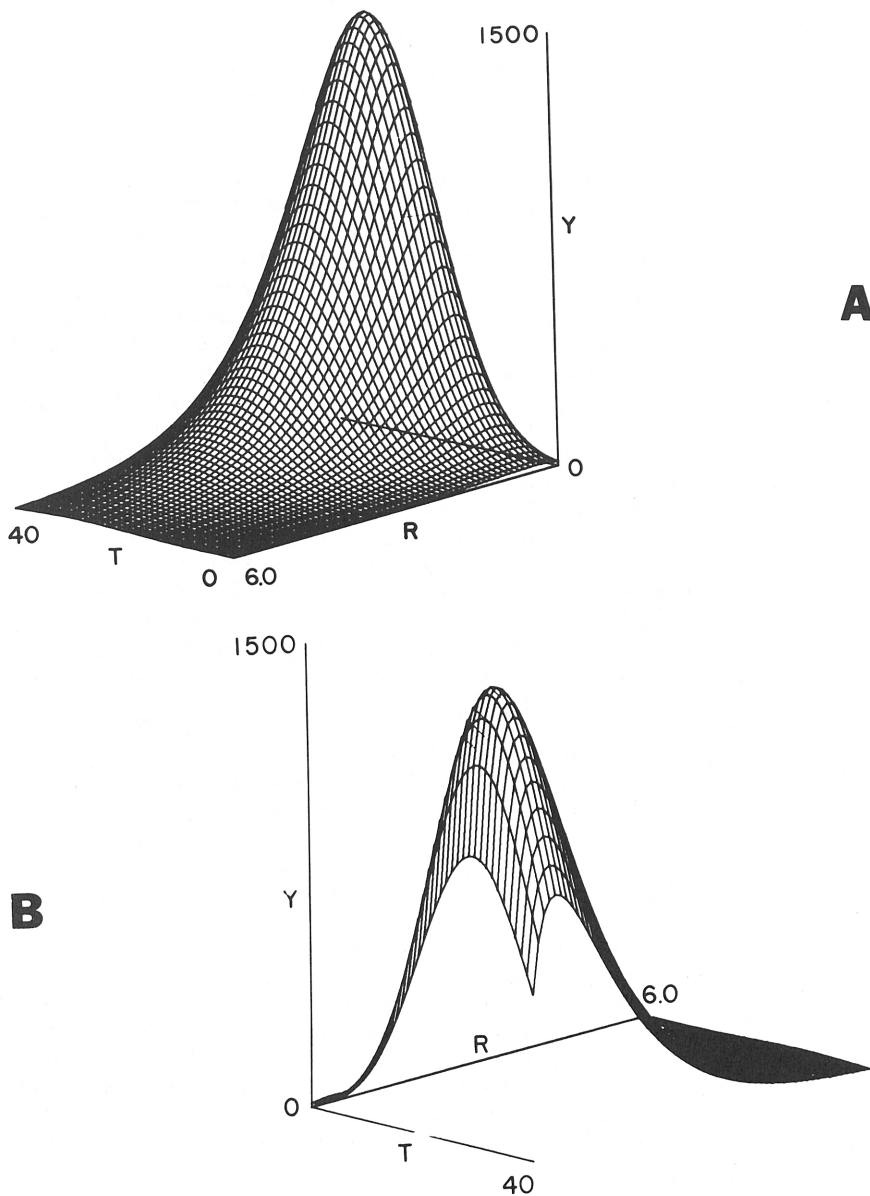


Fig. 6. Foraging intensity of *Gnathamitermes perplexus* predicted by the equation, $\ln Y = 2.39 + 0.31 T - 0.11 R - 0.01 T^2 + 0.54 \ln R$. Y=foraging intensity (0-1500 termites) at 100 rolls of toilet paper, T=daily mean temperature (0-40° C) at the roll-soil interface, and R=daily rainfall (0-6.0 cm).

(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.
 (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.

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 $C_p:p > 1.0$. On this basis equations 3, 6, 7, and 8 (Table 1) were eliminated. 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 by three-dimensional computer graphing methods 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 (one study plot), constitutes the vertical axis for each graph. Equations 1, 2, and 4 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 describing 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 6a, b) 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. Figure 6b shows 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 (Figure 6a). The only area of the response surface not substantiated by actual field observations occurred where very high temperatures (>35°C) and rainfall (>3.0 cm) occurred simultaneously (Figure 6b). 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. 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.

In western Texas, Ueckert et al. (in press) found that the foraging activity of G. tubiformans (Buckley) was most strongly influenced by temperature when seasonal precipitation was abundant. Under more xeric conditions foraging intensity was influenced primarily by soil moisture. With G. perplexus temperature appears to be a more important factor than soil moisture at all times.

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 5) supports this statement. In South Africa, the diurnal and seasonal foraging patterns of Hodotermes mossambicus (Hagen) which forages in the open 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 daily 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 seems unlikely that nutrient availability would affect 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 we did not search for nests. Changes in the caste composition of foraging groups seen at the surface were not evident. It is probable, however, that these and other unrecognized factors such as internal rhythms 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). The average number of G. perplexus foragers/m² over the entire experiment was 6.99. For Heterotermes aureus, the only other termite found on the study area, the mean was much lower, 3.78 (Haverty et al.,

in press). The ability of *G. perplexus* 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.

REFERENCES

- 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 (Isoptera, 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.
- Haverty, M. I., W. L. Nutting, and J. P. La Fage (In Press). A comparison of two techniques for determining abundance of subterranean termites in an Arizona desert grassland. *Insectes Sociaux*.
- 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. Kofoed (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.
- Ueckert, D. N., M. C. Bodine, and B. M. Spears. In Press. Environmental control of the desert termite *Gnathamitermes tubiformans* (Buckley) in a shortgrass prairie. *Ecology*.
- 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.), *Production Ecology of Ants and Termites*, Int. Biol. Programme Synthesis Volume, Cambridge Univ. Press, Cambridge.



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