Life Sciences Vol. 15, pp. 1091-1101 Pergamon Press
Printed in the U.S.A.

# SEASONAL ACTIVITY AND ENVIRONMENTAL CONTROL OF FORAGING OF THE SUBTERRANEAN TERMITE, HETEROTERMES AUREUS (SNYDER), IN A DESERT GRASSLAND

Michael I. Haverty, Jeffery P. LaFage and William L. Nutting

Department of Entomology, University of Arizona

Tucson, Arizona 85721

(Received in final form 5 August 1974)

This research was conducted on a shrub-invaded desert grassland ecotone 40 km S of Tucson, Arizona. To examine the abiotic factors affecting or regulating foraging of subterranean termites a modified bait sampling method using toilet paper rolls was developed. Observations of foraging activity of *Heterotermes aureus* (Snyder) were made during 24-hr periods each week for one year. Pertinent environmental data were collected at each check. *H. aureus* foraged day and night throughout most of the year with minimal activity from December through February. Foraging intensity increased moderately in the spring and fall and was high but erratic during the summer months. The number of foragers generally increased with increasing temperature. Rainfall had little effect on foraging when daily mean soil temperatures were below 20°C (toilet paper roll-soil interface); however, even the slightest amount of rain during the hot summer months greatly increased foraging intensity. Above 33°C, even with precipitation, foraging numbers plummeted. The number of surface foragers at any instant (Y) is best explained by the equation, $\ln Y = -0.985 - 0.0761\ T + 2.928 \ln T + 0.327 \ln R$ where T is the temperature at the roll-soil interface and R is daily rainfall. It appears that foraging activity is not endogenously controlled; rather it is exogenously controlled by temperature and moisture.

This is the third in a series of papers evaluating the role of termites in the detritus cycle of a desert ecosystem. The first (1) set forth our methodology for studying foraging behavior of subterranean termites and the second (2) provided wood-consumption rates for two common species as a function of temperature, wood species and termite biomass. Here we describe the seasonal foraging activity of one of these species and relate it to key environmental parameters.

Subterranean termites have been defined as species that live in more or less diffuse nests of scattered chambers in the soil with no above-ground indication of their presence (3). They are thus difficult subjects for research and have consequently been neglected by most ecologists in favor of the more conspicuous harvesters and mound-building species. Such concentration of effort on the more obvious part of a community has perhaps created the impression that mound builders are ecologically more important than the strictly subterranean species, wherever they occur together (3). Sands, however, concludes that subterranean species are probably the more numerous, and certainly the most significant from the economic viewpoint in the developing countries of the tropics. Our subject, *Heterotermes aureus* (Snyder), a very destructive subterranean termite in southern Arizona and California, has been shown to be one of the most important detritivores in the Sonoran Desert (4).

## Methods

This study was conducted on the US/IBP, Desert Biome research site provided by the U.S. Forest Service on its Santa Rita Experimental Range approximately 40 km S of Tucson, Arizona, at an elevation of 950 m. Annual rainfall averages 330 mm, half of which occurs during the summer monsoon. The remainder is frequently made up, less reliably, during the period from December through February. The area is a shrub-invaded, desert grassland ecotone, characterized by shrubs, cacti and small trees.

To examine the physical factors affecting or regulating foraging of subterranean termites a modified bait-sampling method was developed (1). Most of the standing vegetation on this area had been knocked down by chaining 18 months prior to setting out the bait. In addition all superficial and partially buried wood was raked off the grid area to eliminate any possible competition between natural wood and the bait. Twelve contiguous grids, each containing 100 rolls of toilet paper placed at 1-m intervals, were used as bait. These proved to be very attractive to two subterranean termites, *H. aureus* and *Gnathamitermes perplexus* (Banks).

Foraging activity of *H. aureus* was observed from October 15, 1971, to October 13, 1972. Observations were made during a 24-hr period each week, such that a different test area of 100 rolls was examined every 2 hr. Thus, no single roll was checked more than once a week. Checking for termite foraging activity involved a quick examination of the underside of each roll for the presence of termites and, if present, a notation of the species and their approximate number was made. In this manner 100 rolls could be examined in about 30 minutes without greatly interfering with termite activities. The narrower, deeper and more heavily spotted galleries of *H. aureus* were easy to distinguish from those of *G. perplexus*.

Prior to each 2-hourly check several environmental parameters were measured. Temperature at 1, 3, 5, 10, and 15 cm below the soil surface, in a roll and at the roll-soil interface were measured with copper-constantan thermocouples. Soil surface temperature was measured with surface thermometers. Soil temperatures used in our analysis were means of values measured at two stations within the bait sampling grid. Air, roll-soil interface temperatures, and relative humidity were continuously recorded on the south edge of the test area. Rainfall was measured weekly with two simple, wedge-shaped, plastic collecting gauges.

Five size classes described the number of termites observed in each roll: 1-5, 6-50, 51-150, 151-250 and > 250. The median value of each class (2.5, 27.5, 100.0, 200.0 and 500.0) was used as the estimate of the number of termites foraging at a particular roll. The accuracy of the estimate was determined at the end of the study by examination of 200 rolls from an undisturbed test area, assignment of a size class in the field as usual, and finally a count of the termites in the laboratory. When the relationship was examined by linear regression and correlation, the estimated and observed values of 35 foraging groups showed a highly significant correlation ($r = .955$). Since the numbers of termites were consistently underestimated, the resulting regression equation ($Y = 2.04 + 1.875X$) was used to adjust all estimated numbers of termites.

Seasonal trends in foraging were determined by summing the estimated numbers of termites observed at the surface for all 12 test areas (over a 24-hr period) each week for the 53 weeks of the experiment. These totals were plotted against mean daily temperature (roll-soil interface) for the 24-hr observation period and cumulative rainfall for the preceding week. Preliminary regression analyses had indicated that these two parameters were the most useful in explaining the number of termites foraging at the soil surface.

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

## Results

### Seasonal Activity Trends

*Heterotermes aureus* foraged day and night throughout most of the year. Figure 1 plots the total number of foragers observed at the surface of the study area (1200 $m^2$) during each of 53 24-hr observation periods from October 15, 1971, to October 13, 1972. The corresponding 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. On only two days were no foragers observed (December 17, 1971, and January 7, 1972, when the mean temperatures were 4.8 and 9.9°C). However, foragers were observed on 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 ef-

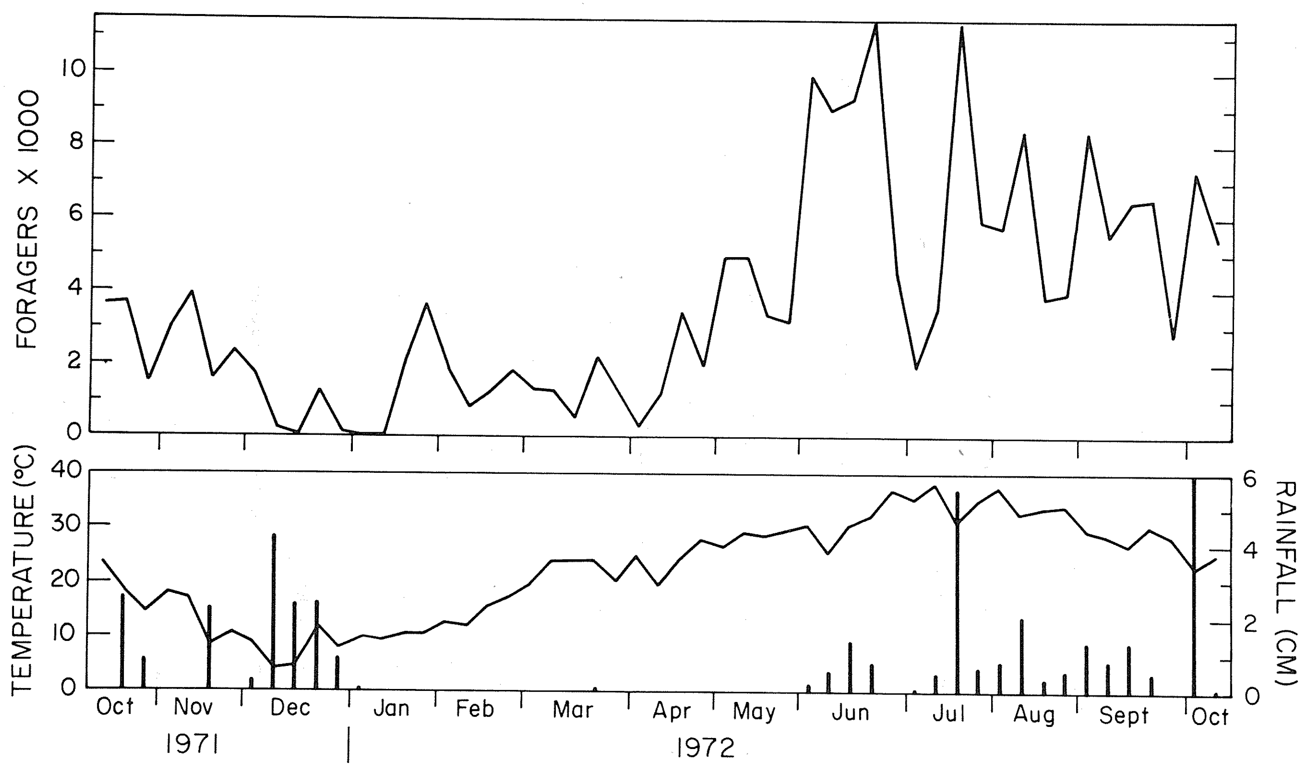


FIG. 1

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

fect 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° (June 29-July 14, July 27-August 4, August 17-25, 1972), even with precipitation, foraging numbers dropped sharply.

Environmental Control of Foraging

*H. aureus* foraged at the rolls within a temperature range of 7.6 to 47°C. This range apparently restricts the time which can be spent foraging. Temperature also determines foraging intensity (number of individuals at the surface per unit area) (1,9).

Plots of foraging intensity vs. environmental parameters indicated that the relationship was not a continuously increasing function. Therefore, four types of curves were examined for each of the environmental parameters:

$$Y = b_0 + b_1 X + b_2 X^2,$$
$$\ln Y = b_0 + b_1 X + b_2 X^2,$$
$$\ln Y = b_0 + b_1 X + b_2/X$$
$$\ln Y = b_0 + b_1 X + b_2 \ln X$$

where Y is the number of *H. aureus* foragers above the soil surface and X is the environmental parameter. From this we determined that temperature at the roll-soil interface would be the most useful. Several equations utilizing this temperature and daily rainfall were then constructed which will predict the number of termites foraging above the soil surface (Table 1). Since all equations have similar multiple regression coefficients they were examined for $C_p$ values (5) to select the best one. Equations in which the $C_p$ to p ratio was > 1.0 were not chosen (equations 2, 4 and 7, Table 1) because of their bias in estimating error. The remaining are all good candidates, but the best equation must also be biologically sound. Equation 8 (Table 1) 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 re-

TABLE 1

Equations Predicting Number of *Heterotermes aureus* Foragers Above the Soil Surface (Y) as a Function of Mean Daily Temperature at the Roll-Soil Interface (T) and Daily Rainfall (R).

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

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

[b] Multiple regression coefficient.

gression coefficient, only three indepent variables, and a low $C_p/p$ ratio indicating a random estimate of error.

## Discussion

There are few reports of seasonal fluctuations in termite foraging activity. Although some authors feel it is difficult to distinguish between endogenous and exogenous control of such activity (6,7), temperature and moisture (or evaporation) are most often the environmental parameters responsible for these fluctuations (6). Bodot (6) investigated the seasonal foraging cycles of *Trinervitermes trinervius* (Rambur), *Ancistrotermes cavithorax* (Sjöstedt) and *Macrotermes natalensis* (Haviland) in an African savanna and found these major trends for each species: 1) foraging is continuous throughout the year with seasonal fluctuations in intensity, 2) foraging intensity increases during the short rainy season, and 3) foraging decreases at the start of the long dry season. The environmental parameters most highly correlated with increased foraging activity differ according to each species' foraging behavior. *T. trinervius* harvests grass on the open soil surface. Its foraging activity has a negative correlation with mean maximum temperature and evaporation, and a positive correlation with mean minimum relative humidity. *A. cavithorax* feeds by covering dead wood and live vegetation with a shield of soil. Its activity shows no correlation with temperature but is positively correlated with rainfall and negatively with evaporation. With *M. natalensis* neither rainfall nor relative humidity has any effect on foraging. The key stimulus is increasing temperature, which increases foraging activity.

Bodine (8) studied the activity of *Gnathamitermes tubiformans* (Buckley) on a temperate grassland, where temperatures vary considerably more than in the tropical savanna. He found that surface foraging activities were most highly correlated with the temperature at 45 cm in the soil. On the basis of an equation containing soil temperature at 45 cm, air temperature, and soil moisture at 45-60 cm, he claimed to account for nearly 100 percent of the variability in numbers of termites at the soil surface. In his regression equation soil temperature has a positive coefficient whereas air temperature and soil moisture have negative coefficients. This implies that increased soil moisture has the effect of reducing foraging populations. This is the only study we are aware of which makes this implication. Bouillon (7) considers moisture to be of utmost importance in determining diurnal foraging cycles of tropical termites. Any weakness in Bodine's attempt to explain the control of foraging activity is probably due to insufficient data.

The results presented in this study agree with Bodot's (6) general conclusions as stated above. Although it is possible that seasonal fluctuations in number of foraging H. aureus were influenced by endogenous rhythms (7), our data strongly indicate that temperature and rainfall are the primary controlling factors. DeBruyn and DeBruin (10) reported a quadratic relationship between ground level temperatures and numbers of Formica polyctena Förster workers on a foraging path. Finnegan (11) reported an increase in foraging activity with increasing temperature for three species of Formica in Quebec. At lower and medium range temperatures H. aureus foraging numbers 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, accentuated the increase in foraging numbers of H. aureus. In contrast ants, which have a more heavily sclerotized cuticle, are less dependent on a low saturation deficit (11, 12) than are termites (6,7).

Notwithstanding these obvious environmental parameters, internal colony pressures may also affect foraging. Bouillon (7) found 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 (6) found that foraging increased with the appearance of reproductive nymphs in a colony and decreased after the appearance of winged reproductives.

With H. aureus any such influence of colony nutrition or alate production was not obvious. When nymphs were present, from late November to early June, foraging was not particularly intense even though temperatures were very favorable.

In the Sonoran Desert, H. aureus forages throughout the year under a wide range of temperatures. While foraging intensity is regulated primarily by temperature, its effect is modified by soil moisture. An equation describing this relationship will be coupled with temperature-dependent wood-consumption rates to estimate the quantity of wood processed by this termite in a desert grassland ecosystem.

## Acknowledgements

The work on which this report is based was carried out as a part of the U.S./I.B.P. Desert Biome, and was supported (in part) by National Science Foundation Grant No. GB-15886. Journal Paper No. 2323 of the Arizona Agricultural Experiment Station.

## References

1. J. P. LAFAGE, W. L. NUTTING, and M. I. HAVERTY, Environ. Entomol. 2 954-956 (1973).
2. M. I. HAVERTY and W. L. NUTTING. Ann. Entomol. Soc. Am. 67 153-157 (1974).
3. W. A. SANDS, Ekol. Polska 20 23-31 (1972).
4. M. I. HAVERTY, The Significance of the Subterranean Termite, Heterotermes aureus (Snyder), as a Detritivore in a Desert Grassland Ecosystem. Ph.D. Dissertation, Univ. of Arizona, Tucson, p. 89 (1974).
5. J. W. GORMAN and R. J. TOMAN, Technometrics 8 27-51 (1966).
6. P. BODOT, Insectes Sociaux 14 359-388 (1967).
7. A. BOUILLON, in K. Krishna and F. Weesner [eds.] Biology of Termites 2 153-280, Academic Press, New York (1970).

8. M. C. BODINE, The Impact of the Termite, Gnathamitermes tubiformans, on Rangeland Herbage Dynamics, M.S. Thesis, Texas Tech. Univ., Lubbock, p. 39 (1973).

9. W. L. NUTTING, M. I. HAVERTY, and J. P. LAFAGE, Proc. 7th Internat. Congr., Internat. Union for the Study of Social Insects, London, p. 298-301 (1973).

10. G. J. DEBRUYN and M. KRUK-DEBRUIN, Ekol. Polska 20 117-127 (1972).

11. R. J. FINNEGAN, Can. Entomol. 105 441-444 (1973).

12. M. G. NIELSEN, Natura Jutlandica 16 83-94 (1972).