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RESEARCH MEMORANDUM

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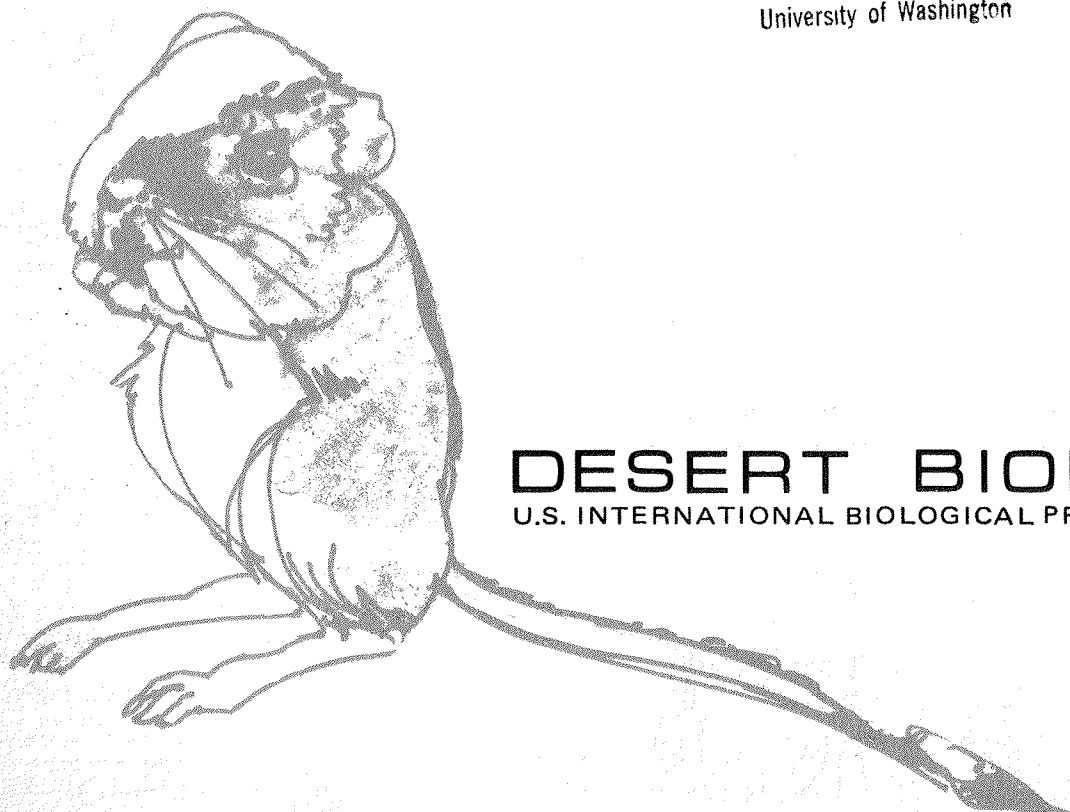
COLONY CHARACTERS OF TERMITES AS RELATED
TO POPULATION DENSITY AND HABITAT

W.L. Nutting, M.I. Haverty,
J.P. LaFage, & R.V. Carr

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DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1971 PROGRESS REPORT

COLONY CHARACTERS OF TERMITES AS RELATED
TO POPULATION DENSITY AND HABITAT

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ABSTRACT

Ecological and demographic studies of termites in the Sonoran Desert are concerned with the determination of colony size, composition, distribution, density, growth and development of at least one dry-wood and one subterranean species. Methods have been designed to relate population data to the distribution and production rates of standing and fallen dead wood, and termite activity to such physical factors as soil temperature and moisture. Seasonal and daily foraging activity of subterranean species is being analyzed through a novel and very productive approach on 100-m² plots of toilet paper rolls, considered as "food units," set out on 1-m² grids.

Four dry-wood and six subterranean species of termites are known from the Santa Rita and Silver Bell Sites. Fallen dead wood at Santa Rita amounts to 2,082 kg/ha, and is produced at a rate of ca. 718 kg/ha/yr. Standing dead wood (3 dominant trees) here amounts to 1,005 kg/ha, and appears at a rate of ca. 262 kg/ha/yr.

Population and biomass estimates for three species of termites at Santa Rita are as follows: *Pterotermes occidentis* (dry-wood), 4.8 colonies/ha, 104.2 termites/ha or 0.48 g/ha; *Heterotermes aureus* (subterranean), 140.7 foraging groups/ha, 23,770 foragers/ha or 8.2 g/ha; *Gnathamitermes perplexus* (subterranean), 705,200 foragers/ha or 374.3 g/ha. Foraging of *Heterotermes* is limited by upper level soil temperatures between ca. 8 and 35°C.

There is obviously a large accumulation of dead plant material, in areas of high termite densities, which is not consumed by termites. Although relationships are probably very complex here, we hope to discover some of the reasons for this anomalous and apparently widespread situation.

INTRODUCTION

All termites use cellulose from a variety of sources (dead and sometimes living wood, leaves, annuals, grasses, roots, dung, and humus) as their principal food. Specialists in most of these categories occur in the Sonoran Desert. As the desert environment becomes colder, either with elevation or latitude, these specialists gradually drop out, probably leaving but a single, general feeder on the colder Desert Biome sites. They are all involved in the comminution and decomposition of plant debris — above, on, or in the soil — with continual assistance from micro-organisms.

Although established colonies have few predators, they seasonally produce large, conspicuous swarms of winged reproductives which probably form a food source of relatively high caloric value for other animals during critical periods of their life cycles.

This study should provide useful information to Desert Biome projects broadly concerned with the detritus cycle, nutrient cycling, plant growth, and predators, both invertebrate and vertebrate. There is particular concern with these projects as they relate to termite ecology, as well as others on plant distribution and productivity, litter accumulation and many abiotic variables, especially in the surface and soil environments. A variety of intensive studies have now been underway in the Tucson Basin for about 17 months. The termite study has concentrated on the Santa Rita Site, but a gradual shift of comparable studies is foreseen to the Silver Bell Site.

OBJECTIVES

Long-term objectives involve as complete ecological and demographic treatments of the termites on the two Tucson sites as possible. More immediately they are to determine colony size, composition, distribution, and reproductive capacity of two or more species of termites in the Tucson Basin as functions of their population density, food supply and physical environment. One dry-wood and one subterranean species are being studied in detail until these are reasonably well understood, and until the methods are sufficiently refined for inclusion of more of the 16 species in the area.

There may be an overlap between some of the termite study measurements and those of the Tucson Basin validation work, such as the determination of the distribution and abundance of dead plant material and local measurements of some physical factors.

METHODS

Distribution, Daily and Seasonal Activity Patterns of Termites as Functions of Available Dead Plant Material and Physical Factors

Activity of specific termites determined by visual examination of all superficial dead plant material in m^2 quadrats (DSCODE A3UNE01) spaced 50 feet apart on transects across study sites. Standing dead wood on trees excluded here but examined under DSCODE A3UNE03.

Distribution of Termites as a Function of Dead Wood Available at Soil Surface

Provides basis for determining host preferences and densities of colonies (or foraging groups) per unit area (DSCODE A3UNE02). All superficial dead wood within 50- m^2 circles is plotted, measured and weighed. Other dead plant material is not considered. Each item containing a termite colony or foraging group is bagged in the field, and the termites later extracted, sorted, counted, and samples of each caste are weighed. Termite data recorded on DSCODE A3UNE04. (Circles are carefully cleared of all dead wood, and the process repeated yearly to determine annual production of surface dead wood.)

Distribution of Termites as a Function of Standing Dead Wood on Individual Trees

This provides the basis for determining host preferences and densities of colonies per unit area (DSCODE A3UNE03).

All dead wood (branches 2 cm diameter and larger) on individual trees is plotted (bearing and height), removed with a chain saw, measured, weighed, and examined for termites. Any termites are later extracted by hand or trapped in damp paper, sorted, counted, and samples of each caste are weighed. Termite data are recorded on DSCODE A3UNE04. Trees are carefully cleared of all dead wood, and the process repeated yearly to determine annual production of standing dead wood.

Termite Colony Size and Composition Data

Provides a basis for analyzing colony growth, maturation, decline, structure, age, and annual alate production (DSCODE A3UNE04). Dry-wood termites are extracted from wood by hand after sawing into short lengths and splitting. Subterranean termites are extracted by hand or by trapping in damp paper towels beneath the wood in open plastic trays. Counting and sorting by caste and sex usually must be done under lower magnifications of a stereomicroscope. Samples of various castes are dried to constant weight in an oven at 60°C.

Population Distribution and Density, and Daily and Seasonal Activity Patterns of Foraging Subterranean Termites as Functions of Physical Factors

Information abstract is not yet submitted and methods are not completely worked out (DSCODE A3UNE06-08).

Ordinary toilet paper is an easily-handled unit of practically pure cellulose which is readily accepted by subterranean termites. A novel and extremely promising approach to the study of their behavior is being developed around 10 x 10-m plots of toilet paper rolls, 100 being set out on a grid at 1-m intervals. The surface was first raked clear of all dead wood and each roll was wrapped with tape before setting out. By late October, 12 contiguous plots had been established so that a different plot could be examined for termite activity every 2 hours, one day each week. As each roll is examined, evidence of termite activity (1 or both of 2 species can be detected) and an estimate of foragers present (1-5, 6-50, 51-150, 151-250, 251+) is recorded. One plot can be checked within a half hour. Air temperature and relative humidity, and soil temperatures at two levels are recorded continuously. Temperatures in and under rolls, and soil temperatures from surface to 125 cm (11 levels), are taken with thermocouples every two hours for 24 hours, one day each week. Soil moisture measurements will be added early in 1972. Plans are to continue these observations for at least a year.

Four additional plots have been set up with a view toward "harvesting" them later this year to check the accuracy of our population estimates, to determine the rate of cellulose consumption, and to measure the quantity of soil brought to the surface by the termites. Additional possibilities being considered here include the use of dyes or tracers to delineate colony territories, and cages or traps to measure seasonal alate production.

The plots are located in the southwest corner of the chained plot on the Santa Rita Site, about 1 mile from the meteorological tower. Eventually, a similar study area will be set up on the Silver Bell Site.

Miscellaneous rearing methods. The development of incipient colonies of two species of dry-wood termites is being followed in the laboratory under constant temperature and relative humidity. Alates, collected during summer flights, are paired on pieces of wood of known weight in plastic dishes or glass sandwiches. Large groups of subterranean termites are maintained at constant temperature in glass aquaria on wood embedded in damp vermiculite. These cultures will be used in wood-preference tests now being planned.

FINDINGS

Methods described for DSCODES A34NE01-03 have provided the following list of four dry-wood and six subterranean termites found on the Santa Rita (SR) and Silver Bell (SB) Sites to date. The most important species are starred(*).

SUBTERRANEAN	DRY-WOOD
* <i>Heterotermes aureus</i> (both sites)	<i>Incisitermes banksi</i> (SR)
<i>Amitermes emersoni</i> (SR)	* <i>Marginitermes hubbardi</i> (SB)
<i>Amitermes minimus</i> (SR)	* <i>Paraneotermes simplicicornis</i> (SR)
<i>Amitermes wheeleri</i> (SR)	* <i>Pterotermes occidentis</i> (both sites)
* <i>Gnathamitermes perplexus</i> (both sites)	
<i>Tenuirostritermes tenuirostris</i> (SR)	

Intensive studies are being made on *Heterotermes*, *Gnathamitermes*, *Pterotermes*, and *Marginitermes*, although some information is accumulating concurrently on the others.

The transect method for examining superficial dead plant material in m²-quadrats (DSCODE A3UNE01) was abandoned in April, 1971, in favor of the more productive procedures specified under DSCODE A3UNE06-08. Although the transect method does generate a good list of termites and host materials, it is most useful as a preliminary survey technique in new study areas. Host materials are listed below under detailed remarks on important species.

A great deal of time is still spent in measuring the amount of fallen (DSCODE A3UNE02) and standing (DSCODE A3UNE03) dead wood on each site, since its distribution is obviously critical in determining the size and distribution of termite colonies. A few preliminary estimates of fallen dead wood in kg/ha have been made for the dominant species (Tables 1-3).

Table 1. Weight of fallen dead wood by species, based on 27 50-m² circles. Santa Rita Undisturbed Site.

Species	Avg wt/circle, kg	s, kg	Range, kg	Est kg/ha
<i>Acacia greggii</i>	3.93	53.63	0-42.41	786
<i>Opuntia fulgida</i> (joints)	1.90	17.99	0-11.00	380
<i>Opuntia spinosior</i>	1.84	11.70	0- 9.72	368
<i>Opuntia fulgida</i> (wood)	1.19	18.45	0-18.09	238
<i>Prosopis juliflora</i>	1.13	13.87	0-12.28	226
Other	0.41	4.25	0- 4.22	82
TOTAL	10.41	52.80	0.60-45.30	2082

Table 2. Weight of fallen dead wood by species, based on 7 50-m² circles. Santa Rita Chained Site.

Species	Avg wt/circle, kg	s, kg	Range, kg	Est kg/ha
<i>Prosopis juliflora</i>	7.62	44.56	0-48.73	1524
<i>Opuntia spinosior</i>	6.39	30.01	0-33.06	1278
<i>Opuntia fulgida</i>	3.65	15.28	0-17.35	730
<i>Acacia greggii</i>	2.47	16.01	0-17.29	494
<i>Opuntia engelmannii</i>	2.40	14.29	0-15.62	480
Other	0.81	2.46	0- 2.55	162
TOTAL	23.34	57.44	1.05-63.16	4668

Table 3. Weight of fallen dead wood by species, based on 9 50-m² circles. Silver Bell Site.

Species	Avg wt/circle, kg	s, kg	Range, kg	Est kg/ha
<i>Cercidium microphyllum</i>	4.56	21.01	0-20.61	912
<i>Larrea divaricata</i>	2.33	7.15	0- 7.06	466
<i>Olneya tesota</i>	1.23	7.43	0- 7.48	246
<i>Opuntia versicolor</i>	1.20	4.81	0- 3.63	240
<i>Opuntia fulgida</i>	0.93	4.50	0- 4.54	186
Other	0.24	1.16	0- 1.30	48
TOTAL	10.47	18.42	2.27-23.13	2095

On the basis of only 10 circles examined a second time on the Santa Rita Site, one year later, the following calculations have been made on fallen dead wood production rates: 3.59 kg dead wood/circle; s, 10.46 kg; range, 0.31-8.53 kg; 71.80 kg/ha/yr. As more circles are sampled a second time, the larger sample size should provide a more meaningful figure.

Although termites associated with fallen wood are collected under this procedure, data on their populations are presented under DSCODE A3UNE04.

Preliminary estimates of standing dead wood in kg/ha (DSCODE A3UNE03) have been made for some of the dominant species (Table 4). Since the sample sizes are small, and the figures on plants/ha are unofficial, we feel that it is not yet worthwhile to present more than this.

Table 4. Weight of standing dead wood by species of dominant plants. Santa Rita and Silver Bell Sites.

Species & Site	no. sampled	no./ha	kg/plant	Est kg/ha
<i>Acacia greggii</i> (SR)	10	32.9 ¹	11.2	367.9
<i>Cercidium floridum</i> (SR)	18	12.1 ¹	8.5	102.6
<i>Cercidium microphyllum</i> (SB)	31	82.4 ²	8.9	732.5
<i>Olneya tesota</i> (SB)	6	12.4 ²	31.2	386.9
<i>Prosopis juliflora</i> (SR)	5	14.4 ¹	37.1	534.2

¹ Estimate from E.B. Fish: ² Estimate from F.G. Werner, U. of Arizona

On the basis of only 24 trees examined a second time, one year later, Table 5 gives an approximation of the annual production weight of standing dead wood which may be expected from three dominant trees on the Santa Rita Site.

Table 5. Annual standing dead wood production rate by species of dominant plants. Santa Rita Site.

Species	no. sampled	no./ha	kg/plant	Est kg/ha/yr
<i>Acacia greggii</i>	10	32.9 ¹	3.4	111.4
<i>Cercidium floridum</i>	9	12.1 ¹	3.8	46.0
<i>Prosopis juliflora</i>	5	14.4 ¹	7.6	104.7

¹ Estimate from E.B. Fish, University of Arizona.

2.3.3.4.-6

Although termites associated with standing dead wood are collected under this procedure, data on their populations are presented under DSCODE A3UNE04.

Following is a summary of population information gathered to date for the dry-wood termite, *Pterotermes occidentis*, in *Cercidium floridum* (standing dead wood) on destructive sampling areas at Santa Rita (DSCODE A3UNE04). Colonies have been disappointingly few and small. Although the method is suspected of favoring large dead branches on the larger trees, there is no basis for this in fact. Small colonies have been found in branches ca. 2.5 cm in diameter.

Pterotermes occidentis in *Cercidium floridum*, Santa Rita -
 Colonies - 7 in 18 trees sampled, 0.4/tree, 4.8/ha
 Termites - Avg 21.7/ colony (range 2-105), 104.2/ha
 Biomass - ca. 0.48g/ha

These figures may be very low, since mature colonies are known to reach at least 2000 individuals. Alate production known to range between 10-30% of colony, July-September each year. One newly established colony has been found out of 10 *C. floridum* sampled a second time one year later at Santa Rita.

Only four small colonies (2 dead) have been found in 31 *C. microphyllum* and 6 *Olneya tesota* sampled at Silver Bell. This termite may also occur in *Cereus giganteus* skeletons at Silver Bell, but none of these has been sampled yet.

Data on foraging groups of *Heterotermes* are presented in Table 6.

Table 6. Composition, biomass and density of foraging groups of *Heterotermes aureus*, Santa Rita and Silver Bell.

	SR, Undisturbed	SR, Chained	Silver Bell
No. circles	27	7	9
Avg no. grps/circle	0.70	1.57	0.56
Avg grp composition	165.32LW	413.0 LW	45.8LW
	3.32S0	7.18S0	1.2S0
	0.26NY	40.45NY	0.4NY
		1.27WS	
Total	189.89	461.91	47.4
Avg grp wt, mg	58.36	176.64	16.55
Est grps/ha	140.74	314.00	111.11
Est termites/ha	23,769.58	145,039.70	5,266.61
Est biomass/ha,g	8.214	55.46	1.84

LW=larva-worker (dry wt, 0.3422mg), NY=nymph (0.7754mg), S0=soldier (0.4776mg), WS= pre-soldier (0.4100mg).

Mature colonies of *Heterotermes* are estimated to reach several tens of thousands. Alate production is estimated at 5-10% of colony strength from June to September each year.

Following is a combined list of hosts from both sites:

<i>Acacia greggii</i>	<i>Fouquieria splendens</i>
<i>Aloysia wrightii</i>	<i>Gutierrezia sarothrae</i>
<i>Baccharis brachyphylla</i>	<i>Larrea divaricata</i>
<i>Celtis pallida</i>	<i>Olneya tesota</i>
<i>Cercidium floridum</i>	<i>Opuntia engelmannii</i>
<i>Cereus giganteus</i>	<i>Opuntia fulgida</i>
<i>Cercidium microphyllum</i>	<i>Opuntia spinosior</i>
<i>Ephedra trifurca</i>	<i>Opuntia versicolor</i>
<i>Ferocactus wislizenii</i>	<i>Prosopis juliflora</i>

Of the other species encountered on one or both sites, *Paraneotermes* has been found 7 times (max. no. 2,357), *Amitermes emersoni* twice (30), *A. minimus* 3 times (1,357), *A. wheeleri* 6 times (229), *Gnathamitermes* 40 times (1,033), and *Terminosritermes* at least 7 times (18) but not during routine sampling.

A few preliminary findings will give a general idea of the type of information expected from the toilet paper plots (DSCODE A3UNE06-08). Only two species are attacking the paper, *Heterotermes aureus* and *Gnathamitermes perplexus*.

Heterotermes aureus: Figure 1 is a diagram of the toilet paper plots showing the distribution of past activity and foraging groups actually present ("up") during 24 hours beginning 0700 hours, October 22, 1971. Table 7 summarizes data collected from examination of 12 of these plots for that period.

Table 7. Summary of *Heterotermes aureus* data on 12 contiguous toilet paper plots, Santa Rita Site, taken bi-hourly for 24 hours beginning 0700 hours, 10/22/1971 (see Fig. 1). Activity index=no. rolls containing foragers/no. rolls attacked to date. Estimated foragers/100m² based on sum of avg no. foragers/roll for each plot. Density= est. no. foragers/m² visited to date.

Hours, MST	Lowest Temp., °C	Activity Index	Est foragers /100m ²	Density
0700	7.6	0.67	5.0	1.67
0900	13.7	1.00	87.5	17.5
1100	16.6	0.0	0.0	0.0
1300	19.3	0.0	0.0	0.0
1500	21.9	0.80	255.0	17.0
1700	22.5	0.89	392.5	20.66
1900	16.1	0.76	120.0	5.7
2100	13.6	1.00	115.0	19.17
2300	12.1	0.89	337.5	18.75
0100	11.3	0.54	65.0	5.0
0300	10.1	0.75	327.5	81.0
0500	9.5	0.71	272.5	19.46

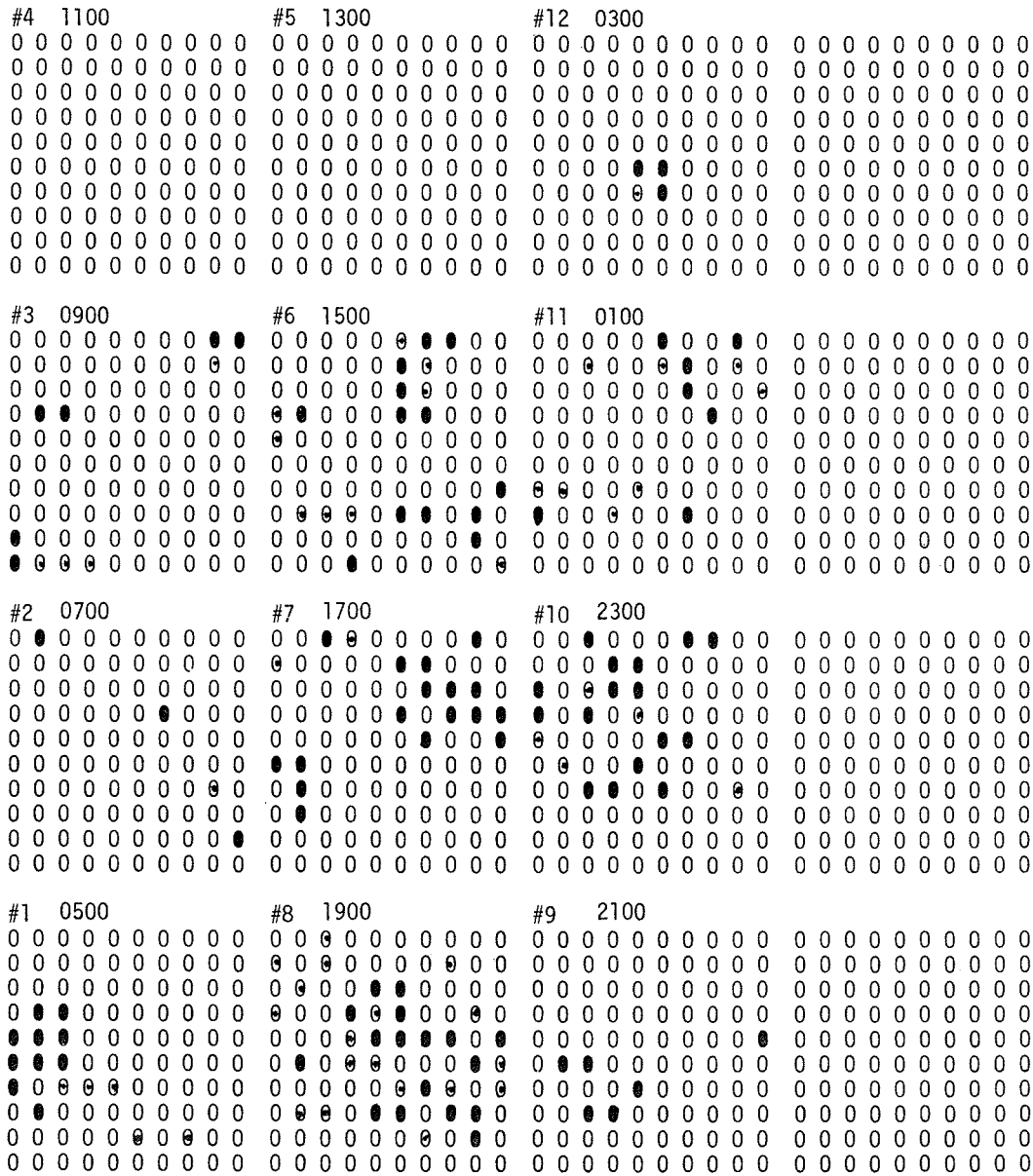


Figure 1. Plan of toilet paper plots, Santa Rita Chained Plot. Distribution and status of *Heterotermes aureus* foraging activity bi-hourly for 24 hrs beginning 0700 hrs, 10-22-71. 0's = toilet paper rolls spaced 1m on centers; ●'s = termites present; O's = evidence of activity, 0's = not attacked.

The maximum estimated number of foraging termites (39,250/ha @1700 hours) compares favorably with that (23,770) based on the circle method on the undisturbed plot, although it is far smaller than the similar estimate (145,039) for the chained plot. It is suggested that there may be ten times as many non-foraging individuals below ground.

In Figure 2, estimated number of foragers up/100m² is plotted as a function of soil or roll temperature (lowest measured) on a semi-log scale. A fairly reasonable relationship may be emerging here, although relationships between activity, numbers and various physical factors should become clearer as data for the remainder of the year are collected. This termite has been found foraging at the surface above a minimum soil temperature of 7.6°C. The upper limit to foraging may be near 35°C.

On the 12 plots there appear concentrations of attacked rolls separated by buffer zones of untouched rolls. It is likely that these represent foraging territories of single colonies. Aside from several isolated on one to a few rolls, two of the largest of these irregular areas measure 5 x 8.5m (ca. 24m²) and 4 x 12 m (ca. 28m²).

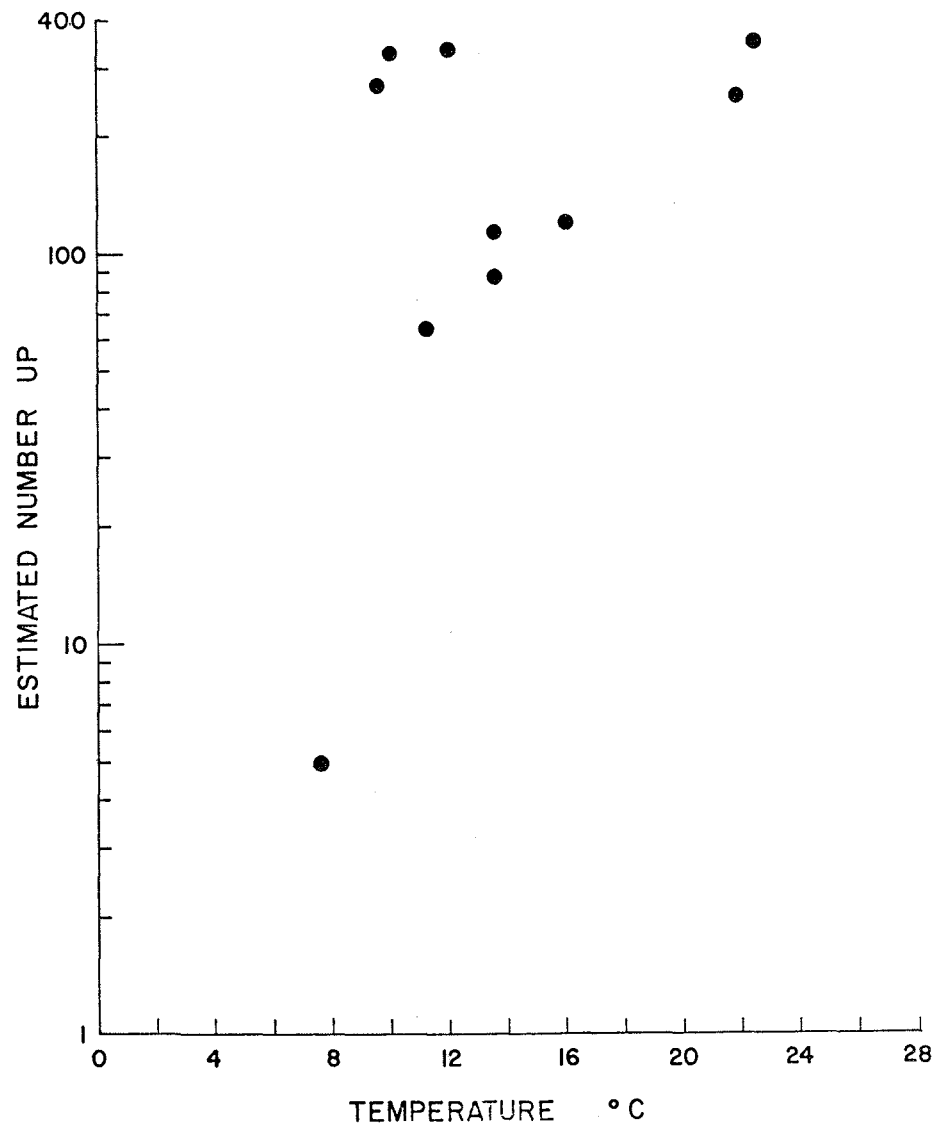


Figure 2. Estimated number of foraging *Heterotermes aureus*/100m² plotted as a function of lowest temperature encountered on each plot. One of 12 plots examined every two hours for 24 hrs. Semi-log scale.

Gnathamitermes perplexus: This species has attacked so many rolls that there is no obvious pattern to suggest colony limits (Figure 3). Foraging groups are very common. A maximum average estimate of foragers, from Plot 1 at 1500 hours on 10/28/71, is 705,200/ha. Based on the average dry weight of one worker (0.5308mg), N=507) this gives 374.3 g of foragers/ha. It forages at the surface above a soil temperature of ca. 10°C.

Mature colony size is estimated between 5,000 and 10,000. Alate production is perhaps less than 5% of a colony, from June to September each year.

Following is a combined list of hosts from both sites:

- | | |
|-------------------------------|-------------------------------|
| <i>Aplopappus tenuisectus</i> | grasses - all spp.? |
| <i>Celtis pallida</i> | <i>Larrea divaricata</i> |
| <i>Cercidium floridum</i> | <i>Olneya tesota</i> |
| <i>Cereus giganteus</i> | <i>Opuntia arbuscula</i> |
| <i>Cercidium microphyllum</i> | <i>Opuntia engelmannii</i> |
| in Cow chips | <i>Opuntia fulgida</i> |
| in Drift | <i>Opuntia spinosior</i> |
| <i>Echinocereus fendleri</i> | <i>Opuntia versicolor</i> |
| <i>Ephedra trifurca</i> | <i>Prosopis juliflora</i> |
| <i>Ferocactus wislizenii</i> | <i>Solanum elaeagnifolium</i> |
| <i>Fouquieria splendens</i> | under Stones |

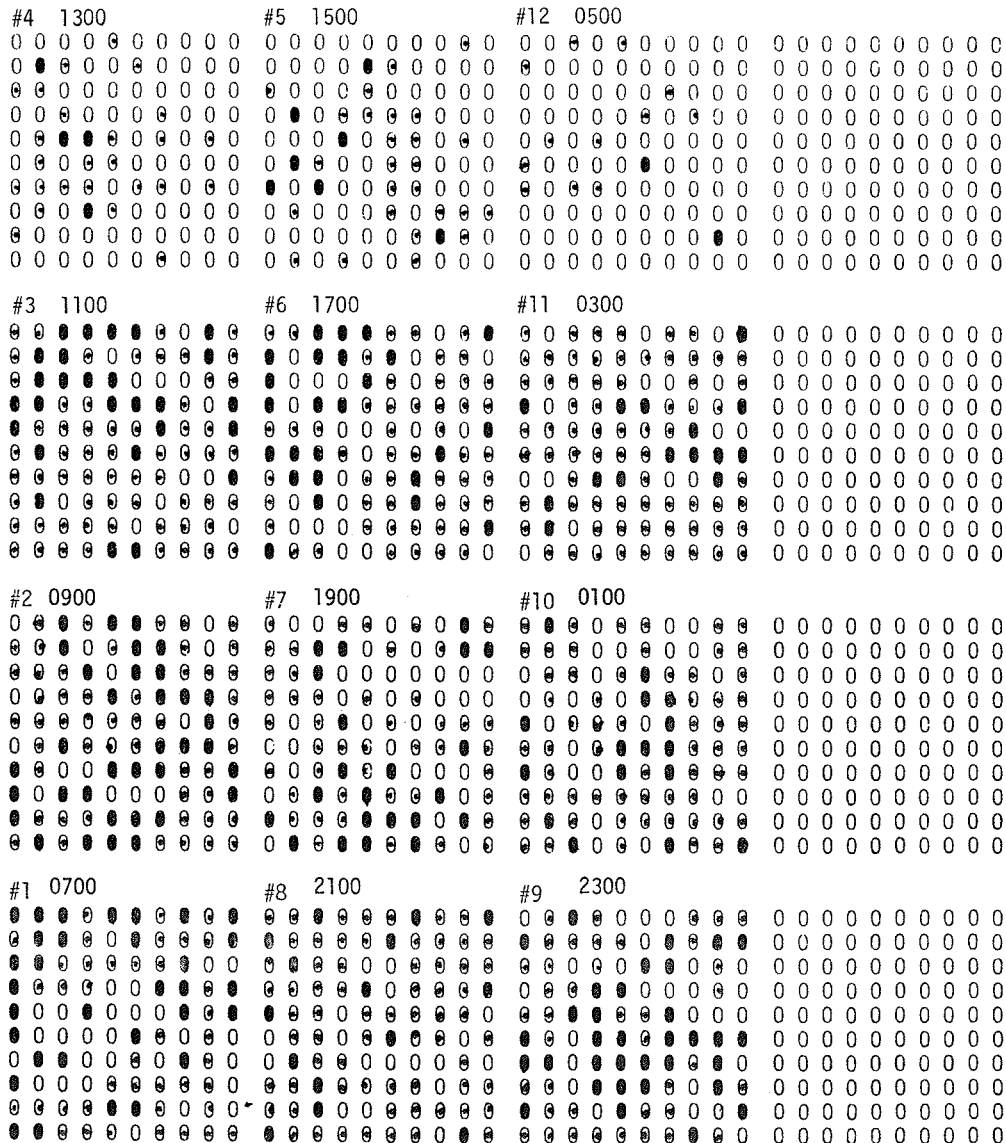


Figure 3. Plan of toilet paper plots, Santa Rita Chained Plot. Distribution and status of *Gnathamitermes perplexus* foraging activity, bi-hourly for 24 hrs beginning 0700 hrs, 10-15-1971. O's = toilet paper rolls spaced 1m on centers. ● = termites present:

Table 8 summarizes the data on incipient colony development for *Marginitermes hubbardi*.

Table 8. Mean number of individuals of *Marginitermes hubbardi* per colony after 6 months, by caste and instar, maintained on birch discs at 32°C and 70% RH. (64 colonies)

Caste of Instar	Mean no./colony	Range	s
Primary Reproductives			
Male	0.79	0 - 1	0.40
Female	0.81	0 - 1	0.38
Eggs	0.26	0 - 4	0.74
Larvae			
1st Instar	0.14	0 - 2	0.38
2nd Instar	0.21	0 - 2	0.44
3rd Instar	2.07	0 - 9	1.72
4th Instar	0.51	0 - 4	0.92
Soldiers	0.50	0 - 1	0.50

Quantities of wood consumed and fecal pellets produced will be determined at the end of a year. Samples of wood and pellets will be reserved for analysis of their constituents.

DISCUSSION

It is relevant to stress that the overall approach of the present study of these cryptobiotic insects has not been attempted on a regional termite fauna anywhere in the world. This bold assumption was based on familiarity with termite research, but Lee and Wood (1971, p. 191) support the contention with the statement that "...no estimate of the total termite population of any soil has ever been made..." However, the work described above is believed to have already produced good estimates of foraging populations and biomass of the two most important subterranean termites in the Sonoran Desert, together with some preliminary indications of foraging territory size for one of them, as well as producing perhaps a fair estimate of the population of one species of dry-wood termite in the same area.

Since at least a year of data collection is necessary to reach the main objectives, analysis of the data has begun in only an exploratory way. Information obtained on dead plant material should permit correlations between its availability and termite abundance. Thus far there is no correlation between the weight of pieces of dead wood and the numbers of termites attacking them. Dry-wood species are considerably more specific in their choice of hosts than the subterranean species. Some studies on wood preference and the rate of wood consumption are in progress, but more are needed.

There is little information available on the influence of specific physical factors on termite abundance and activity. Lower temperatures which limit foraging activity of two subterranean species have already been bracketed, and upper limits will be determined next summer. It does not look as though soil moisture, at least in the upper meter, will be as critical as was originally thought.

There is obviously a large accumulation of dead plant material on these sites which is not — and may never be — eaten by termites. The reasons for this are probably very complex and may involve several factors which limit or prevent termite attack, such as temperature and moisture content of soil and wood, presence or absence of fungi in wood, and feeding deterrents or inhibitors in the wood itself. The widespread occupation of dead wood by existing foraging groups may also determine the availability of new nesting sites to alates which fly each season.

EXPECTATIONS

In addition to the continuation of current studies, the following work is planned for 1972, with anticipation of substantial results on the starred (*) items:

- *1. More refined estimation of foraging group and colony size, and single colony foraging areas, with limits of seasonal variation. Toilet paper rolls treated with dyes or tracers may be tried in the foraging area studies. At least one or two deep excavations are planned this spring to learn as much as possible about underground termite activity.
- *2. Preferred host plants. Host preferences for the abundant species of termites can best be determined from an analysis of data collected during sampling of fallen and standing dead wood. Simple choice tests can be made with laboratory groups of both types of termites.
- *3. Food consumption rates. Harvesting the toilet paper plots will give good cellulose consumption rates in an area where populations of two species are known. Incipient colonies and small laboratory groups can also be used.
4. Reproductive and colony growth rates. Most of this information will probably have to come from laboratory studies. Rates for dry-wood species might be arrived at through analysis of colony size and composition data.
5. Alate production per colony and per hectare. Small cages (ca. 1m^2) were used during the last flight season with little success. Large cages (several m^2) over dead wood work well with dry-wood species and, hopefully, may produce some information on the toilet paper plots.
- *6. Rate of soil movement to the surface. An attempt will be made to measure this in connection with the harvest of one or more toilet paper plots.
7. Correlation of several of the above functions with key environmental factors will depend on progress made in each area.

LITERATURE CITED

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