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Density of Colonies and Spatial Distribution of Foraging Territories of the Desert Subterranean Termite, *Heterotermes aureus* (Snyder)^{1,2,3}

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ABSTRACT

Density of colonies together with size and spatial distribution of foraging territories of the subterranean termite, *Heterotermes aureus* (Snyder), were determined on a 1600-m² bait sampling grid in a shrub-invaded desert grassland on the Santa Rita Experimental Range S of Tucson, Arizona. Bait units (toilet paper rolls) attacked on the first wk of the 52-wk study and those with large, mean weekly forager counts were considered as colony foci. Lateral spread of colony boundaries was followed weekly. After one year *H. aureus* had attacked 22.8% of the bait units. Colony density was estimated at 190.4/ha, mean territory contained 12.5 m² and mean number of individuals/colony was speculated to be 22,632.

This is the 4th in a series of papers detailing the role of termites in the detritus cycle of a desert ecosystem. The first (LaFage et al. 1973) set forth our methodology for studying foraging populations of subterranean termites and their behavior; the 2nd (Haverty and Nutting 1974) reported wood-consumption rates for 2 common species as a function of temperature, wood species, and termite biomass; and the 3rd (Haverty et al. 1974) related seasonal foraging activity of *Heterotermes aureus* (Snyder) to key environmental parameters. Here we present an analysis of extensive field data which describes the foraging populations of *H. aureus*.

To our knowledge spatial distribution of foraging territories and colony size and density of an entirely subterranean species have never been reported. It is plainly difficult to characterize populations of such termites, for without obvious above-ground indications of their presence they are hard to locate and the limits of their colonies nearly impossible to delineate. Estimates of the abundance of subterranean colonies of *Odontotermes latericius* (Haviland) in veld near Boemfontein, South Africa, have been made using data gathered in trenches dug for civil engineering purposes (Hartwig 1966). Territorial boundaries have been determined by observing mutual hostility between workers from different colonies of the subterranean harvester, *Hodotermes mossambicus* (Hagen) (Nel 1968). On the other hand, territories of mound builders have been approximated by measuring the extent of radiating foraging galleries (Greaves 1962).

H. aureus is an entirely subterranean species of considerable economic importance, which occurs in the desert areas of southeastern California and southern Arizona. It forages throughout the year,

with temperature and rainfall affecting the intensity of its activity (Haverty et al. 1974). Nothing is known about the depth or characteristics of its nest and gallery system. It is a general feeder, attacking superficial and buried dead wood from a variety of trees, shrubs and cacti (Haverty and Nutting, unpublished⁵). It enters superficial wood through one or more galleries at the soil-wood interface and typically riddles the interior. Although the older workings may be packed with soil or lined with light brown fecal material, active excavations are clean.

Materials and Methods

The Desert Biome study site was located ca. 40 km S of Tucson, Ariz., on the Santa Rita Experimental Range, at an elevation of 950 m. The area is a shrub-invaded desert grassland, characterized by scattered trees, shrubs, and cacti. The predominant trees are mesquite, *Prosopis juliflora* var. *velutina* (Woot.) Sarg.; blue palo-verde, *Cercidium floridum* Benth.; and catclaw acacia, *Acacia Greggii* Gray. 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. Perennial grasses are scattered along water courses and beneath the crowns of trees and shrubs, with 5 species predominating: 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.

On ¼ of the site, large standing woody plants had been knocked down 18 months before our work began. For the termite studies, a 40×40-m plot was further cleared of any remaining plants with the exception of scattered burro-weed and perennial grasses. It was finally raked clear of all bits of dead wood which had served as food for the *H. aureus*.

¹ Isoptera: Rhinotermitidae.

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⁵ Haverty, M. I., and W. L. Nutting. Density, dispersion, and composition of desert termite foraging populations and their relationship to superficial dead wood. *Environ. Entomol.* (submitted).

On this plot 1681 rolls of toilet paper were set out in a grid at 1-m intervals and served as a substitute food source. Each roll theoretically had the same foraging potential. The rolls of paper, the small shrubs (< .5 m in height) and grasses provided the only shade on the study plot (LaFage et al. 1973).

Detailed observations on the termites foraging here were made during one 24-h period each wk from Oct. 15, 1971, to Oct. 13, 1972. A different subplot of 100 rolls in a block of 12 was checked every 2 h. The fact that no single roll was observed more than once a wk allowed termites time to rebuild connecting galleries. The 4 remaining subplots were reserved for studies of soil movement and paper consumption by termites and were examined for activity but once at the end of the year. A weekly record was kept of foraging intensity for each roll of paper. From this, frequency tables of foraging-number size classes were developed (Haverty et al. 1974) that allowed calculation of the average number of foragers visiting each roll during the year. The weekly records also provided a basis for observing the lateral spread of foraging territories.

We were able to establish boundaries of what we consider to be foraging territories of individual colonies but not by Nel's (1968) ingenious method of noting aggression (or lack of it) displayed between individuals from different areas. Rolls attacked on the 1st wk of the study and rolls with large, mean weekly counts of termites were considered as colony foci. The lateral spread of territories from these points to new rolls was followed weekly. Isolated rolls or groups of 2 or 3 rolls were arbitrarily included with larger aggregations if they were within 2 rolls of the larger clump and appeared to represent a temporal expansion of the original foci.

Weekly activity records were not available for the 4 plots reserved for soil studies or the intermediate rows within the study plot (Figures 1 and 2) since only end-of-the-year evidence of attack was available for these rolls. Consequently, colony boundaries were empirically determined here on the basis of the relative severity of attack on closely associated rolls.

We assumed that each roll subtended 1-m² of territory, so the spatial area of each foraging territory was calculated by summing the rolls attacked in each grouping. Unattacked rolls within such groups were included in the occupied areas since it seems unlikely that they would be attacked by other colonies of *H. aureus*. Areas of colonies on the periphery of the plot were multiplied by two because, on the average, only 1/2 of each such colony would fall within the plot. In determining densities of colonies, we counted colonies wholly within the plot as whole colonies but, according to the preceding assumption, those divided by plot boundaries were counted as half-colonies.

Only one other subterranean termite, *Gnathami-termes perplexus* (Banks) (Termitidae), was abundant on the study plot but its large, open, and rela-

tively clean cavities were easily distinguished from the narrow, deeply penetrating, and heavily spotted galleries of *H. aureus*. The fact that *G. perplexus* attacked 96% of the toilet paper rolls, including 53% of those attacked by *H. aureus*, suggests that it may have influenced the foraging patterns of the latter. We have chosen to defer any consideration of interspecific competition pending completion of our analysis of the foraging populations of *G. perplexus*.

Results and Discussion

The average number of *H. aureus* foragers visiting each roll of paper/check on the 12 subplots is shown in Fig. 1. Figure 2 gives the number of weeks that each roll was part of an active foraging territory. Rolls on the 4 adjacent subplots and in the rows interspersed among them are identified as being attacked (+) sometime during the year or not (-). We do not know whether there were correlations between colony foci and existing dead wood since none of these items was located on our grid maps. This information thus provided the basis for our delineation of probable colony boundaries shown in Fig. 1 and 2. It is entirely possible, however, that our groupings represent foraging areas or subcolonies of a much larger colony.

H. aureus attacked 383 (22.8%) of the rolls of paper. The distribution of the 26 complete and 12 partial (one-half) colony territories is outlined in Fig. 1 and 2. The area of a colony averaged 12.5 m² and occasionally included a few unattacked rolls. By assuming 32 colonies on the study plot and extrapolating from these data, we have calculated that there would be 190.4 colonies/ha. Nel (1968) observed the foraging behavior of 16 colonies of the harvester, *Hodotermes mossambicus*, on a 2980-m² study plot. Of these, 13 were wholly within the area and 3 bisected by its borders. Similar calculations give 14.5 colonies/2980 m² or 48.7 colonies/ha. Other literature reports of colony density are for mound-building species (Lee and Wood 1971).

The average foraging territory of a colony of *H. aureus* (12.5 m²) is very small in comparison with those of other termite species. Nel (1968) found the mean territory of 12 colonies of *Hodotermes mossambicus* to be 92.1 m². Greaves (1962) reported that foraging galleries of *Coptotermes acinaciformis* (Froggatt) radiated from the mound to a maximum of 47.5 m and those of *C. brunneus* Gay to 45.7 m. Colonies of both *C. acinaciformis* and *C. brunneus* were spaced consistently at 90 m apart, each apparently controlling an area of at least 8210 m².

Foraging territories of social insects, particularly those that forage for scattered food, may fluctuate but seldom overlap (Greaves 1962) and there is often a buffer zone between them (Brian et al. 1965, Elton 1932, Nel 1968, and Wilson et al. 1971). The colony territories of *H. aureus* do not appear to overlap and neutral zones occur between most of them. In some cases, however, their bound-

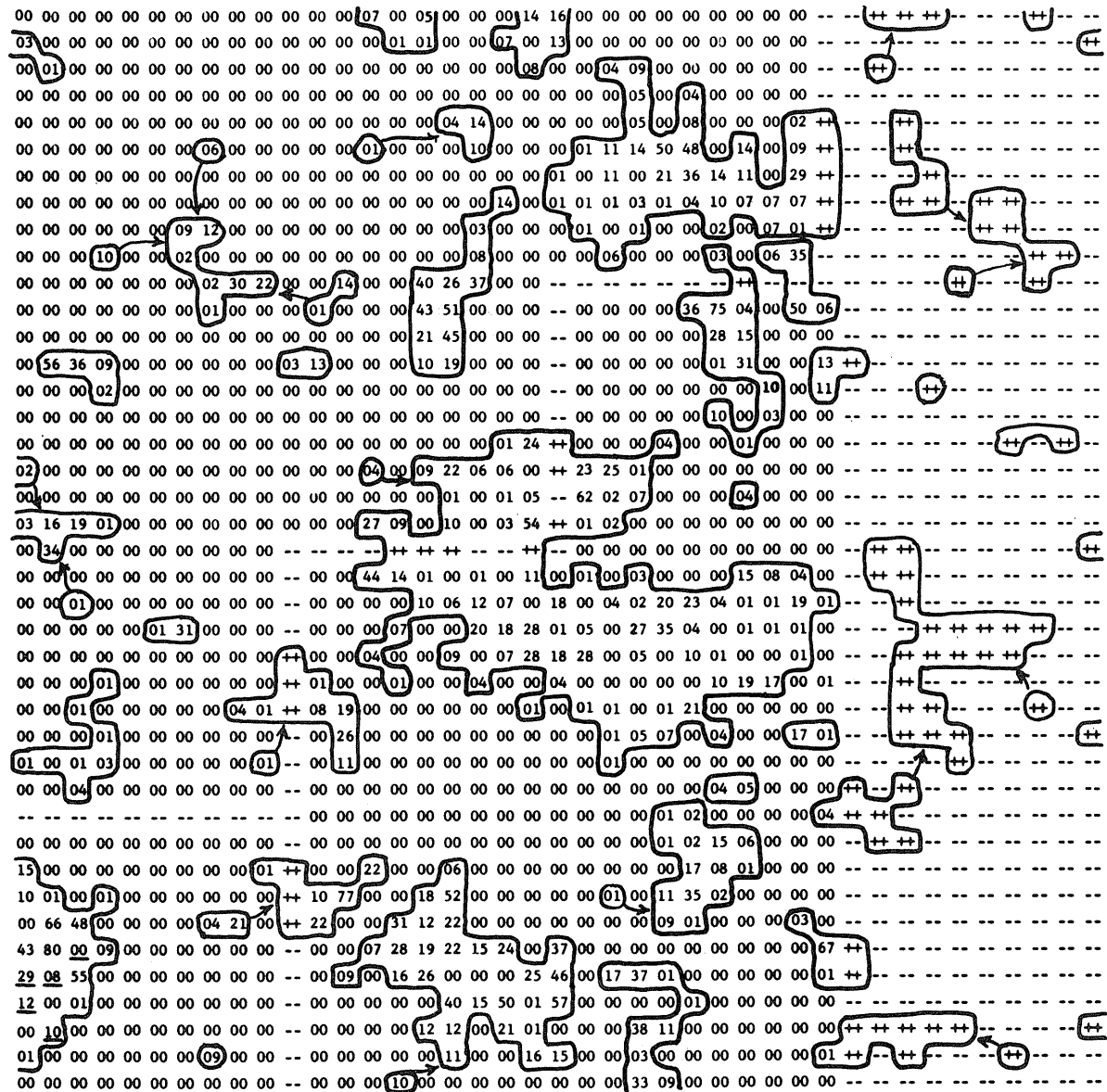


FIG. 1.—Foraging territory pattern and distribution for individual colonies of *Heterotermes aureus* on bait sampling grid of toilet paper rolls, Santa Rita Experimental Range, Pima Co., Ariz. Numerals represent the average number of *H. aureus* foragers observed/roll/weekly check. Underlined numbers are 100 plus the number shown. Pairs of pluses and minuses represent presence or absence of attack upon individual rolls by *H. aureus* as determined at the end of the study period.

aries are tangential, expanding until apparently halted by contact with neighboring colonies (Fig. 2). Since foraging is dynamic, territories on our study plot probably expanded to exploit the new, uniformly distributed food source. Whether or not discrete boundaries are maintained by intraspecific aggressive behavior (Nel 1968) is not known.

In many habitats, including the Santa Rita Experimental Range, there seems to be much unexploited food for termites. Emerson (1955) has observed this in many parts of the world and has postulated

that competition for colonizing and nesting sites is greater than for nutritive resources. Wilson (1971) has also noted that the intrinsic rate of population increase for termites is low. Therefore, it is doubtful that the addition of rolls of paper at the rate of 1769 kg/ha accounted for any increase in termite numbers, and hence an expansion of territory. In fact, the amount of paper was less than the original standing crop biomass of superficial dead wood (2127 kg/ha; Haverty and Nutting, unpubl.⁶). The territorial expansion we observed appears more likely

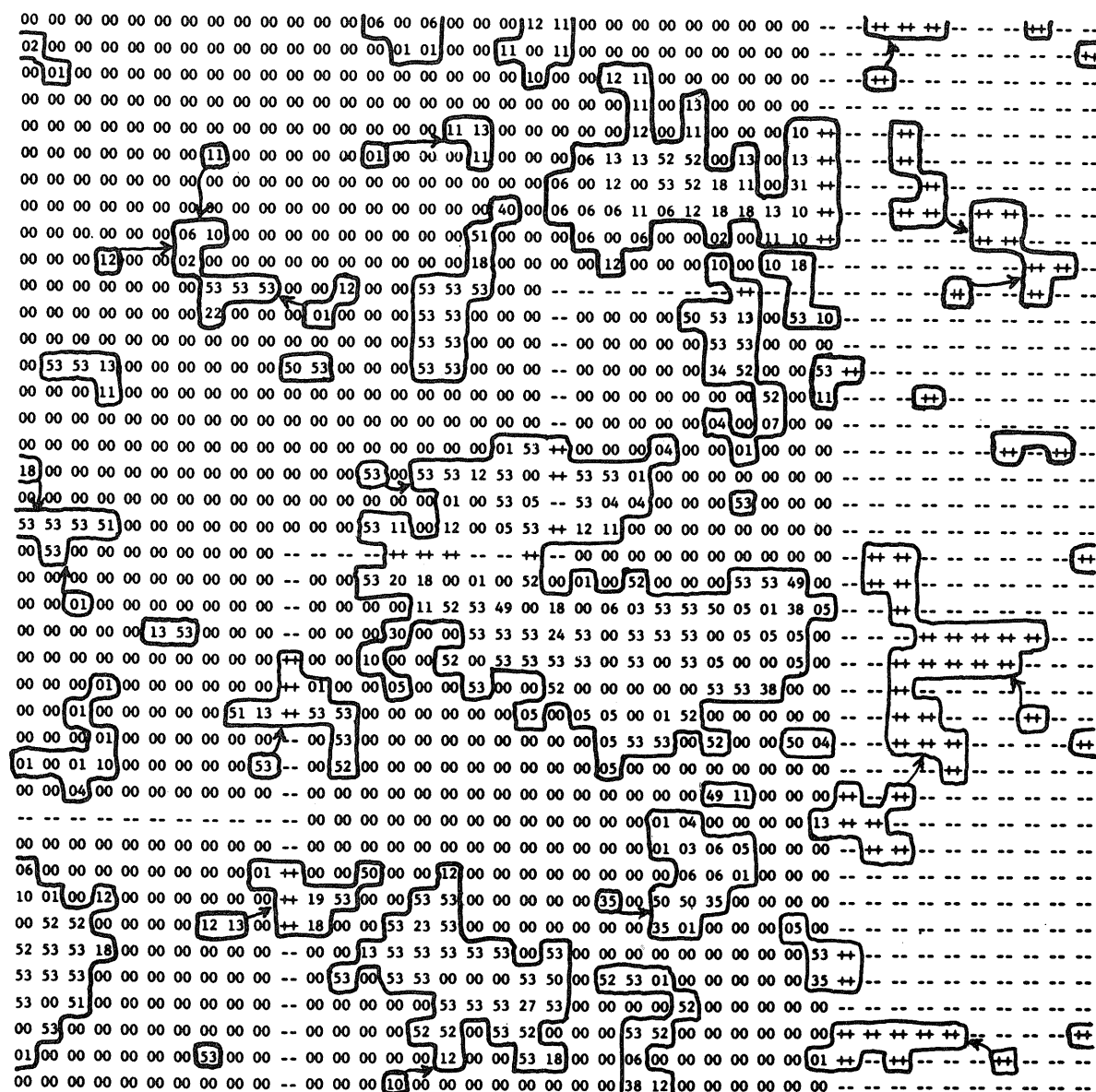


FIG. 2.—Foraging territory pattern and distribution for individual colonies of *Heterotermes aureus* on bait sampling grid, Santa Rita Experimental Range, Pima Co., Ariz. Numerals represent the number of weeks for which each roll was part of an active foraging territory. Pairs of pluses and minuses represent presence or absence of attack upon individual rolls by *H. aureus* as determined at the end of the study period.

to have been the result of a general increase in foraging activity. Most rolls were attacked during the first 5 wk of the study, from Oct. 15 to Nov. 12 (roll values 49–53, Fig. 2), and during the last 18 wk, from June 8–Oct. 13 (roll values 1–18, Fig. 2). This coincides with periods of high foraging activity for this species (Haverty et al. 1974).

The number of individuals in a colony of an entirely subterranean species has never been reported; therefore, we felt that it should be profitable to speculate on average colony size based on the data presented here. During our study we observed an

average of 3.78 foragers/roll/weekly check (Fig. 1). Bodine (unpublished⁶) used soil cores to estimate the density of *Gnathamitermes tubiformans* (Buckley) in the upper 30 cm of soil in a semiarid grassland in Texas. From May through July he observed that the subsurface density was 3797 termites/m², with a surface density of 33.3/m². If we assume that *H. aureus* has the same subsurface:surface proportions (114:1) as *G. tubiformans*, the total density of *H.*

⁶ Bodine, M. C. 1973. The impact of the termite *Gnathamitermes tubiformans* on rangeland herbage dynamics. Texas Tech. Univ., Lubbock, Texas, M.S. thesis, p. 39.

aureus would be 4.31×10^6 termites/ha. Dividing the total number of termites by 190.4 colonies/ha we get an estimated 22,632 termites/colony. This estimate is highly speculative but, in the absence of others for comparison, we feel that it is not at all unreasonable.

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

REFERENCES CITED

- Brian, M. V., J. Hibble, and D. J. Stradling. 1965. Ant pattern and density in a southern English heath. *J. Anim. Ecol.* 34: 545-55.
- Elton, C. S. 1932. Territory among wood ants (*Formica rufa* L.) at Pickett Hill. *J. Anim. Ecol.* 1: 69-76.
- Emerson, A. E. 1955. Geographical origins and dispersions of termite genera. *Fieldiana: Zoology* 37: 465-521.
- Greaves, T. 1962. Studies of foraging galleries and the invasion of living trees by *Coptotermes acinaciformis* and *Coptotermes brunneus* (Isoptera). *Aust. J. Zool.* 10: 630-51.
- Hartwig, E. K. 1966. The nest and control of *Odontotermes latericius* (Haviland) (Termitidae: Isoptera). *S. Afr. J. Agric. Sci.* 9: 407-18.
- Haverty, M. I., J. P. LaFage, and W. L. Nutting. 1974. Seasonal activity and environmental control of foraging of the subterranean termite, *Heterotermes aureus* (Snyder), in a desert grassland. *Life Sciences* 15: 1091-101.
- Haverty, M. I., and W. L. Nutting. 1974. Natural wood-consumption rates and survival of a dry-wood and a subterranean termite at constant temperatures. *Ann. Entomol. Soc. Am.* 67: 153-7.
- LaFage, J. P., W. L. Nutting, and M. I. Haverty. 1973. Desert subterranean termites: A method for studying foraging behavior. *Environ. Entomol.* 2: 954-6.
- Lee, K. E., and T. G. Wood. 1971. Termites and soils. Academic Press, New York. 251 pp.
- Nel, J. J. C. 1968. Aggressive behavior of the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt). *Insectes Soc.* 15: 145-56.
- Wilson, E. O. 1971. The insect societies. Belknap Press of Harvard Univ. Press, Cambridge, Mass. 548 pp.
- Wilson, N. L., J. H. Dillier, and G. P. Markin. 1971. Foraging territories of imported fire ants. *Ann. Entomol. Soc. Am.* 64: 660-5.

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