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Density, Dispersion, and Composition of Desert Termite Foraging Populations and Their Relationship to Superficial Dead Wood[1]

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ABSTRACT

To evaluate the importance of subterranean termites in the detritus cycle it was necessary to determine density and dispersion of termite foraging populations and the types and amounts of wood available to them. Sampling was carried out in a shrub-invaded desert grassland south of Tucson, Ariz. Fifty randomly located, circular quadrats were sampled to study the relationships between foraging termites and the abundance of wood. Standing crop biomass of superficial dead wood was 2127 kg/ha. Five plant species represent 97.6% of the biomass while 6 account for 96.4% of the 450 kg/ha of such wood produced annually. Instantaneous estimates of mean surface foraging numbers of *Heterotermes aureus* (Snyder), *Gnathamitermes perplexus* (Banks), *Paraneotermes simplicicornis* (Banks), *Amitermes wheeleri* (Desneux), and *A. minimus* Light were 6.89, 0.35, 1.31, 1.51, and 0.12 termites/m^2. Caste composition varied between the species and was important in determining total biomass. Neither superficial dead wood nor foraging termites were randomly dispersed; rather, they were aggregated on the site. Estimated total number of all 5 termite species was set at 1025/m^2 with a biomass of 0.414 g/m^2, based on a literature ratio between surface and subsurface foragers of *Gnathamitermes tubiformans*. We have tested the hypothesis that quantity and/or quality of wood available influences termite abundance. Results indicate that the abundance of a particular oligophagous species is correlated with the quantity of a highly perferred wood, where there is no correlation between ploryphagous species and the quantity of any species of wood.

Because of the cryptic behavior of subterranean termites, there are relatively few comprehensive studies which examine their ecology and demography. Most such studies are concerned primarily with the obvious mound building or harvesting species which forage above the ground. Subterranean termites may be defined as those species that normally live in more or less diffuse nests of scattered chambers in the soil with with no above-ground indication of their presence in the form of a mound structure. They are difficult subjects for research and have consequently been neglected by most ecologists, who have favored the study of mound-building species as more convenient subjects. The concentration of effort on the more obvious part of a community has perhaps created the impression that mound-building species are ecologically more important than subterranean species when they occur together. However, Sands (1972) concludes that subterranean species are probably the most numerous, and certainly the most significant from the economic viewpoint, in the developing countries of the tropics.

The absolute density of subterranean termite populations in any particular habitat has never been estimated reliably (Lee and Wood 1971). Relative density or intensity of foraging can be measured with baits, pits, and quadrats (Sands 1972, Haverty et al. 1974, Lee and Wood 1971, Bodot 1967). Soil cores have been used to estimate the numbers of termites in the upper 15 or 30 cm of soil (Sands 1972, Lee and Wood 1971, Bodine, unpubl.[4]). However, soil core-sampling poses problems because subterranean termites tend to be clumped, with their distribution best described by a negative binomial (Sands 1972). For example, during a period of termite activity as many as 87.5% of the cores taken by Bodine (1973) contained no termites. Sufficiently large cores cannot be taken to overcome this problem and yet remain practical.

On our study site 4 species of subterranean termites (as defined above) predominate: *Paraneotermes simplicicornis* (Banks) (Kalotermitidae); *Heterotermes aureus* (Snyder) (Rhinotermitidae); *Gnathamitermes perplexus* (Banks); and *Amitermes wheeleri* (Desneux) (Termitidae). *A. minimus* Light and *A. silvestrianus* Light occur infrequently. At least 3 of these species, *P. simplicicornis, H. aureus,* and *A. wheeleri,* commonly attack sound wood and, since they are therefore economically important in the Sonoran Desert (Snyder 1954), they must also figure importantly in the breakdown and gradual recycling of the superficial dead wood which is continuously produced in the desert ecosystem. An important first step toward evaluating their efficiency in processing this wood involves estimation of their density and dispersion together with the abundance of the wood available to them.

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[4] Bodine, M. C. 1973. The impact of the termite *Gnathamitermes tubiformans* on rangeland herbage dynamics. M.S. Thesis. Texas Tech. Univ., Lubbock.

Methods and Materials

The field work for this study was carried out on one of the US/IBP Desert Biome research sites. The U.S. Forest Service provided the area on its Santa Rita Experimental Range ca. 40 km south of Tucson, Ariz., at an elevation of 950 m. The soil of this site is formed from outwash alluvium characteristic of much of the Sonoran Desert. Annual rainfall averages 330 mm, ca. ½ of which occurs during the summer monsoon season. The remainder is frequently made up, less reliably, during the period from Dec. through Feb. The area is a shrub-invaded, desert grassland, characterized by scattered shrubs, cacti, and small trees. The shrub layer is dominated by burro-weed, *Aplopappus tenuisectus* (Green) Blake; the cactus by cholla, *Opuntia fulgida* Engelm. and *O. spinosior* (Engelm. and Bigel.) Toumey; and the small tree layer by mesquite, *Prosopis juliflora* var. *velutina* (Woot.) Sarg., as well as blue paloverde (*Cercidium floridum* Benth.), and catclaw acacia (*Acacia Greggii* Gray). Perennial grasses are found mainly along the water courses and beneath the crowns of trees and shrubs.

We sampled for superficial dead wood, associated termite activity, and foraging group size on a limited destructive sampling area of an untreated plot. From a grid covering an area of ca. 20 ha which had been used for soil moisture sampling 50 points were chosen randomly and served as the centers of the 50 "circledrats" (circular quadrats). In the beginning sampling was done both day and night to randomize the time of day in which the termite populations were observed. It was soon decided that their foraging activity should be studied separately and intensively; this was done with detailed attention to several environmental variables (LaFage et al. 1973).

At least 2 of the termite species studied, *H. aureus* and *G. perplexus,* are known to forage day and night throughout the year, with temperature governing foraging intensity (Haverty et al. 1974, LaFage unpubl.[5]). Consequently, circledrats were sampled during favorable environmental conditions, with primary attention devoted to dead wood and foraging group size and density.

Using the random points as centers, fifty 50-m² circledrats were "drawn" and sampled between May 3, 1971, and June 7, 1972. To determine dead wood production we resampled each point between May 2, 1972, and June 5, 1973, 1 yr after their initial sampling. Wood accessible to subterranean termites from the ground within the circle was included, wood accessible only from without was not. All the dead wood on the ground was identified and weighed in pounds and ounces on a hand-held, Chatillon® hide scale. Weights were later converted to grams.

When foraging groups were encountered, they were either counted on the spot or the wood containing them was brought back into the laboratory and the termites were extracted from the wood and counted. All counts were exact tallies of every individual in a foraging group. None was estimated. When clean and healthy termites were brought back to the laboratory occasional samples were removed and dried to constant dry weight (to nearest 0.1 mg) at 60°C for 24 h.

The circledrat method yielded data for determining several types of information: biomass of dead wood of each species/ha available to termites, biomass of dead wood of each species produced annually/ha, numbers and biomass of surface foraging populations of several subterranean termites species/ha, and the relationship between the amount of wood available and the termite numbers and biomass.

Wood weights obtained in the field necessarily included a certain amount of moisture, soil, and miscellaneous debris. These field weights have been corrected for moisture content and adhering material as follows. Two collections of random samples of 6 species of wood were made just outside the IBP study area on 2 different dates: after a wet period (Oct. 20, 1972) and a dry period (Sept. 24, 1973). Routine field weights were taken and the wood was brought back into the laboratory for a thorough cleaning and drying. It was brushed and washed in water, dried at 105°C for 24 h, then reweighed on the same scale to determine biomass. A factor for correcting field weights was determined by dividing the weight of a clean, dry sample by its field weight.

No significant difference was found between the correction factors for the wet and dry periods; therefore, data for the 2 seasons were considered together. A significant difference ($\alpha = .01$) between correction factors for wood species was found by analysis of variance. Wood species not processed as above have been assigned a correction factor which is the average of factors determined for the six species. Field weights were multiplied by the appropriate correction factors to give the biomass of superficial dead wood standing crop and annual production of dead wood.

The departure of distributions from a Poisson model was tested by the relationship

$$\frac{\chi^2}{N\text{-}1} = \frac{s^2}{\bar{x}}$$

where s^2 = variance
N = number of samples
$\bar{x}$ = mean
$\frac{s^2}{\bar{x}}$ = coefficient of dispersion.

Values within the 0.95 and 0.05 limits for $\chi^2/N\text{-}1$ are considered to represent a random distribution, whereas those greater than the 0.05 limit imply aggregation (Southwood 1966). Relationships between the standing crop of superficial dead wood and termite numbers or biomass were obtained by linear correlation. Correlations for termite numbers and biomass were examined, using the average biomass for each caste and the corrected biomass of each wood species for each circledrat.

[5] LaFage, J. P. 1974. Environmental factors controlling the foraging behavior of a desert subterranean termite, *Gnathamitermes perplexus* (Banks). M.S. Thesis, Univ. Arizona, Tucson.

Table 1.—Biomass of superficial dead wood standing crop and dead wood produced annually on the IBP untreated plot, Santa Rita Experimental Range, based on fifty 50-m² circledrats.

Wood species	Standing crop			Annual production		
	$\bar{x}$ wt/ circledrat	$s^2/\bar{x}$	Est. kg/ha	$\bar{x}$ wt/ circledrat	$s^2/\bar{x}$	kg/ha Est.
Acacia Greggii	3.162	20.916	632	0.158	1.658	32
Prosopis juliflora	1.801	12.647	360	0.796	14.668	159
Opuntia fulgida	1.766	8.841	353	0.415	9.894	83
Opuntia spinosior	1.562	2.256	312	0.074	1.014	15
Opuntia spp. joints	1.405	4.898	281	0.274	0.923	55
Cercidium floridum	0.688	18.480	138	0.352	8.651	70
Celtis pallida	0.087	3.034	17	0.003	0.062	1
Opuntia engelmannii	0.051	0.608	10	0.102	2.529	20
Ephedra trifurca	0.041	0.390	8	0.023	0.087	5
Gutierrezia Sarothrae	0.040	1.125	8	0.045	0.333	9
Other woods	0.034	0.294	7	0.007	0.068	1
Total	10.636	8.688	2127	2.249	7.839	450

Results

Fallen Dead Wood Available to Termites and Annual Dead Wood Production

Correcting field weights of all superficial dead wood, we estimate that the standing crop biomass is 2127 kg/ha (Table 1). Five dominant plant species (*Acacia Greggii, Prosopis juliflora* var. *velutina, Opuntia fulgida, Opuntia spinosior,* and *Cercidium floridum*) account for 97.6% of the biomass. The coefficients of dispersion for all of the above dominant species are beyond the 0.05 critical limit for $\chi^2/N\text{-}1$ (= 1.354), indicating a nonrandom dispersion of the standing crop biomass.

Biomass of all superficial dead wood produced annually is estimated at 450 kg/ha (Table 1). This estimate does not allow for dead wood produced and consumed by termites during the year. Although we did not measure wood consumption, very few termites were collected in resampling and, hence, the wood consumed was probably minimal. Six plant species (the above plus *Opuntia Engelmannii* Salm-Dyck) account for 96.4% of the biomass produced annually. These production figures might be somewhat high due to the exceptionally cold winter of 1971–72, which brought freezing temperatures and snow. Many peripheral joints of *Opuntia fulgida* and *O. Engelmannii* froze and dropped. The weight of snow appeared to cause many large limbs of *Cercidium floridum* to break and fall. Two such occurences accounted for 92.5% of the annual dead wood production of *C. floridum*. As with standing crop, the coefficients of dispersion indicate a nonrandom pattern in 4 of the 6 dominant species. *Opuntia* spp. joints and *O. spinosior* are exceptional since they appear to display a random dispersion.

Foraging Group Characters

Estimates of numbers of termites and termite biomass/ha are based on foraging groups collected while sampling superficial dead wood. Selected samples of clean termites were taken to determine mean biomass (mg) for each caste (Table 2). The mean number of individuals and biomass of each species

Table 2.—Mean biomass of castes of each of 4 termite species based on samples from foraging groups on the IBP untreated plot, Santa Rita Experimental Range.

Caste	*H. aureus*		*G. perplexus*		*P. simplicicornis*		*A. wheeleri*		*A. minimus*	
	No. indiv. weighed	$\bar{x}$ biomass/ indiv., mg[a]	No. indiv. weighed	$\bar{x}$ biomass/ indiv. mg[a]	No. indiv. weighed	$\bar{x}$ biomass/ indiv., mg[a]	No. indiv. weighed	$\bar{x}$ biomass/ indiv., mg[a]	No. indiv. weighed	$\bar{x}$ biomass/ indiv., mg[a]
Larva	50	0.2640			356	1.0815				
Larva-worker	11,100	0.3408								
Worker			594	0.6455			727	0.4497	483	0.2756
Pseudergate					314	2.3497				
Soldier	200	0.4675	29	0.6000	141	4.0624	43	0.4163	63	0.2825
White soldier	29	0.3862								
Nymph	311	1.0540			463[b]	1.9769[b]				
					494[c]	3.2372[c]				

[a] Biomass determined by oven-drying at 60°C for 24 h.
[b] Nymphs with short wing buds.
[c] Nymphs with long, overlapping wing pads.

Table 3.—Mean number and biomass of 4 species of subterranean termites in each of fifty 50-m² circledrats sampled on the IBP untreated site, Santa Rita Experimental Range.

	Numbers		Biomass (mg)[a]	
	$\bar{x}$	$s^2/\bar{x}$	$\bar{x}$	$s^2/\bar{x}$
Heterotermes aureus	344.58	1599.84	120.74	542.05
Gnathamitermes perplexus	17.32	395.90	11.16	255.53
Paraneotermes simplicicornis	65.44	1723.71	163.44	4546.46
Amitermes spp.[b]	81.58	1636.14	35.59	752.59
All termites	508.20	1379.16	330.93	2422.92

[a] Biomass determined by summing weight of each caste (Table 2) times the number of each caste.
[b] *Amitermes* spp. includes 10 groups of *A. wheeleri,* 1 of *A. silvestrianus,* and 2 of *A. minimus.*

per circledrat are given in Table 3. A greater number of *H. aureus* foragers was found than of all other species combined. With only 12.9% of the mean number for all termites, *P. simplicicornis* accounted for just under 50% of the total mean biomass, due to its much greater individual biomass (Table 2). The coefficients of dispersion of numbers and biomass for each and all termite species are beyond the critical χ^2 level ($\alpha = .05$), indicating a clumped rather than random distribution.

Twenty-six of the 50 circledrats contained 40 foraging groups of *H. aureus,* an average of 0.80 foraging groups per circledrat or 160 foraging groups/ha (Table 4). Average group size was 430.74. Larva-workers (undifferentiated larvae of at least the third instar) comprised 97.2% of the foraging termites collected, soldiers 1.5%, reproductive nymphs 1.1%, and white soldiers and larvae 0.1% each. Biomass figures of individual castes (Table 2) permit calculation of an average group weight of 150.96 mg. With 160 foraging groups/ha it is estimated that there are 68,918 foragers/ha with a biomass of 24.154 g. Similar data for *G. perplexus, P. simpliciconris, A. wheeleri,* and *A. minimus* are presented in Table 4. The foraging biomass figures must represent only a small portion of the total colony biomass since they represent an instantaneous sample of only a fraction of the total foraging force (Bodine 1973).

Relationship between Wood Biomass and Termite Numbers and Biomass

One of the major questions which arises in a study of this nature is "Does a relationship exist between the number of termites in an area and the amount of wood available?" A test for such a possibility was made by linear correlation, even though the distribution of termites and wood do not meet the necessary requirements of normality. Therefore, statistically significant correlation coefficients (r) do not necessarily indicate a significant correlation at a particular probability level, but are used here only to suggest a strong possibility of such a relationship.

Apparently significant relationships exist between

Table 4.—Average composition, density, and biomass of foraging groups of 5 species of termites collected in fifty 50-m² circles on the IBP undisturbed site, Santa Rita Experimental Range.

	H. aureus	*G. perplexus*	*P. simplicicornis*	*A. wheeleri*	*A. minimus*
Avg groups/circledrat (50-m²)	0.80	0.30	0.22	0.22	0.04
Avg group composition:					
Larvae	0.40 (0.1%)		36.00 (12.1%)		
Larva-workers	418.80 (97.2%)				
Workers		56.40 (97.8%)		338.45 (98.6%)	151.00 (99.0%)
Pseudergates			56.36 (19.0%)		
Soldiers	6.28 (1.5%)	1.33 (2.2%)	29.55 (9.9%)	4.64 (1.4%)	1.50 (1.0%)
White soldiers	0.53 (0.1%)		0.36 (0.1%)		
Nymphs	4.73 (1.1%)		92.18 (31.0%)[b]		
			83.00 (27.9%)[c]		
Total	430.74	57.73	297.45	343.09	152.5
Avg group weight, mg[a]	150.96	37.21	742.33	154.13	42.04
Est. foraging groups/ha	160	60	44	44	8
Est. foraging termites/ha	68,918	3,464	13,088	15,096	1,220
Est. foraging biomass/ha, g	24.15	2.23	32.69	6.78	0.34

[a] Biomass figures based on Table 2.
[b] Nymphs with short wing buds.
[c] Nymphs with long, overlapping wing pads.

Table 5.—Matrix of correlation coefficients (r) for 12 categories of standing crop biomass of superficial dead wood and associated numbers and biomass of 5 species of subterranean termites in each of fifty 50-m² circledrats sampled on the IBP undisturbed site, Santa Rita Experimental Range.

Woods	Termites					
	No. *H. aureus*	No. *G. perplexus*	No. *P. simplicicornis*	No. *Amitermes spp.*	Total no. termites	Total biomass termites
Acacia Greggii	—.112	—.041	.686**	.119	.223	.644**
Celtis pallida	—.065	—.036	—.034	—.039	—.091	—.059
Cercidium floridum	—.065	—.029	—.037	—.028	—.088	—.061
Ephedra trifurca	—.083	—.053	—.065	.024	—.094	—.090
Gutierrezia Sarothrae	.090	—.040	—.037	—.043	.042	—.020
Opuntia engelmannii	—.120	—.062	—.047	.205	—.042	—.043
Opuntia fulgida	.017	—.092	—.034	.092	.032	—.022
Opuntia spinosior	.393**	—.046	—.096	—.014	.299*	.012
O. spinosior & *O. fulgida* joints	—.209	—.061	—.063	—.087	—.254	—.147
Prosopis juliflora	—.119	—.019	—.004	—.072	—.140	—.047
Other woods	.018	—.030	.208	—.037	.080	.198
Total of all woods	—.156	—.124	.513**	.066	.084	.449**

* Correlation coefficients significant at the $\alpha = 0.05$ level.
** Correlation coefficients significant at the $\alpha = 0.01$ level.

standing crop biomass of various categories of superficial dead wood and numbers of *H. aureus, P. simplicicornis,* all termites, and biomass of all termites (Table 5). Numbers of *H. aureus* appear highly correlated with standing crop biomass of *Opuntia spinosior. Paraneotermes* numbers are highly correlated with both standing crop biomass of *Acacia Greggii* and total dead wood, apparently because *A. Greggii* standing crop is highly correlated with total dead wood standing crop ($r = .646$). Numbers of all termites show a relationship with *O. spinosior* (Table 5), probably due to the dominance of *H. aureus* in the mean number of all termites observed per circle (Table 3). Biomass of all termite species is influenced greatly by *P. simplicicornis* (Table 3) and, as a result, a significant relationship is indicated between biomass of all termite species and *A. greggii* and total dead wood biomass (Table 5). Neither *Gnathamitermes* nor *Amitermes* exhibits an indication of a significant relationship with any category of superficial dead wood.

Discussion

Caste proportions in termite colonies or foraging groups are known to vary with time of day, season, species, and colony size or age, with the most dramatic manifestations being associated with flights (Bodot 1969, 1970, Sands 1965, Bouillon 1964, Noirot 1969, Nutting 1970). Nutting (1970) presented a record of caste composition in a single foraging group of *H. aureus* in which he found 4% soldiers and 96% nonsoldiers. Nutting et al. (1973) reported foraging groups of *H. aureus* to contain mostly larva-workers and ca. 0.7% soldiers. The average *H. aureus* foraging group in this study contained 430.7 individuals and was composed of 97.2% larva-workers, 1.5% soldiers, and 1.3% divided among nymphs, white soldiers, and larvae. Nymphs were encountered only from late November through late May or early June, in 27.5% of the foraging groups. Neither nymphs nor alates were encountered at the surface during the flight season from late June through September (Nutting 1969). Nymphs may comprise as much as 20.5% of a foraging group. Soldiers were encountered in 75% of the groups and are apparently generally included in the foraging force. Larvae and white soldiers were seldom encountered and are apparently not usually included in foraging parties.

Foraging groups of *G. perplexus* have been reported previously to contain mainly workers and only about 0.4% soldiers (Nutting et al. 1973). During our sampling we found surprisingly few foraging groups of *G. perplexus,* considering its ubiquity in adjacent areas, as determined by a different sampling technique (LaFage et al. 1973, Nutting et al. 1973, LaFage 1974). The average group size was only 57.7 individuals, consisting mainly of workers and only 2.2% soldiers. This appears to be an unusually high percentage of soldiers although a similar figure (2.1%) was reported in surface foraging groups of *G. tubiformans* (Buckley) in Texas by Bodine (1973). The high percentage may be due to the nature of the foraging substrate, mostly twigs and cholla joints, because groups foraging in toilet paper rolls contained only 0.4% soldiers (Nutting et al. 1973). Neither nymphs, larvae, nor white soldiers were encountered in any of the foraging groups, even

though they are sometimes commonly found in foraging groups or "subcolonies" under rocks at higher elevations (Weesner 1970).

Paraneotermes simplicicornis, although taxonomically a drywood termite, behaves much like the truly subterranean termites of the Rhinotermitidae and Termitidae. Groups found in surface wood appear to be outlying portions of a central underground colony or of "foraging subcolonies" (Light 1937, Nutting 1966). Soldier-to-nonsoldier ratio of *P. simplicicornis* foraging groups has been reported to vary greatly, from 4.9% (Nutting 1966) to 22.0% (Nutting 1970). Average foraging group size was 297.5, with a maximum of 2357 individuals. Variation in our study was also great, with the largest mean portion of individuals being nymphs (58.9%) and a high percentage soldiers ($\bar{x} = 9.9\%$). All castes were encountered except primary reproductives, which have seldom been found (Nutting 1966).

Foraging groups of *Amitermes wheeleri* were found as often as those of *P. simplicicornis,* while *A. minimus* was rearely encountered. Groups of *Amitermes* contained only workers and soldiers (1.4% soldiers for *A. wheeleri* and 1.0% for *A. minimus*). These percentages are lower than the 2 and 5% reported for *A. wheeleri* in Texas by Banks and Snyder (1920).

Knowledge of caste composition is necessary for converting termite numbers to an accurate biomass figure. With some species, especially those with a high percentage of one caste, numbers and biomass are highly correlated. But with others, such as *P. simplicicornis,* with several castes of unequal biomass, caste composition is critical for calculating biomass.

Subterranean termites are not usually randomly dispersed in the soil because of their aggregations into colonies and foraging parties (Sands 1972). Our results support Sand's view that termite distributions are best described by the negative binomial (Table 3). Therefore, we must accept sample population values with great variability for extrapolating to larger unit areas.

Estimating the number or biomass of termite/ha is simpler with mound-building species; one need only multiply the number of colonies/ha by the mean number of individuals or biomass per colony. Sands (1965) estimated populations of *Trinervitermes geminatus* (Wasmann) in open savanna of West Africa to be $4.94–12.36 \times 10^6$ individuals/ha or 494–1235.5/m². Bouillon (1969) reported densities for 3 species in an African savanna: *Apicotermes desneuxi* Emerson at 660/m², *A. gurgulifex* Emerson at 43/m², and *Cubitermes exiguus* Mathot at 519/m².

Numbers of subterranean termites per unit area are somewhat more difficult to establish. The method most often used involves taking soil cores, usually to a depth of 15 or 30 cm, and counting the termites. Lee and Weed (1971) presented a summary of data from tropical Africa, South and Central America, and arid and semi-arid regions of Australia. Total termite numbers/m², for all species in each area, ranged from 12 in a desert grassland steppe and a rain forest in Panama to 4450 in a Trinidad rain forest.

Bodine (1973) used soil cores to estimate the density of *Gnathamitermes tubiformans* in the upper 30 cm of soil in a semi-arid grassland in Texas. From February through November the mean was 4135 termites/m², which approached the highest termite density ever recorded (4450/m²) for all species of termites in an area (Lee and Wood 1971). From May through July the subsurface density was 3796.7/m², with a surface density of 33.3/m²—only 0.877% of the measured population.

Rocky soil influenced our decision to sample surface foraging groups rather than subsurface numbers. It is unlikely that absolute colony size, and hence population per unit area, for any of our species could be determined practically, i.e., by digging. It may therefore be of some value to speculate on the size of subsurface numbers of *H. aureus, G. perplexus, A. wheeleri,* and *A. minimus,* based on Bodine's subsurface:surface proportions (114:1) of *G. tubiformans.* From extensive field experience with *P. simplicicornis* we feel that the ratio would be much lower, ca. 10:1. On a basis of the foraging groups collected during 13 months of circledrat sampling, we estimate the average surface foraging force for *H. aureus* to be 6.89, *G. perplexus,* 0.35; *P. simplicicornis,* 1.31; *A. wheeleri,* 1.51; and *A. minimus,* 0.12 termites/m². Using Bodine's subsurface:surface proportion, we estimate the numbers of these species of termites to be 786, 40, 13, 172, and 14 termites/m², or a total of 1025 termites/m². Similarly for biomass, the figures would be 0.275, 0.025, 0.033, 0.077 and 0.004 g/m², or a total of 0.414 g/m². Even though 2 uncommon or cryptic subterranean species are not included in this estimate, total termite density is higher than any cited by Lee and Wood (1971) for arid or semiarid situations. However, it is still less than one fourth of Bodine's figure for *G. tubiformans* in west Texas.

As far as we are aware only 2 efforts have been made to measure the amount of material available to a species or community of termites. Lee and Wood (1971) measured annual litter fall in a dry sclerophyll forest in Australia and found that, of the total 2300 kg/ha, 30.4% or 700 kg was logs and sticks. The standing crop biomass of litter in this same area was 7388 kg/ha (Lee and Wood 1968). Assuming the same percentage of sticks and logs to total litter, their study area would have a dead wood standing crop biomass of 2231 kg/ha. Their dry sclerophyll forest is thus apparently very similar in its standing crop biomass and annual production biomass of dead wood (2231 and 700 kg/ha) to that of the desert grassland of the Santa Rita Experimental Range (2127 and 450 kg/ha). Additional similarities occur in that the most common termite, *Nasutitermes exitiosus* (Hill), is present in numbers (600/m²) comparable to *H. aureus* (786/m²).

Generally, factors such as climate, vegetation, and soil interact in their effects on the distribution and abundance of termites so that it is often not possible

to determine whether or not one is dominant. Within a small geographical area, climate is sufficiently equitable that only soils and vegetation interact to affect termite abundance and dispersion. The major interactions are shade or plant cover, water-holding capacity of soil with a particular vegetation complex, and variety and quantity of food plants (Lee and Wood 1971).

We felt that the standing crop of superficial dead wood must be a key factor in determining the abundance of many of the termites on our study area. As our results indicate, the abundance of only 2 of the 5 termite species appears to be correlated with superficial dead wood biomass: *H. aureus* with *O. spinosior,* and *P. simplicicornis* with *A. Greggii.* These plant species are also among their preferred hosts (Haverty and Nutting 1975). *Gnathamitermes perplexus* is a general feeder and, as a result, shows no such relationship with dead wood biomass. The fact that the *Amitermes* spp. have a definite preference for *A. Greggii* probably explains the high correlation coefficient (Table 5) with dead wood of that plant.

In summary, the dispersion of both the surface foraging populations of 5 species of subterranean termites and the standing crop biomass of their food material is not random in this desert grassland ecosystem. The abundance of the termites appears to be correlated with dead wood standing crop of a particular plant species only in those termites which show strong feeding preferences.

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