

# Foraging Ecology and Relative Importance of Subterranean Termites in Chihuahuan Desert Ecosystems<sup>1</sup>

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## ABSTRACT

Foraging activity of subterranean termites was studied on grids of artificial food units (toilet paper rolls) and on natural foods on the surface using belt transects. Preferred forage items were portions of *Yucca elata* logs and cattle dung which provided large surface area contact with the soil. Foraging at the surface occurred at soil temperatures  $>3-5^{\circ}\text{C}$  at 15 cm depth and at soil moisture tensions between 0 and minus 140 bars. Estimated foraging group densities were 440/ha and 61/ha for 2 areas. Differences in foraging group densities were related to soil texture and depth above the caliche. Mid-summer field determined consumption rates were  $7.9 \pm 2.8$  and  $1.2 \pm 0.04$  kg/ha on the 2 study areas. We concluded that termites account for the consumption of ca. 50% of the production in creosotebush and mesquite-yucca grassland communities in the Chihuahuan desert.

Where they are abundant, termites may be one of the most important groups of organisms in a desert ecosystem. A wide variety of plant material serves as food for termites, including living and dead wood, grasses, herbaceous plants and their debris, fungi, humus, and dung (Lee and Wood 1971). In habitats where most of these food sources are found, a large proportion of the energy resource of the ecosystem is potentially available to termites. Little competition is encountered with other soil animals, since only a minority feed on freshly fallen plant debris or living plants (Lee and Wood 1971).

Unlike most poikilotherms, termites have extremely efficient digestive systems, a trait more common to homiotherms. Poikilotherms, however, are more efficient producers than homiotherms since the animal population of poikilotherms for a given annual population respiration is greater than among homiotherms. If termites were characteristic efficient producers, like other poikilotherms, in addition to possessing efficient digestive systems, they would have a significant impact on the rate and direction of energy flow in many ecosystems, including those that large mammals appear to dominate (Lee and Wood 1971).

The role of termites in a Chihuahuan desert ecosystem has never been extensively studied. To obtain information about the importance of the subterranean termites in Chihuahuan desert ecosystems, studies of foraging activity and consumption rates were conducted over a period of several months. The studies reported here provide insights into the role of termites in the Chihuahuan desert and serve as the basis for future experimental studies designed to further elucidate their role.

## Methods and Materials

The study was conducted from June 1972 through November 1973, at the US/IBP Jornada Validation Site in Dona Ana County, N.M. Two sites were studied. The playa site is a dry lake bed with a

clay-loam to solid clay bottom, surrounded by a fringe of sandy loam. A caliche (calcium carbonate deposition) layer is found ca. 50 cm beneath the soil surface on the fringe. *Prosopis glandulosa* (mesquite) and *Ephedra trifurca* (Mormon tea) are the most common shrubs on the site, occurring at estimated densities of 468/ha.<sup>3</sup>

The 2nd site (bajada) is on an alluvial fan on the upper portion of the watershed draining into the playa. On this site, the soils vary from sandy gravels to sandy loam, with a caliche layer 10-40 cm beneath the soil surface. The bajada is dissected by arroyos (dry water courses) which have somewhat deeper soil than the rest of the area. *Larrea tridentata* (creosotebush) is the dominant vegetation of the drained areas. Along the edges of the arroyos, the principal vegetation includes *Prosopis glandulosa* (mesquite), *Chilopsis linearis* (desert willow), *Yucca baccata* (banana yucca), and *Opuntia violacea* (prickly pear cactus)<sup>3</sup>.

Consumption data were obtained by adaptation of a technique developed at the IBP Santa Rita and Silver Bell sites in Arizona (LaFage et al. 1973). Each plot consisted of 100 toilet paper rolls, 1 m apart on a grid. The rolls were tied with string to prevent unwinding and placed over metal stakes so that one end was in direct contact with the ground. Arranged in this manner, the rolls were a readily acceptable food source for termites. Four identical grids were located on each site in areas representative of the different soil and plant populations.

The original rolls were removed and replaced in March 1973, after 9 months of exposure to estimate total consumption by the termites. Rate of consumption was measured during the 1973 growing season by removing and replacing the same 10 randomly chosen rolls at identical locations on each grid once each month. Casings and litter were cleaned from the food source, and plaster casts were made of the consumed portions of the rolls. The weight of paper consumed was determined from the

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dry weight of plaster using the conversion factor 0.11 g paper = 1 g plaster. The caloric equivalent of the consumed paper was calculated from the standard caloric content of paper, 4.5 cal/g.

Foraging activity of termites was measured using 2 techniques. The 1st method involved visual examination of the surface of the roll in contact with the ground; numbers of termites active on the roll were counted and the roll was quickly replaced. This technique was later modified to eliminate variation due to prior disturbance: 3 different rolls which were known to be sites of frequent activity were checked on each grid at 2 h intervals so that no roll was handled more than once a day. By checking rolls of known activity, a method was available for correlating soil temperature and soil moisture with foraging activity. Soil moisture and soil temperature at a depth of 15 cm were measured at the time and place of each observation by gypsum soil blocks and thermistors buried in the soil of each grid.

The 2nd method, designed to provide an estimate of normal surface foraging activity, consisted of walking two 500 m transects on both the playa and bajada which included samples of the major soil types on each site. All potential food sources in a 2-m belt were examined for activity; the species of the food source and the number of termites in the foraging group were recorded. Available food sources were tabulated on both sites according to species and weight by recording each piece of woody material in 10 randomly chosen 10×2-m strips along the transect lines.

### Results and Discussion

Consumption data for the period June 1972 through March 1973, in kg and kcal/ha, are presented in Table 1. Activity varied considerably between grids, with a range from 0 on some bajada grids to the extensive consumption on the playa grids. Cellulose consumption rates peaked during July and rapidly declined to a trace amount by September. Variation in activity at different locations are evident in Table 1.

Twelve-hour activity checks of the toilet paper grids provided an indication of surface foraging

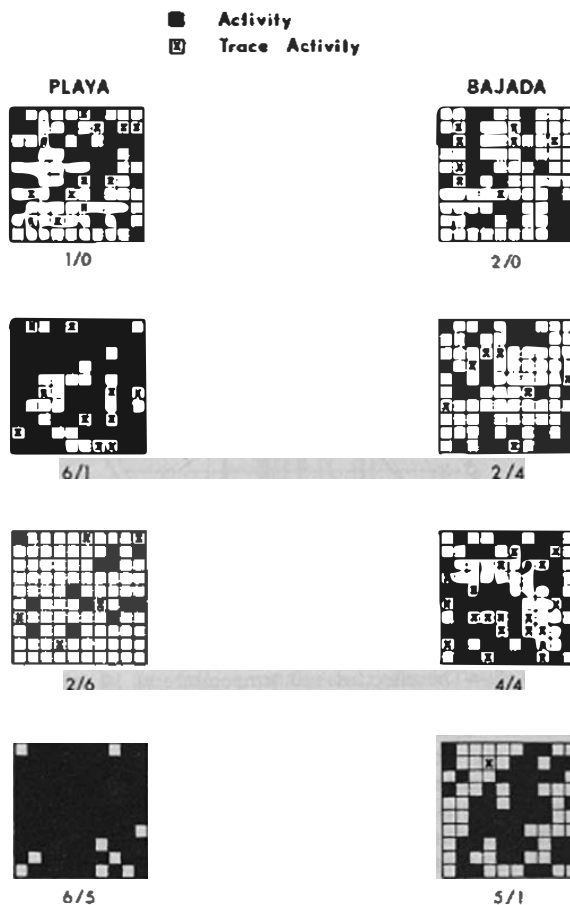


FIG. 1.—The distribution of foraging groups of subterranean termites on the toilet paper roll grids as determined by evidence of consumption or active groups in toilet paper rolls recorded during activity surveys.

activity as a function of soil temperature and moisture. The results of the studies during the period extending from May 18 to Aug. 15 are presented in Fig. 2. Some surface foraging was noted through mid-November, ceasing at soil temperatures ranging between 3–10°C at 15 cm.

Table 1.—Cellulose consumption by termites on toilet paper grids, expressed as kg/ha and as kcal/ha.

Grid	Jun 72–Mar 73		Mar 73–Jun 73		Jul 1973		Aug 1973		Sep 1973	
	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal
Playa										
1/0	15.5	69.8	4.6	20.7	24.8	111.6	4.9	22.3	—	0
2/6	.76	3.4	1.5	6.7	10	45	10	45.6	—	0
6/1	9.6	43.4	2.7	12.2	1.8	8.1	.6	2.6	—	0
6/5	3	13.5	.8	3.6	9.2	41.4	2.2	9.9	—	0
Bajada										
2/0	2.9	13.3	0.7	3.1	0.6	2.7	0.2	0.9	—	0
2/4	4.8	21.7	3.9	17.5	1.8	8.1	—	0	—	0
4/4	4.2	18.8	0.7	3.3	2.9	13.1	—	0	—	0
5/1	11.8	53.2	0.01	0.04	2.3	10.4	1.4	6.2	—	0

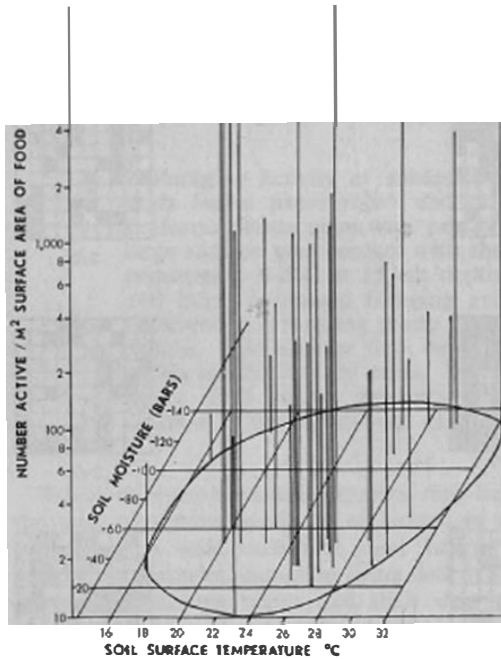


FIG. 2.—The effect of soil temperature at 10 cm and soil moisture at 10 cm on the number of subterranean termites in the toilet paper roll grids.

These data suggest that soil temperature at some depth, probably close to the surface, represents a threshold for surface foraging. The lower threshold temperature appears to be between 3–5°C at 15 cm but is impossible to pinpoint due to diurnal fluctuations in temperature at that depth. The highest soil temperature at which activity was observed was 32.2°C. There was no consistent variation in activity at different soil moisture-temperature regimes.

Attempts to fit these data to a multiple regression model were not entirely satisfactory because the response surface is not symmetrical (Fig. 2). A multiple regression model of the form  $\ll \log_{10} \text{ACTIVITY} = -3.81 + 0.0115M + 0.598ST - 0.0002SM^2 - 0.0145ST^2 - 0.015(SM)(ST) \gg$  gave an  $r^2$  of 0.41 ( $F = 3.86$ ;  $.05 < P < .01$ ) where  $ST$  = soil temperature in °C at 15 cm and  $SM$  = soil moisture in minus bars at 15 cm. This regression is a suitable model for predicting foraging activity but does not accurately predict upper threshold limits. Since only 2 variables were measured, it was not possible to use a step-wise regression to evaluate the relative importance of soil moisture and temperature as factors affecting foraging.

Soil moisture appears to be of less importance as the threshold for foraging near the soil surface than temperature. This finding is not surprising since the relative humidity in the soil interstices only drops to 90% with the change from 0 to minus 140 bars water potential. Using the equation in Slayter (1967) for calculating humidity in soil interstices, the saturation deficit in soil at 30°C is only 15% of that in air at the same temperature and 20% RH.

Studies with toilet paper grids and belt transects documented marked spatial heterogeneity in suitable habitat for subterranean termites. Playa grids 6/5 and 6/1, located in sandy loam ca. 50–90 cm above the caliche layer, had consumption on more than 50% of the rolls, while grids 1/0 and 2/6, on a clay-silt overwash of 5–10 cm depth, exhibited significant consumption on less than 25% of the rolls.

Foraging groups were numerous on the deep sandy soil on the north and east sides of the playa but were virtually absent on the other areas where the caliche layer was within 30 cm of the surface or where the soil was a heavy clay. Other factors which could affect the distribution of foraging groups, such as distribution of suitable food sources, do not differ spatially. Consequently, soil properties appear to be an important factor affecting the density of termite foraging groups on the playa area.

A similar pattern was obvious on the bajada. Consumption was most often associated with grids affected by drainage areas of deep soil, or those grids dissected by small arroyos. Caliche layers are absent in arroyo beds and woody materials are buried in and accumulated along the edges of these watercourses during rainy periods. Most natural activity was also found in areas with deep soil; foraging distribution is likely affected by soil suitability and food distribution.

The relative preferences of subterranean termites for forage materials is presented in Table 2. *Yucca elata* was the favorite food source on the bajada. Nearly all the termites found actively foraging on the transect areas were associated with *Yucca elata*, *Yucca baccata*, and the prickly pear cactus, *Opuntia violacea*. Creosote wood (*Larrea tridentata*) was rarely attacked and mesquite (*Prosopis glandulosa*), though abundant, was never found to host termites. The standing crop of dead wood on the soil surface (Table 2) indicates that certain species of woody material are avoided as a food source by subterranean termites.

On the playa, termites were most often found foraging on *Yucca elata* and cattle dung, which was abundant on the site in early summer of 1973. Cattle were last grazed on the site in October, 1972; no new dung had been added since that time. The number of dung pads present on the playa had decreased considerably by August and had virtually disappeared by the end of November 1973. These findings are similar to those of Ferrar and Watson (1970), who report that an average-sized bovine dung pad disintegrated in ca. 3 months in studies conducted in northern Queensland, Australia. O'Brien (unpubl. data) determined that microbial decomposition in this area is limited by soil moisture. These data, coupled with the findings of Anderson and Coe (1974), who reported that microbial activity in elephant dung is progressively limited by lack of moisture following the initial 48-h period after deposition, suggest that the disappearance of old (dry) dung pads over the summer is almost entirely due to termite activity.

Table 2.—Seasonal shifts in food sources, foraging groups per food source per hectare (FG), and average number of termites per foraging group (N). A + indicates casings around standing dead or procumbent dead plants. Total density of annuals equaled 209,357/ha in August, 1973. Foraging group activity can be compared to standing crop biomass of woody material in the 2 sites indicated in the standing crop column.

Food source genus species	Standing crop	May		Jun		Jul		Aug		Sep		Oct		Nov	
		FG	N	FG	N	FG	N	FG	N	FG	N	FG	N	FG	N
Playa															
Cattle dung	350 units/ha	120	7	200	16.3	45	9.9	3	3.5	35	4.4	20	13.3	15	14
<i>Yucca elata</i>	72 kg/ha	5	4	35	10.4	5	6	5	3	5	2	5	2	5	4
<i>Aristida purpurea</i>														+	5
<i>Hilaria mutica</i>														+	5
<i>Astragalus</i> sp.														+	12
<i>Eriogonum</i> sp.														+	
<i>Perezia nana</i>														+	
<i>Prosopis glandulosa</i>	31 kg/ha													+	
<i>Ephedra trifurca</i>	6.4 kg/ha													+	
Bajada															
Cattle dung		5	100												
<i>Yucca baccata</i>		5	2							5					
<i>Yucca elata</i>	94 kg/ha	5	6	6	50	20	6.5								
<i>Opuntia violacea</i>	4 kg/ha					5	3			10					
<i>Larrea tridentata</i>	150 kg/ha														
<i>Prosopis glandulosa</i>	67 kg/ha														

The toilet paper rolls applied to the ground surface constituted an artificial food source for termites, yet they provided a valid means of estimating consumption as a function of surface area of food applied to the ground and of estimating the number of termite foraging groups per unit soil surface area. The surface area in contact with the soil was much larger than that of small twigs and plant litter. The environment beneath the rolls was sufficiently modified to allow termite activity, whereas such activity is limited on small plant litter by necessary exposure of termites to direct sunlight and drying effects of the air. This modified environment resembles that which is provided beneath yucca logs and cow chips, shown in the data to be favorite food sources of the termites.

Termites were most commonly found in larger pieces of wood and cattle dung when visual observations were made by the transect method. This preference for larger pieces of wood and cattle dung over small twigs and surface litter reflects the fact that the modified environment under a large object on the soil surface is a necessary factor in food suitability. It appears that most small woody materials cannot be utilized, at least during the months of June, July, and August, at the soil surface. These observations support the contention that while soil moisture may not limit access to the soil surface, the moisture content of the air is important. Large objects provide a continuous environment with the soil, thus reducing or eliminating exposure to the drying ambient environment. Factors such as wind and water may be important in modifying the immediate environment around small twigs and annuals. Burial of such detritus presumably enhanced its consumption, since a soil covering of 2–3 cm should allow considerable termite activity.

Late in the fall, annuals and grasses were preferred food sources for the termites. By late November, soil casings surrounded standing dead annuals above the surface of the ground and were abundant on the playa. Consumption of dead annuals surrounded by these casings was extensive at this time, indicating altered availability of plants. While most of the annuals had died by August, termites did not attack them until air and soil temperatures dropped considerably, accompanied by corresponding decreases in the nighttime saturation deficits with high relative humidity. The limiting factor of atmospheric dryness was considerably reduced in the fall with nighttime saturation deficits less than 3 g/m<sup>2</sup>, allowing termite activity above ground at least during the night. These observations are similar to those of Sheppe (1970), who found that *Odontotermes latericius* was most active at night. Since there are no other major consumers of dead annuals, it is not unreasonable to attribute the yearly disappearance of most annuals to termite consumption.

Peak activity occurred in July. This increased activity probably reflects a rise in soil moisture during the rainy season. La Fage et al. (1973) report similar increased foraging intensity in *G. perplexus* in southern Arizona following rain. The data indicate, however, that soil temperature is more limiting to foraging activity than soil moisture. Soil dryness of minus 140 bars did not have a severe effect on surface activity, presumably because desiccation is a threat to survival only upon direct exposure to dry air rather than on contact with dry soils. Soil temperature, in contrast, was responsible for limiting the duration and intensity of activity. During summer months, nearly all surface foraging ceased between 1000–1800 h (MST), when soil temperatures were highest.

One reasonable explanation for the fact that termites do not attack wood of certain species (such as *Larrea tridentata* and *Prosopis glandulosa*) for a considerably long period of time is the possibility of the presence of chemical inhibitory substances in newly fallen woody materials. This might also explain the delay in termite foraging activity in newly fallen yucca logs which has been noted on both sites; termites prefer small pieces of yucca which are noticeably older than larger newer logs. Feeding on older, partially decomposed plant material is likely to be influenced by the growth of fungi and other microorganisms on these substrates. Lee and Wood (1971) suggest that fungi may render wood more digestible and may possibly decompose repellent or toxic substances. Experimental studies designed to evaluate the importance of inhibitory chemicals in food sources are required to test this hypothesis.

Mature colony size for *G. perplexus* has been estimated at between 5000 and 10000 individuals (Nutting, pers. comm.). Haverty and Nutting (1975) reported that the laboratory consumption rate of the subterranean termites *Heterotermes aureus*, which may be comparable to our field experiments, was five milligrams of wood per hour per gram dry weight of termites on natural woods. Estimated consumption of a colony of 10000 individuals weighing 0.5 mg/termite is 18 g wood/colony/month. Consumption estimates ( $\pm$  SE) for the playa and bajada respectively, during the months of July and August were  $7.9 \pm 2.8$  and  $1.2 \pm 0.4$  kg/ha. The great variability of the consumption rates (Table 1) and the presence of zero consumption rates on some grids are consistent with the premise that these rates reflect the densities of termites before the grids were established rather than densities due to the attraction of termites to the grids. Therefore, it appears that the densities of termites in an area are independent of the densities of the rolls, and a valid correlation exists between the number of foraging groups per grid (100 m<sup>2</sup>) and the true densities of termite colonies. The consumption estimates for the playa and bajada give estimated colony densities of 440/ha and 61/ha respectively, based on Haverty and Nutting's estimated consumption rate of 18 g/colony/month. Although any estimates of densities are clearly subject to many sources of error, these density estimates do not appear unreasonable.

Estimates of addition to the detritus pool of the two areas are available from other work done on these sites as part of the Desert Biome Program.

The estimated input of wood and leaves from perennials, stems and leaves of annuals, rabbit and cattle dung on the playa was  $10.3 \times 10^6$  cal/ha in 1972. The estimated consumption by subterranean termites during that period was  $5.3 \times 10^6$  cal/ha. On the bajada, woody detritus production in 1972 was estimated at  $3.7 \times 10^6$  cal/ha and the estimated consumption by termites was  $3.4 \times 10^6$  cal/ha. The bajada litter production estimates, however, do not include samples from arroyos, which have higher productivity than the remaining area. Considering these estimates, it is apparent that subterranean termites consume at least 50% of the net productivity in these Chihuahuan desert ecosystems. The movement of this amount of material through one group of detritivores attests to the importance of these insects in energy flow and nutrient turnover in Chihuahuan desert ecosystems.

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