FORAGING BEHAVIOUR OF TWO SPECIES OF SUBTERRANEAN TERMITES IN THE SONORAN DESERT OF ARIZONA

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Although subterranean termites are very abundant in many parts of the world, field studies on the non-mound-building species are extremely difficult because of their cryptic habits. Most reports of foraging behaviour have dealt with mound builders (Bouillon and Lekie, 1964) or harvesters which forage openly above ground (Bouillon, 1970; Nel, 1968). Some estimates of subterranean populations have been made by baiting or soil-core sampling (Sands, 1972). Using a novel modification of the bait-sampling method, we have recently completed a one-year field study on the activity and behaviour of foraging groups of two common subterranean species in southern Arizona, Heterotermes aureus (Snyder) (Rhinotermitidae) and Gnathamitermes perplexus (Banks) (Termitidae). This approach has provided good estimates of the density and biomass of these groups as functions of certain environmental factors, both daily and seasonal. Additionally, it has produced information on their spatial distribution, the quantities of cellulose consumed, and the amount of soil brought to the surface by them. The study is part of a continuing effort which is being reported in a series of papers dealing with the role of termites in the detritus cycle of desert ecosystems.

MATERIALS AND METHODS The study site was located 40 km south of Tucson, Arizona, at an elevation of 950 m, on the Santa Rita Experimental Range. The area is a shrub-invaded, desert grassland ecotone, characterized by scattered small trees, shrubs and cacti.

The method devised to observe foraging behaviour (LaFage, et al., 1973) involved clearing dead wood from an area 40x40 m with subsequent division into 16 contiguous plots, each 10x10 m. One hundred rolls of plain white toilet paper, wrapped with tape to prevent raveling, were placed on each of the plots on grids at 1-m intervals. The paper served as a food source which attracted the termites to the surface where their foraging behaviour could be studied on a continuing basis. Observations on these plots were made during one 24-hr period each week from October 15, 1971, through to October 13, 1972. A different plot of 100 rolls in a block of 12 was examined every 2 hr; thus, no single roll was checked more than once a week.

Checking for termite foraging activity involved a quick examination of each roll, notation of the species and approximate number present or, if none was present, any evidence of past activity. In this manner, 100 rolls could be checked in about 30 min. Work of the two species which frequented the rolls regularly was easily identified since each attacked the paper in a characteristic way.

Prior to each check several physical factors were measured: Temperatures at the soil surface, inside and under rolls, and at several sub-surface levels down to 125 cm. In addition, air temperature, relative humidity, temperature under a roll and at depths of 3, 5, 10 and 15 cm were recorded continuously. Rainfall and soil moisture (at depths of 0-15, 15-30, 30-60, and 60-90 cm) were measured weekly.

At the end of the year, 200 rolls were randomly harvested from the four undisturbed plots to check our population estimates, to determine the amount of paper consumed, and to measure the quantity of soil moved to the surface by the two species.

RESULTS AND DISCUSSION Although we are still processing the data, certain preliminary findings should serve to demonstrate the usefulness of the method. The two most abundant termite species on the site worked the rolls through most of the year. Extrapolating from our data on the 12 plots during periods of intense foraging activity, we conservatively estimate the maximum density of *Heterotermes* foragers at 478,500/ha (or 161.3 g/ha, dry wt), and for *Gnathamitermes* at 705,000/ha (or 484.7 g/ha, dry wt). From other studies we have determined that foraging groups of *Heterotermes* may contain from one to ca. a thousand individuals, mainly larvae-workers and ca. 0.7% soldiers; those of *Gnathamitermes*, from one to ca. a thousand, mainly workers and ca. 0.4% soldiers. We have speculated that mature colonies of *Heterotermes* might number in the tens of thousands, those of *Gnathamitermes* perhaps 5,000-10,000, and that the underground force might outnumber the foragers 10 to 1.

Heterotermes foraged within a temperature range of 7.6-47.0°
and *Gnathamitermes* between 9.0-49.0°C (extremes measured in the series from under a roll down to a soil depth of 15 cm, with accompanying activity). From laboratory studies (Collins, et al., 1973) we know that both species can survive periods of several minutes at 53°C, so that it is highly probable that they continue to make trips to surface debris even at temperatures in the low 50's. We know, then, that these species work continuously, day and night throughout the year, whenever soil temperatures permit. Whereas temperature governs the time which can be spent foraging, and to some extent foraging intensity (number of individuals at the surface), periodic rises in soil moisture following rain also increase foraging intensity. Regression analyses show that the lowest soil temperature (from under a roll to 15 cm) is correlated significantly with numbers of foragers at the surface.

Distributional data from the 12 contiguous plots indicate that the two species have very different foraging behaviours. *Heterotermes* attacked relatively few rolls here (14%) and apparently forages intensively within limited and relatively stable areas. *Gnathamitermes* worked nearly every roll (96%) and seems to forage over wide and changing areas. One isolated area of 28 m^2 may represent the foraging territory of a mature *Heterotermes* colony.

Based on data from the four undisturbed, 100-m^2 plots, *Heterotermes* foraged over 22% of the surface area and *Gnathamitermes* over 88%, while their territories overlapped on 12% of the area. By extrapolation we estimate that Heterotermes consumed paper (essentially pure cellulose) at a rate of 19.5 kg/ha/yr, Gnathamitermes at a rate of 100.1 kg/ha/yr, while both comsumed 14.4 kg/ha/yr from their overlapping territories. The two species, therefore, consumed paper at a combined rate of 134 kg/ha/yr. (Weights were obtained with the paper at ca. 25^{o}C and 30% RH.)

Both species pack their workings with soil, as do many other termites (Lee and Wood, 1971, p. 48), and we have suggested (Collins, et al., 1973) that this habit may contribute to the reduction or stability of temperature within their above-ground cavities. Again, using the territorial data from the same four plots, we have estimated that Heterotermes moved soil to the surface at a rate of ca. 72 kg/ha/yr, Gnathamitermes at a rate of ca. 559 kg/ha/yr, while the two species together in the area of overlap brought up soil at a rate of 93 kg/ha/yr. In sum, the two species moved soil to the surface at a combined rate of 724 kg, or nearly 3/4 metric ton, /ha/yr. Analyses are in progress to determine what effects these two species have on the chemical and physical properties of this soil. So far as we know there are no earthworms in the area, although there are large ant populations which must also contribute substantially to the turning over of the desert soils.

These and other data from related studies on both dry-wood and sub-terranean termites are being used in a computer model designed to answer questions about long-term interactions between termites, dead wood and critical abiotic factors. Hopefully, this model will generate information which can be used in a predictive, general purpose model of desert eco-systems.

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