Location of Food Sources by Subterranean Termites[1]

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ABSTRACT

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Chihuahuan desert subterranean termites, *Gnathamitermes tubiformans* (Buckley) and *Amitermes wheeleri* (Desneux) readily located surface foods but failed to utilize buried foods of the same type. The termites attacked both natural cowdung pats and artificial(polyurethane) cowdung pats at the same rate as estimated by holes chewed through plastic film barriers placed between the soil and both kinds of pats. There was smaller diel excursion of temperatures in the upper 20 cm of soil under dungpats than in the soil not under dung. We suggest that desert subterranean termites locate relatively large size surface foods such as cattle dung and *Yucca* sp. logs by sensing the thermal shadows cast by such items.

Introduction

Foraging distribution patterns of some species of North American desert termites have been studied by La Fage et al. (1973), Haverty et al. (1975) and Johnson and Whitford (1975). These authors used artifical bait units (toilet paper rolls) to attract termites to the surface. Johnson and Whitford (1975) reported that large surface objects such as cattle dung pats and *Yucca* spp. logs exhibited the highest frequency of attack by termites. Neither of these studies addressed the question of the mechanism used by these subterranean termites initially to locate suitable food items.

Lee and Wood (1971) reviewed the foraging strategies employed by subterranean-nesting species. The majority of galleries of these species are either on or near the surface where the concentration of food sources is greatest. However, they cite no studies of the methods used by the termites to locate suitable food items, i.e., whether they forage randomly, use chemical stimuli, or detect differential temperature gradients in the soil. This study was designed to investigate which of these strategies, or combination of strategies, are used by the desert termites *Gnathamitermes tubiformans* (Buckley) and *Amitermes wheeleri* (Desneux).

Methods and Materials

All studies were carried out on the Jornada Experimental Range, 40 km NNe of Las Cruces, Dona Ana County, New Mexico, on an area described by Johnson and Whitford (1975).

The first experiment in 1977 was designed to differentiate between chemical and physical cues used by termites to detect prospective food sources on the soil surface, and to investigate whether termites search randomly. Four sites were selected on the fringe of a playa (ephemeral drainage basin) where termite activity was known to be high. At each site, the following three treatments were assigned at random, on 3 parallel lines, one m apart: (1) We excavated a shallow, flat-bottomed trench, 2 cm deep, about 35 cm wide and 2 m long. A sheet of polyethylene film (0.2 mm thickness) 30 cm wide and 2 m long, was carefully laid in the bottom of the trench. The corners of the sheet were secured and marked with nails pressed into the ground, and the excavated soil was carefully smoothed back over the sheet. (2) A similar treatment was prepared but with 4 dungpats spaced evenly on the soil over the film. (3) For a control we placed 4 dungpats in the same orientation as in (2), but without the polyethylene film underneath.

Dungpats are highly attractive to termites, which enter them and eventually completely destroy them (Johnson and Whitford, 1975). Those used for treatments were collected from a dry lake bottom where no termites occur. Fairly uniform, thoroughly dry pats, about 20 to 30 cm diameter, were selected; all were from a single grazing session some six months previously.

This study was set up on 25 April 1977. After 150 days the dungpats were examined; the number of entrance holes on the underside was noted, and the amount of feeding and tunnelling in the pat rated from 0 (no damage) to 3 (heavily damaged). Then the film sheets were carefully uncovered, labelled as to position and orientation, and rolled onto paper rollers. In the case of (2), the location of the center of each dungpat was marked on the film. The films were spread out on a bench in the lab. Two sets of data were collected. First, the sheets were divided into four sections by ink lines and the termite holes in each section were marked and counted. The distance of each hole from the center of the nearest dungpat was measured. There were different sorts of holes in the sheets due to germinating plants and mechanical damage by other animals. However, termite holes were easily distinguished because the center of the hole was cleanly removed. Density of holes under and around a target and damage rating were analyzed as 4 replications.

An additional study was set up in 1978. Ten sites were selected. The set-up at each site was essentially similar to the 1977 experiment except that instead of using 4 dungpats in treatments, the following 3 targets were used:

(1) One dungpat (2) a 20 cm diameter circle of aluminium-coated, foamed polyurethane building insulation board, and (3) a 20 cm length mesquite wood, about 7 cm diameter, was split and one half used, split face down, in each treatment. The ten sites were divided at random into two groups, one being read at 100 days and

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the other at 150 days. Data collected were the same as in the 1977 trial.

We measured the temperature profile under a dungpat by digging a hole about 15 cm diameter and 20 cm deep and inserting thermocouples such that one set of 3 thermocouples lay under a dungpat and the other set of 3 in the soil 25 cm away; the soil was tamped back and two weeks elapsed before readings were taken. Temperatures were measured at depths of 20, 10 and 2 cm; a thermocouple mounted in a needle was used to measure surface temperature by thrusting it along just under the surface of the soil or dungpat. Temperatures were read directly on a Bailey electronic thermometer (Bailey Instruments, Saddle Brook, N.J.) on 4 dates during the early summer.

We also examined the suitability of newspaper as a bait material. In one series, newspapers were rolled into tight rolls, bound with wire, a wooden tag attached to the wire and buried 10 cm in the soil at a nearby site on 13 April 1977. The labels were left above the soil surface. On 29 June 1977, a different form of bait was made by folding newspaper into a compact, flat pad 20 cm square and 2 cm thick. Eight of these were secured to the soil surface, in two lines, 50 cm apart, using long nails. An additional nine were buried 10 cm in the soil.

Field experience had indicated that the performance of toilet paper rolls as baits (La Fage et al., 1973) seemed to be enhanced by covering these with a flat stone slab. Ninety-five rolls were laid out at the nodes of a 10 x 10 grid with one m spacing (5 nodes on one side were omitted). Half were randomly selected and covered with a slab of cinder-block and the remainder were left uncovered and secured with a steel pin.

There were 216 measures of the distance from the termite tunnel holes in the sheets to the nearest dungpat center. The mean distance was 17.0 ± 8.90 cm and the data are slightly right-skewed. The appearance of the films suggests that the holes tend to be grouped around the edge of the dungpat. To test this, a computer simulation was run, allowing random attack around a dungpat. As the film was only 30 cm wide, some termite tunnel openings could fall outside the strip of film. There were 216 termite tunnel holes on the four strips of film with the radial distance from the center of the pat to the gallery punctures varying from one to 41 cm. Thus, many holes within the observing radius of 41 cm would occur outside the film strip, and the data gathered by measuring distances from a point are biased against some greater distances. This sampling distribution was computer simulated by generating a random number between one and 40, and then generating this number of points randomly on an 80 x 80 matrix and truncating two opposite sides symmetrically to obtain a 30 x 80 matrix. The cartesian coordinates of these points were converted to polar coordinates from the center of the matrix, and these radial distances were treated in the same fashion as the field data. This process was repeated until 220 valid points were accumulated. This simulation resulted in a much more symmetrical distribution than the one observed, and the mean distance from the centers to the holes differed significantly ($t = 5.032$, $p < 0.01$). The observed distribution was clustered around the median (and mode) of 16, which is approximately the radius of the dungpats used. This supports the field observation that termites tend to enter the dungpats around the periphery. The simulation yielded a mean distance of 21.9 ± 11.20 cm. These data were more symmetrically distributed. The measured distances and simulation distances were significantly different ($t = 5.409$, $p < 0.001$) by the modified t-test for unequal variances (Snedecor and Cochran, 1967).

Results

In the 1977 experiment involving polyethylene sheeting and cowpats there were ($\bar{X} \pm SD$) 13.5 ± 2.83 on the control film. The analysis of variance showed significant difference between presence and absence of dungpats ($p < 0.01$), but no differences between sites.

The attack rates and the number of gallery entrances on the dungpats were strongly correlated ($r = 0.788$, $p < 0.001$). A paired comparison t-test of number of entrance holes between treatment and control dungpats was not significant.

In the 1978 experiments, there were 19.8 ± 5.93 termites holes per dungpat at 100 days and 57.0 ± 60.77 at 150 days (this mean is distorted by one single figure of 161 holes below one dungpat; if this is removed, the value is 36.0 ± 20.45). Corresponding figures for the polyurethane artificial dungpats are 15.8 ± 8.04 holes and 23.2 ± 2.59 holes. The pieces of mesquite wood had 10.8 ± 1.64 and 9.20 ± 5.17 holes in the film at 100 and 150 days respectively. The films with no surface food materials had 9.20 ± 4.38 and 16.73 ± 8.44 holes per section at 100 and 150 days.

There were no significant differences between the dungpats and the artifical dungpats at either time, but there were significant differences between these and the mesquite wood controls. Attack was significantly greater after 150 days compared with 100 days. There was no significant difference between mesquite wood and control.

The distribution of attack holes under both the dungpat and the artifical dungpat in the 1978 study was very similar to the distribution observed for the dungpats in 1977, i.e. 15.0 ± 8.44 for the artifical dungpats. These measurements did not differ significantly from one another nor from the 1977 data.

While the dungpats were all more-or-less completely destroyed, attack on the artifical dungpats was limited to occasional penetration of the aluminium foil covering and two short galleries between the aluminium and the foam.

Temperatures under dungpats and soil not under dungpats were taken at 4 dates in early summer when general climatic conditions were similar. There were no significant differences in temperatures under dungpats or open soil at 20 cm and the total daily temperature excursion was 3.0 – 3.3°C at that depth. There were significant differences in temperatures under dungpats and open soil at 10 cm and 2 cm depth at the surface ($F = 11.52$, $p < 0.0001$) (Table 1). The total daily temperature excursion was greater in open soil than under the dungpats (Table 1).

Of the 24 buried newspaper logs, only 15 were recovered due to loss of the tags and wires following disturbance of the site by cattle. Of the 15 recovered, 10 were deeply buried and showed only slight surface erosion on two, while several had galleries attached to the roll but no actual damage to the paper; only one showed a single deeper gallery, 4 cm long, 1.5 cm wide and 3 mm deep. Three newspaper logs were buried rather superficially, and two of these had extensive surface working: about 4 cm^2 on each. Two newspaper logs which had been excavated by cattle and were lying on the surface were heavily attacked. Two of the wooden lables lying on the surface were heavily attacked and covered by gallery carton, but the underlying rolls were undamaged.

The 95 toilet rolls with and without brick covers were rated for termite damage (0 = no damage, to 2 = heavy damage) on 13 September 1977. Of th covered rolls, 88% were damaged, average rating 1.44; of the standard rolls, 57% were attacked, with average rating of 0.91. These ratings for damage differ significantly ($p < 0.01$) when tested by Chi-square for ordinal data (Siegel,1956).

Discussion

The observations of baits (newspapers as rolls or pads, toilet rolls with and without covering slabs) suggest strongly that termites detect prospective food items much more readily on the surface of the soil than when the food is buried. This is supported by the finding of Santos (1979) that termites only attack surface litter bags. He found that 30 surface bags were all heavily attacked by termites, with up to 6 gallery entrances per bag; however, of 140 bags buried at 15–20 cm for one month, 40 bags buried for 3 months and 20 buried for 6 months, none had any termite attack nor were any termites extracted from the litter. Thus, position in the soil profile seems to be much more important than composition, which (in the present study) varied from highly purified cellulose (toilet rolls), cruder paper dungpats and totally indigestible, chemically inert polymerised hydrocarbon.

The species present on the Jornada Site, *Gnathamitermes tubiformans* (Buckley) and *Amitermes wheeleri* (Deseux), do not forage on the soil surface during the summer. It seems reasonable to surmise that some sort of underground "shadow" cast by the food object is detected by the termites. This could be temperature anomaly, a soil-water anomaly or a chemical trace. It seems unlikely that termites should recognize the chemical trace(s) of so many different food types, but this does not discount the possibility that they detect exudates from pioneer saprophytic fungi. It also seems improbable that chemicals emanating from the plastic foam would be attractive to termites and it certainly was not attacked by desert saprophytes. Detection of soil-water anomaly seems improbable, as even at very high soil-water tensions on the Jornada site, air in the pore spaces in the soil is close to 100% relative humidity (Slayter 1967). Further, termites do not attack dungpats until they have dried completely.

The data on soil temperatures under dungpats and open soil provide a logical modality for the location of large sutiable food items by subterranean termites. The significant differences in soil temperatures produced by the thermal shadow of dungpats up to 20 cm depth and the reduced thermal excursion under dungpats can most probably be detected by termites. Indeed a temperature differential of greater than 2°C can probably be detected by most organisms.

In the experiment using polythylene film, it was expected that the film would prove at least a partial barrier to chemical stimulants, in which case there should have been greater damage in the treatment where dungpats were present without the film than where the film was beneath the dungpats. However, this difference did not appear in the data. If the termites investigated the soil randomly, there should not be any statistical difference between the density of holes in the film in treatments (1) and (2), which appears to be true, and termite holes should be randomly dispersed on both 1 and 2.

The essentially identical pattern of attack on the artificial dungpats, which resemble their model only in size and in being highly insulative, would seem to eliminate chemical traces as an orientation mechanism and strongly support our hypothesis that the termites respond to a temperature anomaly. Termites respond strongly to temperature (Lee and Woods, 1971) and this would seem a reliable modality for orientation to surface objects. One might speculate that subterranean termites, which live in diffuse colonies, may detect temperature gradients in the soil and construct exploratory tunnels upward towards the soil surface. If a suitable food source is found, further tunnels would be constructed to capitalize on the source as quickly as possible. This would tend to define the edge of the source, leading to a concentration of galleries. In this case, where fairly uniform food objects of 20–30 cm diam were intentionally used, this would lead to a peak in the curve at about 16 cm as shown in the simulation model. The galleries at distances less than and greater than this would rep-

Table 1.—Mean soil temperatures ± 1 standard deviation of exposed soil and soil under cow dungpats for four dates 15 May, 22 May, 5 June and 6 June. Temperatures pairs significantly different by Tukey's Q(>2.29°C) are indicated by different letters a,b.

	20 cm		10 cm		2 cm		Surface	
Time	Soil	Dungpat	Soil	Dungpat	Soil	Dungpat	Soil	Dungpat
0600h	22.0 ± .8^{a}	23.3 ± 1.5^{a}	17.5 ± 1.9^{a}	21.0 ± 1.8^{b}	12.0 ± 2.8^{a}	16.0 ± .8^{b}	8.0 ± .8^{a}	9.0 ± 0.8^{a}
1200h	21.0 ± .8^{a}	21.0 ± .8^{a}	27.0 ± 1.8^{b}	24.0 ± .9^{a}	38.0 ± 1.8^{b}	24.0 ± .8^{a}	50.5 ± 2.6^{b}	46.0 ± 0.8^{a}
1800h	24.0 ± 1.8^{a}	23.0 ± .8^{a}	29.5 ± 1.3^{b}	27.0 ± .8^{a}	24.0 ± 4.1^{a}	22.0 ± .9^{a}	25.0 ± 0.8^{b}	22.3 ± 1.0^{a}
Total Excursion	3.0	3.3	12.0	6.0	26.0	8.0	42.0	37.0

resent variation in size of the food source and exploratory tunnels.

Finally, it could be argued that the pattern of attack on dungpats can be explained as initial discovery by random chance, followed by recruitment to a favorable food source resulting in a large number of feeding tunnels being formed. If this mechanism occurred one would intuitively expect either a concentration around the original gallery or a random pattern of galleries under the dungpat, not the observed pattern of galleries oriented to the edge of the dungpat. More convincing, however, is the similar number and pattern of galleries leading to the circles of aluminium-covered, foam plastic discs used to mimic the dungpats. This strongly suggests a purely mechanical response to a physical modality, which we argue is a temperature anomaly caused by an insulating surface object.

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