

**FORAGING DISTANCES AND FORAGER POPULATION SIZES OF THE
DESERT TERMITE *GNATHAMITERMES TUBIFORMANS* (BUCKLEY)
(ISOPTERA: TERMITIDAE)**

A Thesis

by

ANNE MICHELLE NARAYANAN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2004

Major Subject: Entomology

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August 2004

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ABSTRACT

Foraging Distances and Forager Population Sizes of the Desert Termite *Gnathamitermes tubiformans* (Buckley) (Isoptera: Termitidae). (August 2004)

Anne Michelle Narayanan, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Roger E. Gold

The desert termite *Gnathamitermes tubiformans* and its unique foraging tubes are a common fixture in rangelands across Arizona, New Mexico, northern Mexico, and Texas. Although it is a native species and has thrived for millions of years, recent droughts have made its activity more visible and raised questions about its impact on vegetation. Since *G. tubiformans* prefers grasses as food, there has been a concern about competition between livestock and termites. Monitoring of desert termite activity was conducted through two experiments focusing on foraging distances and forager population sizes.

The foraging distances experiment used circular grids in 5 m x 5 m plots to map the movement of marked *G. tubiformans* released from the center of the grid. Analyses showed no significant correlations between distances moved and abundance or type of vegetation. Movement of marked termites did not favor any compass directions.

The second experiment used a mark-recapture estimation model to predict *G. tubiformans* forager populations in 5 m x 5 m plots. Linear regression analyses showed a significant positive correlation between size of the forager population and amount of total vegetation. In addition, linear regression analyses showed a significant positive

correlation between total estimated number of collected termites during early recruitment and amount of vegetation cover, specifically grasses.

Desertification of rangelands used by *G. tubiformans* and livestock is a worry with few known solutions. Elucidating answers to this problem involves ferreting out the sources of the degradation. The results of this thesis shed light on the role *G. tubiformans* plays in its habitat, and infer that degraded habitats with low amounts of vegetation will exhibit low termite populations.

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INTRODUCTION

In general, termites are thought of as wood-consuming, urban pests. Termites cause billions of dollars in damages annually in the United States, yet outside of an urban setting, they are valuable recyclers of dead wood and other material containing cellulose. These recyclers thrive not only in the deciduous forests of the Eastern United States, but also in the arid and desert regions of Arizona, New Mexico, and Texas. Some desert termites, like those in the genus *Gnathamitermes*, do not feed extensively on wood and prefer other cellulose sources like dead grasses, forbs, and animal dung.

All termites are insects belonging to the order Isoptera. There are approximately 2,700 species of termites in the world with most of those in seven different families (Nalepa 2000). Termites are eusocial and have been called “white ants”, even though ants belong to the order Hymenoptera. Termites and ants do not share much in common besides their eusociality. As eusocial insects, termite colonies are comprised of castes with overlapping generations. In the desert termite *Gnathamitermes tubiformans* (Buckley), three castes can be found within a colony: (1) reproductives, primary and supplemental, which include the king and queen; (2) sterile workers that gather the food, feed others and build the nest; and (3) soldiers that defend the colony. The supplemental or secondary reproductives can replace the king and queen if something happens to the founding pair (Borror et al. 1992).

This thesis follows the format of the Journal of Economic Entomology.

All termites are soft-bodied and have paurometabolous metamorphosis that includes the stages of egg, nymph and adult. Even with soft bodies, termite fossils in substrates like amber date back over 100 million years (Pearce 1997). The oldest fossilized termite is approximately 130 million years old and is in the family Hodotermitidae (Thorne et al. 2000). Also, fossils of primitive cockroaches show a similar age (Nalepa and Bandi 2000). Through shared morphological features and the existence of a wood eating cockroach, *Cryptocercus punctulatus* Scudder, termites are related to cockroaches, yet their social behavior is much advanced compared to cockroaches past and present (Nalepa and Bandi 2000).

Termite colonies begin with a king and a queen that burrow into wood or soil after swarming from their colonies of origin. They dehisce their wings after landing and begin the mating ritual. These nuptial flights usually occur after rainfall so that moist conditions will insure that the new reproductives can burrow easily to begin their nest (Pearce 1997). Once the primary pair excavates a small chamber, then eggs are laid. The king and queen rear the first workers by feeding them from their body reserves and the protein from their degenerated flight muscles (Pearce 1997). As more workers are produced and developed, they begin foraging and caring for the brood and the royal pair.

Desert termites, such as the species *Gnathamitermes tubiformans*, belong to the termite subfamily Termitinae in the family Termitidae. This is considered the highest or most recently evolved family of termites (Noirot 2001). Differences from other termite families include gut structure and fauna along with external morphology. Within the termite hindgut are protozoa and bacteria that digest cellulose into useable sugars

(Pearce 1997). Termites in the family Termitidae have only bacteria in their hindguts (Pearce 1997). This could explain some differences in diets between some species of termitids and other groups. The oldest Termitidae fossils are between 50 and 40 million years old (Thorne et al. 2000). A fossil of a species of *Gnathamitermes* dates back to the Miocene period (approximately five to 20 million years ago). These fossils are markedly younger than those of the 130 million year old hodotermitid, and this adds to the likelihood that the termitids have evolved more recently than the other families of termites.

Gnathamitermes tubiformans has a diet that deviates from other termites that use dead wood. They prefer grasses, forbs, surfaces of dead wood, and certain types of mammal dung, especially that of cattle (Bodine and Ueckert 1975). Allen et al. (1980) found that 46% of the diet for *G. tubiformans* consisted of standing dead grass; 34% was grass litter; and 16% was live grass. Colonies of *G. tubiformans* are found in the soil and foraging occurs within tubes built from soil particles and feces glued together by the saliva of the worker termites (Nutting et al. 1987, Schaefer and Whitford 1981). These tubes are straw-like structures that completely enclose the food substrates like grass culms and leaves. When feeding occurs on a flat surface like that of dead wood, the area is covered in a sheet of soil particles cemented with saliva. The use of the coverings is not entirely understood, but MacKay et al. (1985) suggest that the galleries are protection from desiccation and predators including lizards, birds, and ants (Schaefer and Whitford 1981). Birds are predators of the alate termites during mating swarms (Schaefer and Whitford 1981).

Gnathamitermes tubiformans has a distribution that stretches from northern Mexico to Arizona, New Mexico, and Texas (Bodine and Ueckert 1975). Studies conducted in Arizona, New Mexico and Texas have evaluated the benefits and detriments caused by *G. tubiformans*. There are no clear answers to whether *G. tubiformans* is truly beneficial or detrimental to arid and semi-arid environments. Elkins et al. (1986) affirm that even with beneficial and detrimental effects, *G. tubiformans* is a keystone species in the northern Chihuahuan desert.

As a keystone species, the presence of *G. tubiformans* affects the structure of the environment in which it inhabits. Like other termites, *G. tubiformans* is a beneficial decomposer of decaying plant matter. In southern-central New Mexico near Las Cruces, from July to September 1979, Whitford et al. (1982) found that *G. tubiformans* was responsible for the breakdown of 19.5% to 100% of cattle dung. In a separate experiment, Whitford et al. (1982) observed that fifty percent of leaf litter from shrubs, grasses, and forbs were removed by *G. tubiformans*. Schaefer and Whitford (1981) noted that *G. tubiformans* was a key to desert nutrient cycles. By feeding upon dead grasses, forbs, wood, and dung, the termites move nutrients into the soil. Termite foraging tubes were found to be high in nitrogen (Schaefer and Whitford 1981). Rainfall melts this tube material and nitrogen is released into the soil (Schaefer and Whitford 1981).

The subterranean lifestyle of *G. tubiformans* is important to water infiltration into desert soil. *Gnathamitermes tubiformans* colonies create an extensive network of tunnels and chambers within the soil. When *G. tubiformans* was chemically removed

from an area, soil porosity was reduced, which in turn reduced water infiltration (Elkins et al. 1986). Reduced water infiltration leads to valuable water being lost to run-off. Through this reduced water infiltration, the intershrub plant communities suffered. Fluffgrass (*Dasyochloa pulchellum* (H.B.K.) Rydb.), a perennial grass, almost completely disappeared in the absence of termites (Elkins et al. 1986). The loss of grass coverage resulted in increased erosion (Elkins et al. 1986). Whitford et al. (1982) also concluded that the removal of termites was detrimental to *D. pulchellum* and thus altered the structure of the ecosystem.

Even as a key player in the desert ecosystems that *G. tubiformans* inhabits, some of its behaviors are considered detrimental. Although *G. tubiformans* consumes dead plant matter, a portion of the nutrients become locked deeply in the soil within tunnels and galleries. These nutrients are not available to plants with shallow roots, such as grasses (Schaefer and Whitford 1981). The termite practices of cannibalism and fecal feeding insures that nutrients move to other termites and not into the environment. Only predation of termites allows for a quicker turnover of nutrients into the environment (Schaefer and Whitford 1981).

The reduction of ground litter has been indirectly linked to termite foraging. Too much reduction of ground litter lessens the condition of topsoil. Though water infiltration may increase in the presence of termites, loss of water due to run-off occurs with the complete absence of plant litter on the soil surface. This litter keeps the soil temperature and evaporation of soil moisture lower (Bodine and Ueckert 1975). The decomposition of more plant litter increases soil organic matter. Nash and Whitford

(1995) found a “highly significant negative correlation between termite abundance/activity and soil organic matter” with an r -value of -0.97 . Nash et al. (1999) later showed that feeding activity at baits gave an inverse relationship with abundance of *G. tubiformans* natural diet. It is likely that lower bait (toilet paper rolls) activity was measured in sites with more ground litter because desert termites preferred their natural food sources over toilet paper rolls. This may have led to a false low measure of activity in some sites. In another study that compared areas with termite activity and added straw mulch, plots where termites were present and straw mulch was added, nitrogen soil levels were significantly higher than levels in plots where termites were absent and straw mulch was added (Brown and Whitford 2003). Thus Brown and Whitford (2003) concluded, “subterranean termites are a major determinant of soil nitrogen levels.”

The condition of any environment is dictated by climatic factors such as precipitation, temperature, humidity, and evaporation. Within arid and semi-arid environments, the amount of precipitation an area receives is key to the survival of the plant communities of that area. Survival of the animals that feed upon the plants increases and decreases as precipitation levels fluctuate. When an area receives a high amount of precipitation, the plant communities thrive along with the *G. tubiformans* colonies that feed on the plants. Their population will grow during years of more precipitation and will consume more as a result (Bodine and Ueckert 1975). Conversely, in drought years, the number of desert termites decreases (Bodine and Ueckert 1975). Drought years along with desert termites have caused concern for ranchers across western Texas. Even though *G. tubiformans* numbers are lowest during drought years,

their feeding becomes more noticeable as they compete with cattle for forage (Bodine and Ueckert 1975).

For all that is known about *G. tubiformans*, some basic and fundamental biology and ecology questions have not been answered. This thesis focused on foraging distances and forager population sizes in areas of varying amounts of standing vegetation. The first set of experiments tested the null hypothesis that foraging distances do not vary with the amount of standing vegetation. The second set of experiments tested the null hypothesis that estimated population sizes of desert termite foragers do not vary with the amount of standing vegetation. Through these experiments and others, the interaction between these termites and their environment can be elucidated.

MATERIALS AND METHODS

Plot Sites and Vouchers. All study plots were located approximately 8 km East of Big Spring, Texas in Howard County, ranging from 32° 14' 15" N to 32° 14' 18" N and 101° 21' 23" W to 101° 21' 30" W. The ten-acre pasture area had been excluded from grazing for five years. The study was conducted from September 20, 2003 to October 22, 2003. Ten 5 m x 5 m plots with active *G. tubiformans* foragers were used. A quadrant-based count of standing vegetation (grasses and forbs) was taken of each plot. A 1 m x 1 m frame was randomly placed five times within a plot, and standing grasses (two culms = one grass) and standing forbs were counted (Figure 1). The counts were averaged and then multiplied by 25 to give an estimated total count for each plot. Five plots were randomly chosen for each experiment. Voucher samples were collected from each plot to verify that the desert termites were *G. tubiformans* (Weesner 1965). Vouchers were placed in the Texas A&M University Insect Collection and are identified as number 648. The collection is located on the second floor of the Minnie Belle Heep Building on Texas A&M University West Campus.



Figure 1. A quadrant-based count of standing vegetation was taken in each 5 m x 5 m plot using a 1 m x 1 m frame. During five random placements of the frame, standing grasses (two culms = one grass) and forbs were counted. Counts were averaged and multiplied by 25 to yield a total count for each plot.

Baits and Termite Marking. For both experiments, cow manure baits were used to collect desert termites. Baits were made according to Taylor et al. (1998). Fresh, semi-liquid manure was collected from the Texas A&M Beef Center in lined 5-gallon buckets. Cylindrical containers (10 cm diameter, 12.5 cm height), with the top end open and bottom fitted with wire mesh (0.6 cm x 0.6 cm openings) were used as molds and holders for the manure in the field (Figure 2).



Figure 2. Termite bait trap (10 cm diameter, 12.5 cm height) with mesh (0.6 cm x 0.6 cm openings) bottom exposed.

The manure filled the containers to a depth of 3.5-5 cm (0.275-0.393 L). Manure was added as consumption occurred to maintain equal levels in all baits. On the evening prior to bait collection all baits were watered with approximately 0.5 L to entice termite feeding. Small colored flags marked the baits within each plot. After termites were allowed to forage over a five-day period, baits were collected and termites were separated from the manure (Figure 3). The mean body mass of worker termites was determined by weighing ten groups of five individual workers. The total number of termites from a bait was measured by dividing the total mass of the combined worker termites per bait by the mean mass of *G. tubiformans* workers. Although this technique

took time, it gave a reliable estimated count of the captured termites without the more time consuming process of counting individuals.



Figure 3. After the five-day foraging period, *G. tubiformans* were separated from the manure bait using a sorter constructed from an inclined plastic shoebox lid with tubing leading to the collection box below. Exposed termites moved down through the tubing.

Captured termites were marked with Krylon Fluorescent Indoor/Outdoor Paint (The Sherwin-Williams Company Consumer Group, Cleveland, OH) using the technique developed by Forschler (1994). To mark termites, approximately 50 termites were placed in a 100 x 16 mm plastic Petri dish. The dish was placed inside a 56 x 33 x 41 cm (L x W x H) cardboard box. Paint was sprayed from about 50 cm away and 50 cm above to allow a drift to fall and mark the termites.

After being marked, termites were released back to the same spot of ground surface covered by the manure bait. To prevent termites from escaping, an empty bait container without the mesh bottom was used to fence in the released termites. This forced the released termites to re-enter the holes formed during foraging of the manure bait.

Foraging Distances Experimental Design. Within each foraging distance plot, two manure baits were set in the center and termite foraging was allowed for five days. After the foraging period, the baits were collected and the captured termites were separated, estimated, marked, and released. After releasing the termites, fourteen manure baits were set in a circular grid around the center in each plot (Figure 4). Center baits were not replaced. The grid consisted of three rings at the arbitrary distances of one meter, two meters, and three meters. Two manure baits were set at one meter from the central point in opposite directions to the north and south. Similarly, four baits were set at two meters from the central point, and eight baits were set at three meters from the central point. Baits within each ring were offset by 45° from the baits within the previous ring. This method follows Turchin's (1998) method for recapturing marked insects with attractive baits.



Figure 4. Circular grids were set up for the foraging distance experiment. Grids consisted of two baits, four baits, and eight baits at one meter, two meters, and three meters, respectfully, from the center of the grid. Marked *G. tubiformans* were released in the center, and baits were monitored for their movement.

After marked termites foraged for five days within the distance grid, baits were checked for marked termites. Baits were checked in the field by emptying the manure in a 40 cm x 28 cm plastic tray. The tray was then placed into a box to be viewed by a Spectroline UV-4B blacklight (Spectronics Corporation, Westbury, NY) (Figure 5). Marked termites were easily identified by the fluorescent paint mark. Positions of marked termites in the grid were recorded. Manure and viewed termites were carefully placed back into the corresponding baits. Grid baits were checked in this manner three more times with five-day foraging periods between each check.



Figure 5. Foraging distance plot samples were viewed by black light in a darkened box to detect marked *G. tubiformans*. Any marks were recorded and released back to the location of capture.

Statistical analyses (Microsoft[®] Corporation 2000, SPSS Inc. 2001) were used to determine relationships among movements of marked termites and counts of vegetation within plots. Nine linear regression models were tested between percent recaptures of marks at one to three meters and total vegetation per plot, grasses per plot, and forbs per plot (SPSS Inc. 2001). Any preferences of marked termite movement relative to compass directions (north, north east, east, south east, south, south west, west, and north west) within grid plots were observed using analysis of variance (SPSS Inc. 2001).

Forager Populations Experimental Design. Five manure bait traps were placed within each plot. Bait locations corresponded with active foraging tubes. After bait placement, foraging commenced for five days. Following the five days, baits were collected and the captured termites were separated, estimated, marked and released in

the same fashion as the previous experiment. Once all released termites re-entered the soil, the manure bait traps were replaced to allow for another five-day foraging period.

Then, as the foraging period elapsed, manure baits were collected and the captured termites were extracted from the manure. Each bait collection was viewed by black light and the number of marked termites was recorded. The entire collection from each bait was then estimated, marked, and released back to the same bait station. Another five-day foraging period commenced. Termites were collected and marked for three more periods.

Begon's (1979) weighted mean model was used to estimate forager populations within plots: $N = (\sum M_i n_i) / [(\sum m_i) + 1]$

N = estimated forager population

M_i = number of marked termites at risk on day i

n_i = number of termites caught on day i

m_i = number of marked termites caught on day i

Standard error of $N = N \sqrt{(1/(\sum m_i + 1) + 2/(\sum m_i + 1)^2 + 6/(\sum m_i + 1)^3)}$

Statistical analyses (Microsoft[®] Corporation 2000, SPSS Inc. 2001) were used to assess relationships between estimated forager populations and counts of vegetation within plots. Three linear regression models were tested between estimated forager populations and total vegetation per plot, grasses per plot, and forbs per plot (SPSS Inc. 2001).

The first two collections of termites were combined as a total estimated number during the first ten days of recruitment to the baits. These numbers were analyzed to determine relationships between total estimated number of collected termites recruited in

the first ten days and vegetation counts in plots. Three linear regression models were tested between the total estimated number of collected termites in the first ten days and total vegetation per plot, grasses per plot, and forbs per plot (SPSS Inc. 2001).

RESULTS

Vegetation Counts. The dominant shrub species was honey mesquite (*Prosopis glandulosa* Torr). The dominant cactus species was prickly pear (*Opuntia phaeacantha* Englem). Dominant grass species included King Ranch bluestem (*Bothriochloa ischaemum* (L.) Keng), curly mesquite (*Hilaria belangeri* (Steud.) Nash), tobosagrass (*Hilaria mutica* (Buckl.) Benth.), Halls panicum (*Panicum hallii* Vasey), and little bluestem (*Schizachyrium scoparium* (Michx) Nash). The dominant forb species was annual broomweed (*Amphiachyris dracunculoides* (DC.) Nutt). Total vegetation counts ranged from 630 plants/plot to 2,870 plants/plot (Table 1). Grass counts ranged from 10 grasses/plot to 2,085 grasses/plot (Table 1). Forb counts ranged from 310 forbs/plot to 2,195 forbs/plot (Table 1).

Table 1. Plot vegetation counts and locations.

Plot #	Grasses/plot	Forbs/plot	Plants/plot	Longitude	Latitude
1	10	975	985	32° 14' 18" N	101° 21' 26" W
2	125	1110	1235	32° 14' 18" N	101° 21' 25" W
3	165	2195	2360	32° 14' 17" N	101° 21' 28" W
4	2085	785	2870	32° 14' 15" N	101° 21' 24" W
5	1605	420	2025	32° 14' 16" N	101° 21' 23" W
6	170	460	630	32° 14' 17" N	101° 21' 25" W
7	145	565	710	32° 14' 18" N	101° 21' 25" W
8	865	310	1175	32° 14' 17" N	101° 21' 29" W
9	750	830	1580	32° 14' 17" N	101° 21' 30" W
10	1875	965	2840	32° 14' 15" N	101° 21' 26" W

Termite Mass. Due to the small mass of a single worker *G. tubiformans*, five termites were placed in each group to secure a reading from the balance. The mean body mass of worker termites was 0.00343 g (Table 2).

Table 2. Group masses of *G. tubiformans* worker termites based on groups of five individuals.

Group #	Mass (g)
1	0.0160
2	0.0173
3	0.0167
4	0.0170
5	0.0180
6	0.0187
7	0.0180
8	0.0160
9	0.0175
10	0.0163

The group mean was 0.01715 g and was divided by five individuals to yield 0.00343 g per termite.

Foraging Distances. The mean percent recaptures for all distance plots was 1.03 \pm 0.83%. Total percent recaptures for all distance plots was 6.66%. The mean percent recapture rates for 1-3 meters ranged from 0.23 to 0.64 (Table 3). There were no significant or strong correlations found between percent recaptures at one to three meters, and total vegetation per plot, grasses per plot, and forbs per plot (Table 4).

Table 3. Percent recaptures of marked *G. tubiformans* in plots 1-5 at 1 meter, 2 meters, and 3 meters.

Plot #	1 meter	2 meters	3 meters
1	0	1.6950	0.1695
2	0	0	0.6787
3	0.71940	1.1990	0
4	0.28570	0	0
5	1.27800	0.3195	0.3195
Mean	0.46 ± 0.55	0.64 ± 0.77	0.23 ± 0.28

Table 4. The R² and P-values for percent recaptures of marked *G. tubiformans* at 1 meter, 2 meters, 3 meters, and vegetation counts.

	R ²	P
Total vegetation		
Recaptures (%) at 1 meter	0.207	0.44
Recaptures (%) at 2 meters	0.080	0.65
Recaptures (%) at 3 meters	0.403	0.25
Grasses		
Recaptures (%) at 1 meter	0.198	0.45
Recaptures (%) at 2 meters	0.380	0.27
Recaptures (%) at 3 meters	0.092	0.62
Forbs		
Recaptures (%) at 1 meter	0.013	0.86
Recaptures (%) at 2 meters	0.191	0.46
Recaptures (%) at 3 meters	0.092	0.62

Preferences of marked termite movement to compass directions within grid plots were tested using analysis of variance (Table 5). Mean number of termites recaptured for the eight compass directions was not significantly different ($p = 0.49$).

Table 5. Movement of marked *G. tubiformans* to compass directions.

	North	NEast	East	SEast	South	SWest	West	NWest
Plot 1 recaptures (%)	0	0	0	1.6950	0	0	0.1695	0
Plot 2 recaptures (%)	0	0	0	0	0.2262	0	0	0.4525
Plot 3 recaptures (%)	0	0	0	0.4796	0.7194	0	0	0.7194
Plot 4 recaptures (%)	0.2857	0	0	0	0	0	0	0
Plot 5 recaptures (%)	0.9585	0	0.3195	0	0.3195	0.3195	0	0
Mean recaptures (%)	0.2488	0	0.0639	0.4349	0.2530	0.0639	0.0339	0.2334
Standard deviation (%)	0.4156	0	0.1429	0.7344	0.2961	0.1429	0.0758	0.3345

Estimated Forager Populations. Using Begon's (1979) weighted mean model, the mean estimated forager population for plots 6-10 was $61,181.24 \pm 48,449.48$ (Table 6).

Table 6. Estimated *G. tubiformans* forager populations.

Plot #	Estimated Population	Standard Error
6	51,354.70	4,965.04
7	35,545.30	4,160.90
8	29,765.00	4,489.10
9	42,600.00	4,417.90
10	146,641.20	14,665.40

Linear regression analysis suggests that there is a positive relationship between estimated forager populations and vegetation counts, most notably with grass counts and total plant counts (Table 7). However, though the relationships appeared to be strong, they were not significantly different from random except for total plant counts ($P = 0.05$, Table 7).

Table 7. The R^2 and P-values of apparent *G. tubiformans* forager populations and vegetation counts.

	R^2	P
Grasses	0.696	0.08
Forbs	0.543	0.16
Total plants	0.763	0.05

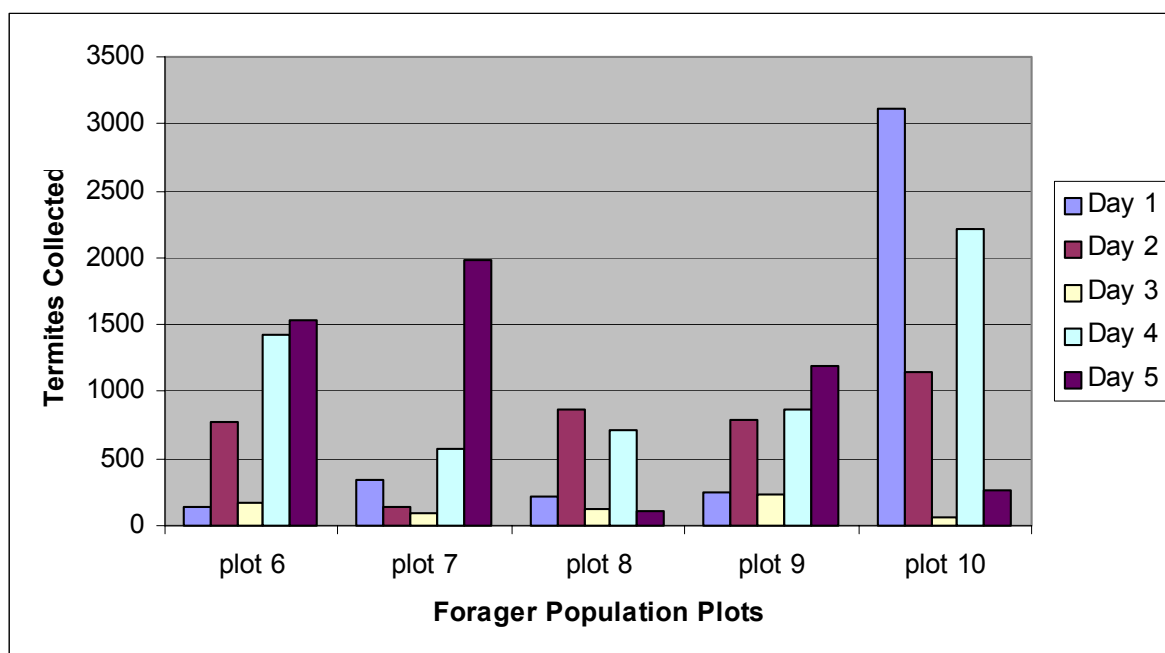


Figure 6. Total *G. tubiformans* collections for forager population plots. Each day represents a 5-day foraging period between collections.

By graphing the total number of termites collected each foraging period, trends in recruitment to the baits can be observed (Figure 6). Plots 6, 8, and 9 show increasing recruitment from the first to the second foraging periods. The third collection may have shown an increase in recruitment if not for inclement weather conditions that resulted in 1.02 centimeters of rain and a consequent drop in the number of foraging termites in all

five plots. Plots 6, 7, and 9 show increasing recruitment from the fourth to the fifth foraging periods with large numbers of foragers in all three of these plots. Since experiment two aimed to evaluate foraging populations in a given plot with varying amounts and types of vegetation, as recruitment climbs with the use of attractant baits, a biased account of foraging termites in that given plot seemed probable. The attractant baits may have influenced the number a foragers within plots. Based on these observations, the first and second collections were combined and the third, fourth, and fifth collections were deleted from the linear regression analyses so as not to show bias due to over-recruitment (Tables 8 and 9).

Table 8. Collection numbers for *G. tubiformans* foragers for day 1 and day 2.

Plot #	Day 1	+	Day 2	=	Combined collection
6	134		769		903
7	335		138		473
8	217		870		1,087
9	248		787		1,035
10	3,110		1,139		4,249

Table 9. The R^2 and P-values for correlations of combined first two collections of *G. tubiformans* foragers and vegetations counts.

	R^2	P
Grasses	0.869	0.02
Forbs	0.475	0.20
Total plants	0.877	0.02

The resulting linear regression analyses showed significant positive correlations between numbers of termites and density of vegetation. Specifically, as grass cover and total plant cover increased, so did numbers of foraging (Table 9). There was no significant relationship between forb density and termite activity.

DISCUSSION AND CONCLUSIONS

By studying *G. tubiformans*' movements and forager population numbers, it seems likely that vegetation composition and amount actually impact the dynamics of their activity. Although experiment one, foraging distances, showed no significant or strong correlations with movement of marked termites away from grid centers and vegetation counts, experiment two yielded extremely strong, positive linear relationships that were significant at the 95% confidence interval. As total vegetation increased estimated forager populations also increased. Also, total collected termite numbers for the first ten days of recruitment increased as total vegetation and grasses increased.

Based on the results in experiment one, the data supported the acceptance of the null hypothesis that foraging distances of *G. tubiformans* do not vary with the amount of standing vegetation. Correlations between movement of marked individuals to certain distances and standing vegetation counts were weak at best with no significant differences. It was expected that plots with low standing vegetation would show more recaptures at the outer grid ring. This expectation was supported by the idea that foraging to the outer portion of the grid would be evident when the food supply was low, in an effort for termite foragers to secure more food resources. Likewise, when there was abundant food in plots with high counts of standing vegetation, movement would be more restricted to the inner portions of the grid. In future experiments, the use of manure as bait should be closely evaluated with other food choices. Even though manure is excellent bait for *G. tubiformans*, it may have influenced the usual foraging

patterns of the termites. Besides the use of other bait materials, future replications of this experiment would benefit from a larger sample size with more plots tested. Due to the cryptic behavior of these subterranean insects, it was difficult to map their movements. Lastly, for experiment one, analysis showed that foraging termites did not favor any compass directions (Table 5, $p = 0.49$).

Results from experiment two supported the rejection of the null hypothesis that estimated population sizes of *G. tubiformans* foragers do not vary with the amount of standing vegetation. Clearly, as plot vegetation counts increased, so did forager populations. This relationship seemed to be influenced by the amount of grasses within a plot. Begon's (1979) model used to estimate apparent forager populations gave a strong correlation for total plants ($R^2 = 0.763$, $p = 0.05$) that was significant at the 95% confidence interval. This relationship was predicated by the correlations of early recruitment (first ten days) collection numbers with grasses ($R^2 = 0.869$, $p = 0.02$) and total plants ($R^2 = 0.877$, $p = 0.02$). This reaffirms past studies that show *G. tubiformans* prefers grasses as a food source (Allen et al. 1980).

The observation that recruitment to attractant baits kept increasing through 25 days of foraging in some plots was a useful and unexpected result of this study. Results of previous studies, like that of Nash and Whitford (1995) and Nash et al. (1999), may have been biased by this increasing recruitment. Their study monitored baits at two-week intervals for a span of eight months (Nash and Whitford 1995). Their second collection period showed some evidence of high, increasing recruitment. The Nash et al. (1999) study monitored baits on a yearly basis. They even recognized that "termites

utilize surface baits with intensity inversely related to the availability of natural foods” (Nash et al. 1999). Realizing the potential for increasing recruitment of desert termite foragers to baits will be vital in shaping future experimental studies of these insects.

As the results of this study have shown, vegetation make-up and amount governs termite foraging populations. *Gnathamitermes tubiformans* has been a native of the western portions of Texas for millions of years (Thorne et al. 2000). Degradation of rangelands where desert termites are found is alarming; yet, this study shows that areas of low vegetation, like those in degraded areas, will harbor low numbers of desert termites. If *G. tubiformans* was part of this degradation process, a negative correlation with vegetation amounts and termite numbers would be more likely. Studies outside the realm of entomology are probing the causes of desertification and may hold the answer of how to stop depletion of resources in rangelands.

Portions of the native habitat of *Gnathamitermes tubiformans* have experienced some radical changes over the past two centuries including shifts of perennial grass dominated lands to less productive areas with an abundance of annual grasses, forbs, and woody shrubs. In a review by Van Auken (2000), he lists the various terminologies that these changes have been given as follows: “desertification, shrub invasion, woody plant invasion, and bush or brush encroachment.” Other similar terms that have been coined include “savannization,” “aridization,” and “xerotization” (Verstraete 1986). The term desertification is being used worldwide. The United Nations (1978) held a conference on desertification that created a general definition for desertification as the diminishment “or destruction of the biological potential of the land, and can lead ultimately to desert-

like conditions.” Different definitions for desertification are specific to the areas that experience the degradation. For arid and semiarid regions of the United States, desertification is defined as the “degradation of desert grasslands to less productive shrublands” (Kerley and Whitford 2000).

Many studies have focused on the causes of desertification. Van Auken (2000) concluded that the creation of shrublands was due to “chronic high levels of domestic herbivory” that led to less production of grasses that fuel and promote natural range fires that could lower woody plant growth to favor more grass growth. Archer et al. (1988) agreed with Van Auken, but added that a slow climate change coupled with the above cause could expedite the conversion of grasslands to shrublands.

It is known that halting and even reversing desertification is a lengthy task if possible at all. A study by Valone et al. (2002) compared a range area that had been excluded from grazing for 39 years with a range area that had been excluded from grazing for 20 years. The 20-year exclusion showed no difference in vegetation with the adjacent grazed area, and both were dominated by shrubs (Valone et al. 2002). The 39-year exclusion showed four times more grass coverage than the adjacent grazed area (Valone et al. 2002). This suggests that, in at least some cases, recovery from desertification is a long process of more than 20 years.

Dung fouling from livestock, such as cattle, is a concern in grazed pastures. Since accumulated dung pads cover ground area, grass forage productivity decreases and in turn leads to desertified conditions (Anderson et al. 1984). As was pointed out, *G. tubiformans* was found to remove 19.5 to 100% of cattle dung in studied pastures

(Whitford et al. 1982). Whitford et al. (1982) also stated that without termites, only 4% removal occurs by weathering and fungi. Desert termites are vital to the reduction of dung in pastures since fewer arthropod decomposers are present in arid and semi-arid areas outside of the brief rainy period. Although some may view *G. tubiformans* as detrimental because it feeds on grasses and competes with livestock for food, evidence such as its role in decomposing cattle dung and the results of this thesis support the opposite view.

REFERENCES CITED

- Allen, C.T., D.E. Foster, and D.N. Ueckert. 1980.** Seasonal food habits of a desert termite, *Gnathamitermes tubiformans*, in West Texas. Entomol. Soc. Am. 9(4):461-466.
- Anderson, J.R., R.W. Merritt, and E.C. Loomis. 1984.** The insect-free cattle dropping and its relationship to increased dung fouling of rangeland pastures. J. Econ. Entomol. 77:133-141.
- Archer, S., C. Scifres, C.R. Bassham, and R. Maggio. 1988.** Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58(2):111-127.
- Begon, M. 1979.** The models, pp. 6-23. *In* Investigating animal abundance: capture and recapture for biologists. Edward Arnold Limited, London.
- Bodine, M.C. and D.N. Ueckert. 1975.** Effect of desert termites on herbage and litter in a shortgrass ecosystem in West Texas. J. Range Management 28(5):353-358.
- Borror, D.J., C.A. Triplehorn, and N.F. Johnson. 1992.** An introduction to the study of insects. Harcourt Brace & Company, Orlando, FL.
- Brown, M.F. and W.G. Whitford. 2003.** The effects of termites and straw mulch on soil nitrogen in a creosotebush (*Larrea tridentata*) dominated Chihuahuan Desert ecosystem. Journal of Arid Environments 53:15-20.
- Elkins, N.Z., G.V. Sabol, T.J. Ward, and W.G. Whitford. 1986.** The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. Oecologia 68:521-528.
- Forschler, B.T. 1994.** Fluorescent spray paint as a topical marker on subterranean termites (Isoptera: Rhinotermitidae). Sociobiology 24(1):27-38.
- Kerley, G.I.H. and W.G. Whitford. 2000.** Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores and granivory. American Midland Naturalist 144:78-91.
- MacKay, W.P., J.H. Blizzard, J.J. Miller, and W.G. Whitford. 1985.** Analysis of above-ground gallery construction by the subterranean termite *Gnathamitermes tubiformans* (Isoptera: Termitidae). Environ. Entomol. 14(4):470-474.

- Microsoft® Corporation. 2000.** Microsoft® Excel 2000. ver. 9.0.3821 sr-1. Microsoft Corporation, Redmond, WA.
- Nalepa, C.A. 2000.** Wood-destroying insects- termites, pp. 112-116. *In* R.E. Gold and S.C. Jones [eds.], Handbook of household and structural insect pests. Entomological Society of America, Lanham, MD.
- Nalepa, C.A., and C. Bandi. 2000.** Characterizing the ancestors: paedomorphosis and termite evolution, pp. 53-75. *In* T. Abe, D.E. Bignell, and M. Higashi [eds], Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Nash, M.H. and W.G. Whitford. 1995.** Subterranean termites: regulators of soil organic matter in the Chihuahuan Desert. *Biol. Fertil. Soils* 19:15-18.
- Nash, M.S., J.P. Anderson, and W.G. Whitford. 1999.** Spatial and temporal variability in relative abundance and foraging behavior of subterranean termites in desertified and relatively intact Chihuahuan Desert ecosystems. *Applied Soil Ecology* 12:149-157.
- Noirot, C. 2001.** The gut of termites (Isoptera) comparative anatomy, systematics, phylogeny. II. - Higher termites (Termitidae). Abstract. *Ann. Soc. Entomol. France* 37(4):431-471.
- Nutting, W.L., M.I. Haverty, and J.P. LaFage. 1987.** Physical and chemical alteration of soil by two subterranean termite species in Sonoran Desert grassland. *J. Arid Environ.* 12:233-239.
- Pearce, M.J. 1997.** Termites: biology and pest management. CAB International, New York, NY.
- Schaefer, D.A. and W.G. Whitford. 1981.** Nutrient cycling by the subterranean termite *Gnathamitermes tubiformans* in a Chihuahuan Desert ecosystem. *Oecologia* 48:277-283.
- SPSS Inc. 2001.** SPSS for Windows. Chicago, IL.
- Taylor, H.S., W.P. MacKay, J.E. Herrick, R.A. Guerrero, and W.G. Whitford. 1998.** Comparison of field methods to detect termite activity in the northern Chihuahuan Desert (Isoptera). *Sociobiology* 32(1):1-15.

- Thorne, B.L., D.A. Grimaldi, and K. Krishna. 2000.** Early fossil history of the termites, pp. 77-93. *In* T. Abe, D.E. Bignell, and M. Higashi [eds], Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Turchin, P. 1998.** Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc. Publishers, Sunderland, MA.
- United Nations. 1978.** United Nations conference on desertification: round-up, plan of action and resolutions, 29 August-9 September 1977, United Nations, New York.
- Valone, T.J., M. Meyer, J.H. Brown, and R.M. Chew. 2002.** Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. *Conservation Biology* 16(4):995-1002.
- Van Auken, O.W. 2000.** Shrub invasions of North America semiarid grasslands. *Annu. Rev. Ecol. Syst.* 31:197-215.
- Verstraete, M.M. 1986.** Defining desertification: a review. *Climatic Change* 9:5-18.
- Weesner, F.M. 1965.** Termites of the Southwestern United States- Area D, pp. 57-63. *In* The termites of the United States; a handbook. National Pest Control Association, Elizabeth, NJ.
- Whitford, W.G., Y. Steinberger, and G. Ettershank. 1982.** Contributions of subterranean termites to the "economy" of Chihuahuan Desert ecosystems. *Oecologia* 55:298-302.

VITA

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