
If you think you know everything about termite biology and evolution, you can make sure by reading this article. Adapted from a well-liked speech at the Purdue Pest Control Conference, this article lends insight into termite control in the future.

TERMITES

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Biographical Sketch: *Michael I. Haverty, a native of Fresno, California, attended the University of California, Davis, where he received his Bachelor of Science degree in zoology in 1968. From 1968 to 1969 and from 1971 to 1974, he worked in the Department of Entomology at the University of Arizona, receiving his Master of Science degree in 1970 and his Doctor of Philosophy degree in entomology with a minor in zoology in May 1974. While there, his research involved a study of the role of termites in the desert ecosystems.*

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The pest control operator needs to understand termite biology to effectively control the pests and to qualify for state certification under the Environmental Protection Agency's new requirements. Researchers in the Forest Service are continuing to delve into termite behavior and ecology to find weak links that could be exploited as new control measures. What I would like to do here is give you a brief review of termite biology, then point out those aspects of termite ecology and behavior that may help you in implementing old control techniques or may lead to the discovery of new ones.

SOCIAL INSECT

Termites have two characteristics that distinguish them from most other insects: they are social insects, and they use cellulose as food. The only other truly social insects are some of the bees, ants, and

wasps. The only other insects that eat cellulose are some of the beetles, ants, cockroaches, and the silverfish.

You have probably heard termites referred to as social insects before. This is not simply because they live in colonies. Many insects exhibit gregarious or communal behavior. All of you have seen bag worms or heard of locust droves destroying grain fields in the Middle East. These animals are living in communal groups, but they are not social insects. Social insects can be distinguished by three traits: individuals cooperate in caring for the young; sterile individuals work in behalf of the reproductive individuals; and there is an overlap of at least two generations working in the colony and thus offspring assist parents.

Social behavior makes a species highly efficient in achieving its goals. Social insects are selfless. Ter-

mites show uncalculated consideration of, and regard for, the interests of the other members of the colony. All their efforts are directed toward the success of the colony. Worker termites gather food not so much for themselves but so the queen may be nourished in order to produce her numerous eggs and the reproductive nymphs can be fattened for their nuptial flight.

EVOLUTION

In a literal sense, termites can be considered nothing more than social cockroaches. Unfortunately, there are no living ancestors common to both the wood eating cockroach, *Cryptocercus*, and the most primitive termite, *Mastotermes darwiniensis* Froggatt, which occurs in Australia. Both of these insects do possess many features in common which lead us to believe they did have, at one time, a common

ancestor. These common features include among other things:

1. Morphological features — wing venation, genitalia, terminal leg segments.
2. Bacteria and flagellate protozoa in the digestive tract.
3. Primitive termite lays eggs in batches similar to egg cases of cockroaches.

During the transition from wood eating roaches, termites evolved truly social behavior, deciduous wings, and a caste system. From the primitive ancestor, termites have evolved into five major families.

There are two major branches in the evolutionary tree of termites. The first branch goes to the primitive family Mastotermitidae which has only one representative species living today, *M. darwiniensis*. From this group evolved the Kalotermitidae or drywood termites. The major change in this step

of evolution is in wing and leg morphology. Also the eggs are now laid singly rather than in batches. The second branch leads to the harvester or rottenwood termites (Hodotermitidae) and subterranean termites (Rhinotermitidae). This branch terminates with the group known as the higher termites (Termitidae). These insects are quite different from the other termites in that they have almost all lost the symbiotic protozoa; thereby relying mostly on bacteria and fungi for the digestion of cellulose. The Termitidae also have a "true" worker caste which is missing in the other termites.

TYPES OF TERMITES

For all practical purposes, we have three types of termites in the continental United States: dampwoods, drywoods, and subterranean. Dampwood termites locate their colonies in damp, decaying wood, but once established they can extend their activities into sound and even relatively dry wood. Drywood termites establish their colonies and continue to live in undecayed wood with little moisture. Colonies of both these kinds of ter-

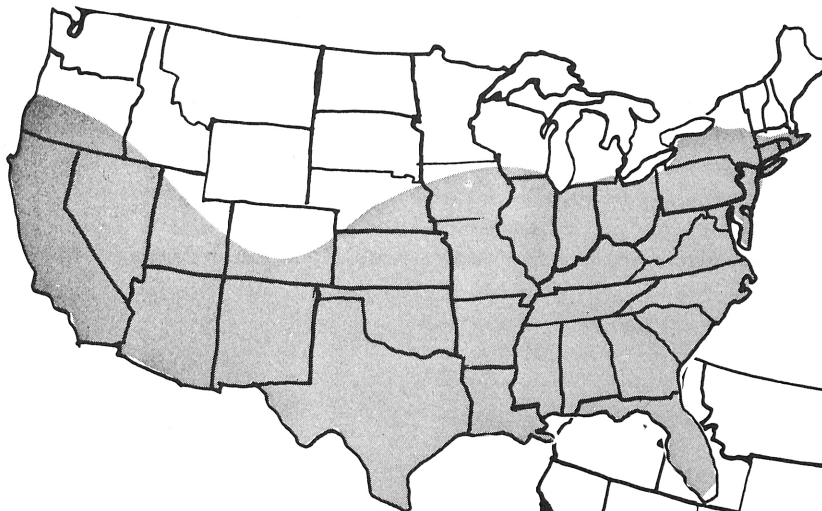


Figure 1.—Relative hazard of subterranean termite infestation in the United States is indicated by red area (from Johnston et al. 1972).



Figure 2.—Map showing northern limit of recorded damage by drywood or dampwood termites in the United States (from Snyder 1950).

Table 1.—Feeding (mg/8 weeks) on 11 species of wood by the Formosan termite, *Coptotermes formosanus*, and the eastern subterranean termite, *Reticulitermes flavipes* (from Smythe and Carter 1970).

Wood	<i>C. formosanus</i>	<i>R. flavipes</i>
Loblolly pine	381	493
Slash pine	367	270
Sugar maple	455	113
Western larch	167	81
Black walnut	74	59
Redwood	43	37
White oak	22	20
Black cherry	12	18
Baldcypress	19	17
Douglas-fir	107	14
Ponderosa pine	20	14

Table 2.—Feeding (mg/8 weeks) by the eastern subterranean termite, *Reticulitermes flavipes*, on five species of decayed and nondecayed wood (from Smythe et al. 1971).

Wood	Decayed	Nondecayed
Sugar maple	726	438
Loblolly pine	706	436
Slash pine	701	508
Western larch	669	335
Ponderosa pine	660	333
Average	692	410

Table 3.—Consumption of wood by theoretical colonies of the Formosan termite, *Coptotermes formosanus*, and the eastern subterranean termite, *Reticulitermes flavipes*.

	<i>C. formosanus</i>	<i>R. flavipes</i>
Wood consumption rate (mg wood/gram of termite/day)	23.4	33.2
Weight of worker (mg)	3.79	2.50
Wood consumption/termite/day (mg)	0.89	0.083
Estimated number of workers/colony	350,000	60,000
Wood consumption/colony/day (grams)	31.04	4.98
Days to consume one board foot of pine ¹	38	236

¹ This calculation assumes that pine weighs an average of 0.5 gram/cc with 2359.7 cc/board foot or 1179.9 grams/board foot.

mites are confined to the wood. Subterranean termites nest in the soil and ordinarily must maintain contact with moist soil. When feeding on dry wood above the ground, these termites maintain a humid environment in the wood by constructing "shelter tubes" from the soil to the wood and lining their galleries within the wood with fecal material. These differences in nesting habits require different techniques for both prevention and control.

Subterranean termites are found in every State except Alaska (Fig. 1). Years ago termite damage was concentrated in the southern half of the United States. Now, however, with more and more homes having central heating, subterranean termite damage is becoming more common in the Northern States. Drywood and dampwood termite damage is mostly restricted to the Southern States, especially Florida, Arizona, California, and Hawaii (Fig. 2). However, drywood termites are easily distributed around the United States because they can infest commonly transported articles such as boxes, crates, and furniture. Moreover, their small colonies can tolerate long periods of low moisture.

LIFE CYCLE

The life cycle of termites is unique among the insects. Nonsocial insects generally undergo either incomplete or complete metamorphosis (Fig. 3). In the incomplete life cycle, a nymph hatches from the egg and molts, or sheds its skin, several times as it grows into an adult. Even the first nymph resembles the adult insect somewhat. Grasshoppers and cockroaches undergo this type of development. In the complete life cycle, a larva hatches from the egg and molts several times as it increases in size. Larvae are quite different in appearance from the adult and require a pupal stage during which the insect rearranges its cells

The termite undergoes incomplete metamorphosis but differs substantially from the other insects because it exhibits polymorphism, or has many forms. The main forms are egg, larva, reproductive nymph, soldier, worker,¹ alates (also known as swarmers), and supplementary or replacement reproductive. For example, in *Reticulitermes*, the most common subterranean genus in the United States, larvae can molt into either a worker, soldier, reproductive nymph, or supplementary reproductive, depending on the needs of the colony (Fig. 4). Likewise, workers can change into soldiers, nymphs, or supplementary reproductives; nymphs to alates or supplementary reproductives and possibly even to soldiers. The most intriguing fact about termite metamorphosis is that termites have the ability to "grow" backwards. In other words, a nymph that has begun to develop wing buds may actually lose them with additional molts and go back to the worker stage. Workers may molt without increasing in size or may actually become smaller. Soldiers, alates, and supplementary reproductives are terminal castes and cannot undergo further molts. The important thing to remember is that most of the individuals in a termite colony are adaptable. If the colony "needs" more soldiers, there will be an increase in the incidence of soldier molts by larvae and workers.

New termite colonies can be started from an initial male and female pair (incipient colony) or from an isolated (orphaned) portion of a large colony. Pair formation occurs after the flight of the reproductives (see Fig. 4). Mated pairs usually begin laying eggs immediately; 10 to 12 eggs are in the initial batch. The second and subsequent batches

INCOMPLETE METAMORPHOSIS

EGG $\longrightarrow$ NYMPH₁ $\longrightarrow$ NYMPH₂ $\longrightarrow$
ADULT $\longleftarrow$ NYMPH_N $\longleftarrow$

COMPLETE METAMORPHOSIS

EGG $\longrightarrow$ LARVA₁ $\longrightarrow$ LARVA₂ $\longrightarrow$
PUPA $\longleftarrow$ LARVA_N $\longleftarrow$
ADULT

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graph TD
    FP[FOUNDING PAIR] --> E[EGG]
    E --> L[LARVA]
    L --> S[WORKER]
    L --> N[NYPH]
    L --> SR[Supplementary & Replacement Reproductives]
    SR --> S
    SR --> N
    SR --> E
    S --> N
    N --> A[ALATE]
    A --> F[FLIGHT]
    F --> P[PAIRING]
    P --> E
    A -.-> S
  
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The diagram illustrates the life cycle of the honey bee. It begins with a **FOUNDING PAIR** leading to an **EGG**. The **EGG** develops into a **LARVA**, which then branches into three paths: **WORKER**, **NYPH**, and **Supplementary & Replacement Reproductives**. The **Supplementary & Replacement Reproductives** can further develop into **WORKER** or **NYPH**, or return to the **EGG** stage. The **WORKER** and **NYPH** stages both lead to the **NYPH** stage. The **NYPH** stage leads to the **ALATE** stage, which then leads to **FLIGHT**, **PAIRING**, and finally back to the **EGG** stage. A dashed arrow indicates a feedback loop from the **ALATE** stage back to the **WORKER** stage.

Figure 4.—Generalized life cycle of *Reticulitermes*.

of eggs are larger than the first and may number 30 or 40. The third batch is laid at about 9 months, after which egg laying becomes more frequent and colony development accelerates. At the end of a year a colony may have grown to only 75 individuals because not every egg laid hatches nor does every larva reach maturity. Very few of the reproductives that fly each year ever pair up and establish a new colony; and very few of the colonies established ever reach maturity.

Termite colonies can also reproduce by division. Colonies often send workers to look for new food sources. If a new supply is found, then more individuals are recruited to the site. After a while a subcolony is established with a continuous exchange of individuals between this group and the main portion of the colony. Then, for any number of reasons, the subcolony may be cut off from the mother colony, and the exchange of individuals terminated. This subcolony can produce its own reproductives

(Fig. 4) and develop rather rapidly as an independent colony. Some Forest Service researchers believe colony division to be the principal mode of dispersal in northern areas where the winters are too severe for an incipient colony to survive.

The ecology and behavior of termites — a subject not usually covered in discussions of termite biology — offers new and useful insights to the pest control operator. I have worked in this field of research for the past 5 years, mainly with the termites of the desert Southwest. Since all of you are concerned primarily with subterranean termites, I will try to limit my discussion to the *Reticulitermes* species and their relatives.

FORAGING

Since subterranean termites usually do not build their nests in wood, they must forage for food away from the nest. In most parts of the country, foraging is essentially curtailed by winter or extremely dry periods. However, in Arizona

several species can forage year-round, though the intensity of foraging varies with the season. My colleagues and I at the University of Arizona used a sampling grid of 1200 rolls of toilet paper to see how weather affected foraging (Fig. 5). The number of foragers generally increased with increasing temperature. Foraging was minimal from December to February, moderate in spring and fall, and high but erratic during summer (Fig. 6). From October through December, when temperature under the toilet paper rolls was consistently below 68°F, rainfall appeared to have little effect on the number of foragers. However, during the hot summer months of June through September, even a slight amount of rain increased the number of foragers, provided the mean temperature did not rise above 92°F. Above this temperature, even with rainfall, foraging numbers plummeted. These optimum conditions for foraging — warm temperatures and high soil moisture — are usually present under and around buildings.

FEEDING

Termites do not like all woods equally well. One of the best ways to assess wood preference is to present termites with several types of wood and see how much of each wood they eat. Forest Service research in Gulfport, Mississippi, demonstrates that the Formosan termite, *Coptotermes formosanus* Shiraki, prefers woods such as sugar maple, slash, and loblolly pines over white oak, redwood, or ponderosa pine. Likewise, the eastern subterranean termite, *Reticulitermes flavipes* Kollar, prefers slash and loblolly pine over a variety of other woods (Table 1). Not only does the type or species of wood matter, but the condition of the wood is important also. Decayed wood is eaten faster and preferred over sound wood (Table 2). Termite workings in the wood increase its moisture content and

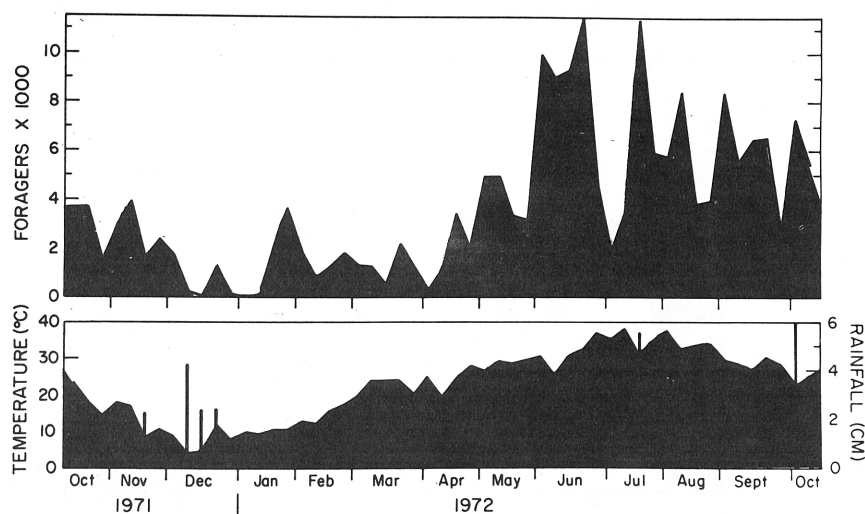


Figure 6.—Seasonal foraging intensity of *Heterotermes aureus* (Snyder) and accompanying temperature and rainfall on the sampling grid (see Fig. 5). Foraging numbers represent the sum of 1200 observations each day. Temperature is the average under the toilet paper rolls over a 24-hour observation period; rainfall is a weekly total (from Haverty 1974).

facilitate decay. Therefore, it is no accident that termite damage in a home is often associated with decay.

The major species of subterranean termites in the United States all consume wood at about the same rate; that is, somewhere in the neighborhood of 2 to 3% of their body weight each day. What really makes some species potentially more voracious than others is the environment in which they live (termites eat more wood when conditions are optimal over a longer period of time), the size of the insect (larger insects eat more wood), and the number of insects (more insects eat more wood). For these reasons, you would expect a colony of the Formosan termite to be more destructive than a colony of the eastern subterranean termite.

An average, mature colony of the eastern subterranean termite would probably contain about 60,000 workers (Table 3). Under ideal conditions, which are usually found under and in the walls of homes, such a colony will consume about 5 grams of wood each day. This is less than 1/5 of an ounce of wood. At this rate it would take this colony about 157 days to totally consume a 1-foot length of a pine 2x4.

The Formosan termite usually has many more individuals in its colonies. A mature colony could easily contain 350,000 workers, which will consume about 31 grams, or a little more than 1 ounce, of wood each day. Thus, it would take them only 25 days to totally consume a 1-foot section of a pine 2x4.

Digestion of wood really begins before the termites take their first bite. Decay fungi in the wood break down cellulose into smaller units. Termites can digest sound wood, but the decay fungi make their work much easier. Termites need the help of protozoa and bacteria in their gut to digest wood. What's more, termites need all the normal protozoan species in their gut. Experi-

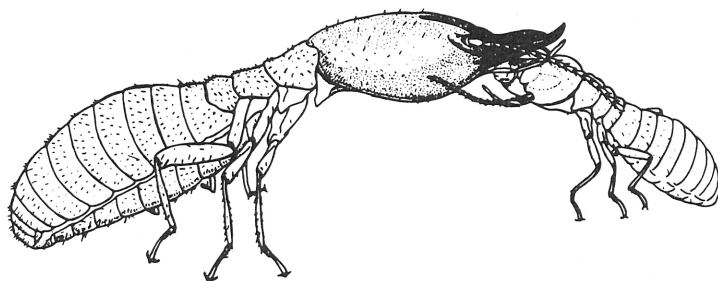


Figure 7.—Small worker of *Bellicositermes natalensis* (Haviland) giving stomodeal food to a large soldier (from McMahan 1969. Used with permission of Academic Press).

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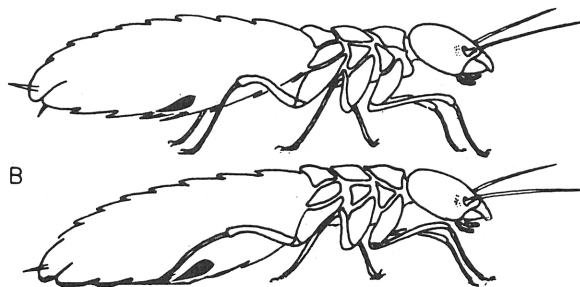


Figure 8.—The nymph of *Zootermopsis nevadensis* (Hagen) lays odor trail upon being stimulated. The location of the sternal gland on the lower portion of the abdomen is indicated by cross hatching in this individual, which is shown in both resting (a) and trail-laying (b) posture (from Wilson 1971. Used with permission of the Belknap Press of Harvard University Press).

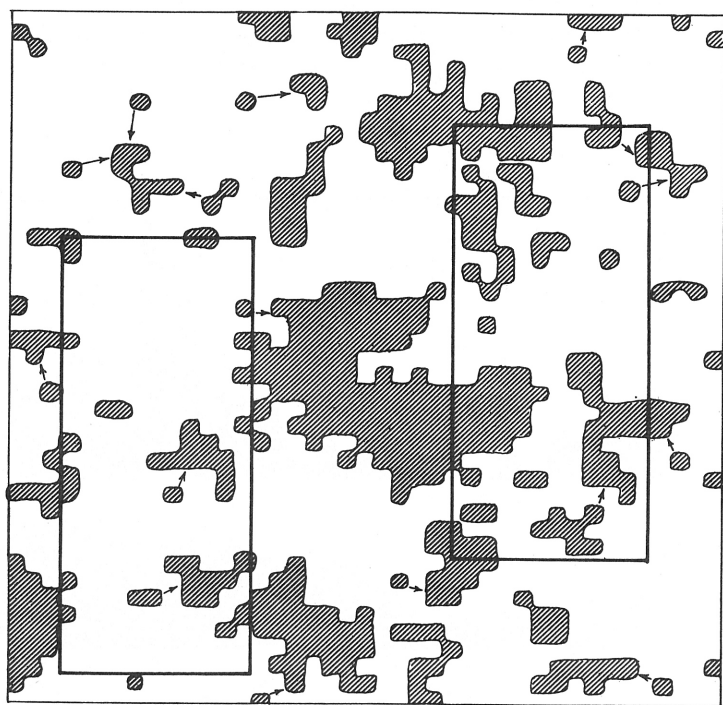


Figure 9.—Foraging territory pattern and distribution for individual colonies of *H. aureus* (shaded areas) on sampling grid of toilet paper rolls (see Fig. 5). Rectangles simulate a house slab covering approximately 2400 square feet (after Haverty et al. 1975. Used with permission of Entomological Society of America).

ments in our Gulfport laboratory show that when one species of protozoa is removed the termites begin a downhill slide toward death.

COMMUNICATION BY TROPHALLAXIS

Communication within a termite colony is extremely important to maintain efficient social integration and division of labor. One of the chief means of communicating is trophallaxis, or the mutual exchange of nutrients between colony members. Trophallaxis permits the efficient use of nutrients, recognition of colony members, distribution of chemicals involved in caste regulation, and the transfer of cellulose-digesting protozoans. There are two methods by which termites exchange food, from the mouth, or stomadeal feeding (Fig. 7), and from the hind gut, or proctodeal feeding. Many members of a termite colony cannot feed themselves; so the only way they can obtain food is to solicit it from members that have it.

Each colony has its own characteristic odor or "taste," if you will, by which members recognize each other. This odor is probably acquired from whatever they are eating and possibly from some chemicals produced by the reproductives. When a forager comes into the nest area from the outside, it is closely inspected by other members of the colony. If this outsider does not "smell" or "taste" right, it is usually quickly killed.

The proportion of the castes in the colony is regulated chemically. The different dependent castes, such as soldiers and reproductives, produce chemicals that are passed around by trophallaxis. These chemicals inhibit the production of additional soldiers or reproductives. If there are too many soldiers, for example, there will also be too much of the soldier-inhibiting chemical(s) being passed around. Termites react to an increase in this chemical by killing some of the excess soldiers and thereby maintaining the proper balance of the different castes.

When termites shed their skin during the growth process, they also get rid of their entire hindgut contents, including all the protozoa they need for digesting wood. As I mentioned earlier, without these protozoa termites soon die. Therefore, to get a new supply of protozoa they need to do some proctodeal feeding. It may not seem very pleasant, but it is necessary.

So as you can see, this exchange of food and chemicals is important to the functioning of a colony. It is important to us as researchers too because it is a method by which we might distribute some control agent, an insecticide or even an antibiotic to eliminate the protozoa, throughout the colony.

COMMUNICATION BY TRAIL LAYING

Communication also goes on outside the nest area. When subterranean termites locate food, the foragers go back to the nest to recruit other workers. The successful forager tells other workers where the food is by laying a trail.

Along the underside of a termite's abdomen is a gland called the sternal gland (Fig. 8). This gland produces a chemical (or chemicals) which affect(s) the behavior of other termites in many ways. When a forager encounters a tasty source of food, it quickly returns to the nest dragging its abdomen along the surface. While dragging the abdomen, the termite extrudes a trail from the sternal gland. When another termite encounters this chemical trail, it follows it to the new food source.

These trails do not last forever. They slowly dissipate unless they are reinforced. If a recruited forager also finds the new food source tasty, it quickly returns to the nest dragging its abdomen, thus reinforcing the trail. When the food is totally exploited, the returning termites probably no longer drag their abdomens and the trail deteriorates.

POPULATION BIOLOGY

The majority of the population biology work on termites has been

done in Africa and Australia, where the termites build large mounds that are easy to observe. In the United States, the most common type of nest system is the subterranean type. It consists simply of a network of galleries extending into the ground and enlarged in places into more spacious chambers. Since these nests have no sharp boundaries and the location of the chambers and galleries varies at different times, the study of whole colonies and populations is difficult.

In Arizona we used our toilet paper grid (Fig. 5) to get estimates of the size and density of colonies and of the foraging territory for one subterranean termite species, *Heterotermes aureus* (Snyder) (Haverty et al. 1975). Such a study has never been attempted anywhere else in the United States. In this desert grassland we found an estimated 77 colonies per acre, each having a foraging territory of about 135 square feet (Fig. 9) and an average of 22,632 individuals. This foraging territory is not as spectacular as that of the Formosan termite, which can cover about 1 1/2 acres with galleries extending from 200-400 feet out from the main colony (King and Spink 1969).

What we found out is not only interesting from a biological standpoint but should also be of interest to the pest control operator. Consider if you will the possibility of building a home on our study site without first pretreating the soil. If a homebuilder places a slab with an area of 2,400 square feet on either of the two locations shown (Fig. 9), he would expose it to 11 or 12 colonies containing over 250,000 hungry termites. All the natural wood should have been cleared before the slab was poured; therefore, all the termites have left to eat is the wood in the house built above them. This bit of ecological work emphasizes the importance of pretreatment.

As research on termite ecology and behavior progresses, we hope to develop new control techniques to supplement or replace present procedures. What I have discussed here are some of the avenues we will try.

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