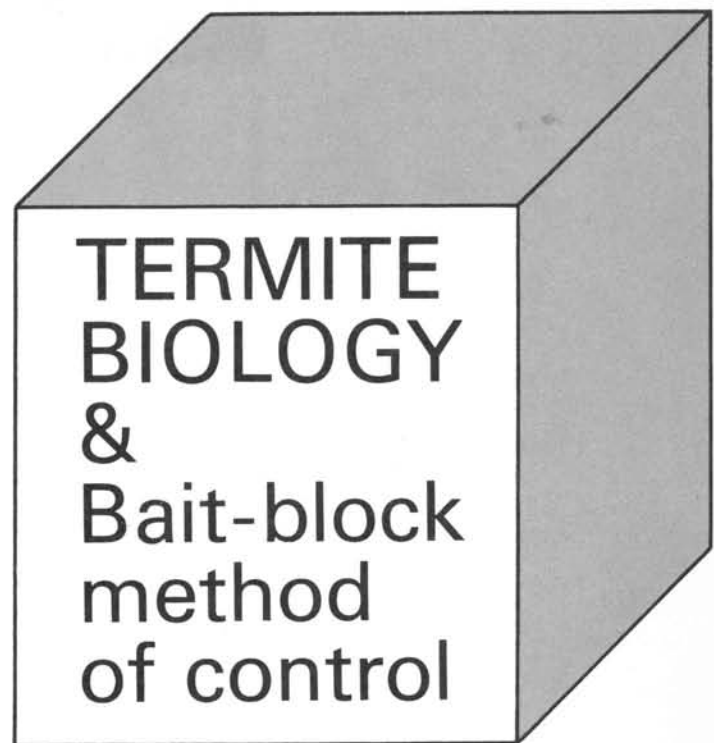


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# Termite Biology

The general biology of termites has been well documented (see Snyder 1956, 1961, 1968; Krishna and Weesner 1970). Previous publications of this Station (Turner and Townsend 1936, 1939; Turner 1949, 1961, 1968; Beard, 1974) have discussed the eastern subterranean termite and suggested methods of control.

Termites are represented in Connecticut by a single established species, the eastern subterranean termite (*Reticulitermes flavipes* (Kollar)). Among Connecticut insects of economic importance, the termite has few rivals, but the extent of its damage to structural wood or other cellulosic materials is difficult to appraise. More and more dwellings are being constructed in woodlands—the natural home of the termite—, and existing structures in areas long modified from the original habitat have served as termite preserves from which more colonies can disperse.

Current control methods emphasize the placement of a chemical barrier between infested or threatened wood, upon which termites feed, and the soil, where termites obtain necessary moisture. Although techniques of treatment may require special equipment and skills, the biological principles upon which treatment is based are simple. Soil treatment around and under a building with a persistent insecticide is sometimes ill-advised because of possible contamination of water resources and becomes increasingly undesirable as the ecological consequences become better understood.

The need for alternative control measures is great. A most promising method is a bait-block method described by Esenther and Gray (1968) and Esenther and Beal (1974) for area control of termites. This bulletin reports a modification of this technique applied to more discrete types of infestation. Because successful application of this method requires more detailed information about termite biology than has been available, studies are also reported that pertain to members of the termite colony, their feeding behavior, social relationships, caste development,

colony founding, foraging activity, natural enemies, and other hazards.

#### Materials and Methods

For laboratory use most colonies were taken from stumps or logs in woodlands, but some were from infested buildings. Stock colonies were maintained in containers of various sizes, and supplied with food and moisture. Three forms of food material served experimental needs. Suitably moistened cellulose in the form of filter paper, cellucotton, or toilet tissue was used. Wood was used in the form of partially decayed blocks, approximately 5 cm cubes, prepared from freshly cut tulip tree (*Liriodendron tulipifera* L.). This is a low density wood especially acceptable to termites when partially decayed (Esenther and Gray 1968). A kerf was sawed through the center to a depth of 4.5 cm to increase the surface area of each block and to provide a sheltered crevice for termites. Moist sawdust from mixed hardwoods, including some partially decayed, was used as a medium to provide moisture and food simultaneously. When sawdust was not used, soil or a soil substitute provided moisture.

Experimental colonies were maintained appropriately for the particular situation, as will be discussed. Special techniques will also be described as they are applicable.

#### Members of the Colony

Termite colonies comprise members of castes that differ both in appearance and function. The simple functional classification of workers, reproductives, and soldiers has some practical value, but is unsatisfactory in suggesting developmental relationships. On the other hand, a complex classification of all possible castes may not apply to all species. Consistent with present terminology (Miller 1969, Wilson 1971) the following members are found in colonies of *R. flavipes*.

*Larvae* are immature individuals that have no evidence of wings or wing pads. They emerge from eggs and molt an

indefinite number of times. Up to the third instar they cannot feed themselves, and must be fed by older larvae. After a molt, even an older larva does not feed for several days. Thus, young larvae or molting larvae are dependent on older ones. Later stage larvae are independent and may retain larval form or differentiate into other castes; a few change into soldiers, passing through a pre-soldier form; still others may differentiate into nymphs or ergatoid reproductives. Larvae are the predominant workers and are chiefly responsible for feeding dependent individuals, for foraging, and for building and repairing shelter-tubes.

The *soldiers* are easily identified by their large heads with prominent mandibles. They are straw-colored with a darker head. The pre-soldier form is recognizable as it shows features of the soldier but is less developed and less pigmented. Because soldiers are strong defenders against raiding enemies in some species, many investigators have assumed this to be equally true for *R. flavipes*, but King (1897) reported soldiers are inept at defense. Thus, soldiers appear to be a relic of evolutionary development in this species.

*Nymphs* differ from larvae in possessing wing pads and being whiter and larger. Intermediate between the larvae and mature reproductive forms, they molt several times, each time acquiring more prominent wing pads. Nymphs have often been mistaken for secondary reproductives.

The final molt of the nymph into a mature, *primary reproductive* is dramatic, when dark pigmentation develops. The mature reproductive appears as a black-bodied insect with long, grey, gauzy wings. This is the caste that gregariously leaves the colony in dispersal swarms.

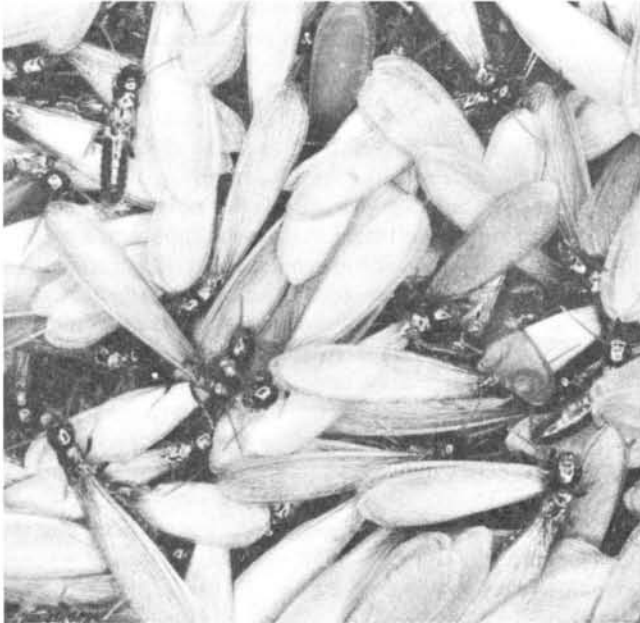
Fig. 2 Termite nymphs



Fig. 1 Termite larvae (workers) and soldiers



Fig. 3 Swarming adult termites



Supplementary or *replacement reproductives* may develop. They may be *ergatoid reproductives* resembling larval forms without wing-pads, or *nymphoid reproductives* derived from nymphs and retaining wing-pads. These forms are about the size of nymphs, but are straw-colored and have distinctive keel-shaped (laterally compressed) abdomens initially; later the female abdomen may be distended like that of a gravid primary queen.

Higher termites are said to possess a definitive worker caste, whereas the lower termites, of which *R. flavipes* is a representative, are said to possess a *pseudergate* (false worker) caste. The pseudergate is a larval form that functions as a worker but is competent to differentiate into other castes. It has not been clearly established whether *R. flavipes* has definitive workers or not, but some evidence will be presented to show that it does. If a definitive worker caste does exist, the term larva may be inappropriate except for individuals that have the capacity to differentiate. At present, competency for differentiation cannot be visibly recognized. For practical reasons it is important to know the potentiality of isolated groups of individuals for developing reproductives and thus regenerating a complete colony.

#### Colony Development and Caste Differentiation

New colony formation is initiated by the dispersal flight of swarming, mature, winged reproductives including both males and females. These swarms may number into the thousands of individuals. Maturity of these individuals is not reached simultaneously, but emergence occurs during a very short period, usually during the morning hours. More than one swarm can come from one infestation at different times. Just what triggers the emergence of so many individuals at one time is not known, but it is presumed to be a combination of environmental conditions. Mature termites have developed in December and January in this laboratory but in Connecticut buildings, swarms usually

Fig. 4 Gravid primary queen (dark) and gravid ergatoid reproductive



occur first in February, with peak emergence in March and April. Swarming occurs later in more exposed areas.

In buildings, swarms emerge from cracks and crevices not too far from the site of infestation. Swarming termites are evidence of the presence of a colony, but they indicate its size and age only in a relative way.

Although in some species winged adults develop only in large established colonies, this is not so with *R. flavipes*. Snyder (1915) quoted Joutel who kept a colony of only 2 or 3 doz. individuals, some of which matured and swarmed each year. In this laboratory, one group of 20 larvae was reduced to 7 larvae and 4 nymphs 6 mo. after isolation; after another 6 mo. the "colony" consisted of 4 larvae, 1 soldier, and 1 mature reproductive. Other isolated larval groups, few in number, have also produced one or a few winged adults, usually unpredictably. Out of some 14 isolated groups of nymphs, none survived beyond 6 mo. and none produced any winged forms or nymphoid reproductives. This suggests some requirement for differentiation that may be supplied by larvae.

Most winged termites emerging within a building fly toward the light and die in their efforts to find breeding sites. It would be rare for any of these to start a new colony indoors. Such termites emerging to the outdoors are highly vulnerable to predation by birds, ants, and other insectivores. Thus the probability of their finding suitable sites for colony founding is low. After what is usually a short flight, the termites lose their wings, the female assumes a "calling" posture by raising her abdomen, and one or more males may follow her in tandem. This behavior sequence often precedes the finding of a nesting site and subsequent mating.

Laboratory observations suggest that pairs of termites are fastidious in choosing sites for new colonies or are inherently weak at this stage. In several hundred trials with different media that included soil and wood or wood products, all termites failed to survive and reproduce. For example in one trial, 6 materials (sawdust, wood chips, 2

forms of pine bark, redwood bark, and wood blocks, each replicated 6 times, were placed in a Latin square on soil in a greenhouse bench and covered with plastic containers. The soil was kept appropriately moist. Ten winged termites were placed inside each container. Not a single living termite was found 3 mo. later.

On the other hand, one technique has proved reliable in starting incipient colonies. Moist sawdust from mixed hardwoods, some of which were partially decayed, is placed in screw topped vials. When a tandem pair is placed in such a vial, the probability is high that the pair will survive, reproduce, and start a colony. A moist, but not wet, environment must be maintained.

One or 2 eggs may be laid promptly after mating, followed by 10 or 12 others within a few days. Snyder (1915) noted that eggs of *R. flavipes* hatched in 2 wk. Bready and Friedman (1963) found that eggs from secondary reproductives hatched in 26 to 29 days at 27°C. I have observed that eggs require 4 wk. or more to hatch at 25°C.

The initial brood is cared for by the founding pair, and another clutch of eggs is laid after the young larvae have reached the third to fourth instar. These larvae help care for the new brood. The second and subsequent clutches of eggs are larger than the first and may number 30 or 40. Between each of the first three clutches of eggs is a time interval until the larvae reach the third or fourth instar. After the third clutch, or at colony age of about 9 mo., eggs are laid more frequently and colony development accelerates.

Caste differentiation can begin early in colony development. In each of 10 out of 13 incipient colonies, a single soldier developed at the fourth instar in the initial group of brood. This occurred as early as 2 mo. after the first eggs hatched. No other obvious differentiation occurred during the first year.

Ten incipient colonies after 1 yr. were remarkably similar and were constituted as shown in Table 1.

Table 1. Composition of 1-yr-old incipient colonies

Colony	Reproductives	Soldiers	Independent larvae	Dependent larvae
1	2	1	51	22
2	2	1	34	12
3	2	1	35	12
4	2	0	40	18
5	2	1	32	19
6	2	1	23	9
7	2	1	37	15
8	2	1	35	11
9	2	1	42	25
10	2	0	38	13

The colony can be self-sufficient as long as the founding pair produces larvae that can forage and care for their nest-mates. The other castes must develop to fulfill the biologic urge to multiply and disperse.

The soldier caste is definitive—its members do not

differentiate further. As mentioned, a relatively small proportion of the colony is of this caste. Just what limits their numbers is not known, but pheromones are likely the controlling agent.

An orthogonal development of larvae would lead through a series of instars of increasing size to the differentiation of nymphs showing shorter, then longer wing-pads, and to the final molt into sexually mature winged adults. Some larvae continue to molt, but retain their larval appearance and fail to develop wing-pads. From some, ergatoid reproductives develop, presumably in the absence of primary reproductives. Similarly, nymphoid reproductives presumably develop from early stage nymphs. In these studies, this caste has been seen only once, when large numbers were developing into winged forms in a colony preparing to swarm. It appeared as if a development block had occurred to shunt many individuals into this form instead of permitting complete development to winged sexuals. When these were retained for observation, many died, but the survivors did not lay eggs (for at least 6 wk.) indicating they were not functional reproductives.

More primary reproductives than a single pair can live compatibly in one "nest", but according to current theory (see Miller 1969, Wilson 1971) these primary forms secrete inhibiting hormones that prevent the development of replacement reproductives. When primary reproductives die, or when larval termites become isolated from their colony, the absence of this hormone permits the differentiation of replacement reproductives. This concept has been accepted largely on the basis of Lüscher's work on *Kaloterms flavicollis* (Fabricius) (see Miller 1969). Little work has been done on caste differentiation in *R. flavipes* since that of Thompson (1917), who believed that individual termites were genetically predetermined to develop into certain castes. This view has gone unsupported, and it is reasonable to conclude that this species generally develops as do other species of *Reticulitermes* (outlined by Miller 1969). Even when hormones regulate development of reproductives, all larvae are not equally competent to become sexually mature.

This ability to acquire reproductives by isolated colonies requires assessment for practical reasons to be discussed. Complete lability would permit all isolated larvae to differentiate into reproductives, but this does not happen. A number of field-collected colonies without reproductives and of different sizes have been brought into the laboratory and maintained for over a year without reproductives developing. In such cases larvae that die are not replaced. In a more specific test, a reproducing colony was established in a 5 l plastic container with moist soil and adequate wood reserves. Connected to this by soil-filled plastic tubes were smaller, satellite plastic containers also containing suitable media. The satellite sites were invaded by foraging termites, which were isolated and maintained separately. In only 2 out of 6 isolates did reproductives appear within 6 mo. after separation from the parent colony. The number of individuals in each isolate was not determined.

In another test (A) in which different numbers of larvae

were isolated in soil media, most isolates died, although a few acquired reproductives after long delay when the original number was 50 larvae or more. Sawdust medium permitted better survival, and so 40 isolates (Test B) were prepared (June 10, 1973) with 10 replicates of 20, 40, 80, and 160 larvae each. After 6 and 12 mo., reproducing groups were as indicated in Table 2. Reproduction was considered accomplished only if fertile eggs were deposited. Reproductives may have been produced in other groups, but eggs were either absent or failed to hatch.

Table 2. Number of isolated groups developing reproductives

No. of groups	No. larvae per group	Number reproducing within	
		6 mo.	12 mo.
10	20	0	3
10	40	1	9
10	80	4	7
10	160	5	8

The greater the number of individuals present in the isolate, the greater is the chance of reproductives developing more quickly. Given a longer time, smaller groups may catch up. The potential for differentiation is not uniform, but competency and factors triggering differentiation are not understood. These data, together with observations of other isolated larval groups maintained for over a year without developing reproductives, are evidence that a definitive worker caste may exist that has lost its ability to differentiate.

This variable lability need not be genetically determined as Thompson (1917) maintained, but may relate to physiological events such as the stage in the molting cycle as demonstrated by Lüscher (reviewed by Miller 1969, Wilson 1971) with *K. flavicollis*. Judging from Lüscher's (1953) observations, larval isolates of *K. flavicollis* develop reproductives much more readily than do isolates of *R. flavipes*. Thus we should not assume that the regulating mechanisms are the same.

The reluctance of larval isolates (in Test A) to produce reproductives during winter months suggested a seasonal variation in lability. This was explored by repeating Test B using larvae isolated October 5, 1973 from field-collected termites (Test C). Among the 40 isolated larval groups (10 replicates of 20, 40, 80, and 160 larvae), no differentiation and no reproduction occurred within 6 mo. (After 8 mo. one group of 160 larvae began reproduction.) During the same time period, additional groups in Test B began reproduction indicating that the condition of larvae in Test C rather than the rearing environment accounted for the lack of differentiation. Diapause is a likely explanation.

Many writers have believed that nutrition may play a role in differentiation, and this may indeed be true of *R. flavipes* as has been proposed by Esenther (1969) who also noted seasonal variations in caste composition. Paralleling the larval isolates of Test B, two groups each of 20, 40, and 80 nymphs were isolated. After 6 mo. no differentiation

had occurred, although nymphal molts may have gone unnoticed. Other groups of isolated nymphs have also failed to differentiate. This indicates that nymphs are less labile than larvae, and nutrition could be a possible reason; feeding behavior is different in the two stages, as will be discussed later. The influence of larval nest-mates on nymphal differentiation remains to be determined. In fact, caste development in this species should be critically restudied.

If replacement reproductives develop only in the absence of primary reproductives, it does not follow that primary reproductives develop only in the absence of secondary sexuals. In one isolated group starting with 160 larvae, 1 replacement reproductive developed prior to the appearance of 3 winged adults. Being confined, the latter lost their wings and adapted to life in their "home" colony. The possibility of successful mating between reproductive castes does not seem to have been investigated. Literature records the question, but not the answer, as to whether offspring of replacement reproductives can develop into primary reproductives. Circumstantial evidence strongly indicates that such development is routine.

The ability to produce replacement reproductives allows colonies of *R. flavipes* to fragment and for different isolates to become independent colonies. It is not unlikely that this is a more common method of colony formation than that of starting from a founding pair.

A third method of colony founding (Harris 1958) is for primary reproductives to migrate with a portion of the colony from one site to another, leaving the residual colony to develop replacement reproductives. This has not been observed in *R. flavipes*, and its occurrence is unlikely.

#### The Nest of Established Colonies

It is commonly believed that the subterranean termite nests in the soil and forages in wood. If by "nest" is meant a kind of brood chamber or nursery occupied by reproductives and their developing offspring, soil sites are not essential and may be less common than sites within wood when the colony is well established. Soil locations for a brood chamber have not been clearly demonstrated, but breeding sites in wood are frequent. In a thriving colony, multiple sites may be present, interconnected by channels for service by foraging members of the colony. The breeding site is not distinctive structurally, but in each may be found reproductive forms, the developing young, and also members of other castes. Other channels and feeding sites are occupied predominantly by older larvae, but soldiers and sometimes nymphs are present.

Evidence for soil nesting sites was sought in soil of a greenhouse bench where termite infested logs were on the surface. The soil area was 85 x 155 cm, 13 cm deep. The infestation had been in place 7 mo., and some termite traffic could be seen from soil to log. All soil was carefully examined by moving small portions with a table fork. No concentration of termites nor "nest" was found; only 15 foragers and 1 soldier were observed. On the other hand, reproductive centers with reproductives, attendants, and

young larvae were present within the log.

The soil is presumed to be a winter refuge for termites living in exposed areas (Snyder 1935, Esenther 1969) as well as a source of moisture, but the daily and seasonal activities of termites below ground have not been adequately studied. Termites can survive the winter in above-ground nest sites. This was shown by enclosing infested logs in plastic bags and placing them outdoors on a metal sheet; thus moisture would be retained but termites would not reach the soil. Placed in October while termites were still active, the logs were brought indoors at the end of January. Although ambient air temperatures had been as low as  $-17^{\circ}\text{C}$ , the termites resumed activity promptly when placed on soil in a greenhouse. Esenther (1969) observed that *R. flavipes* cannot long survive temperatures of  $0^{\circ}\text{C}$ . If this is generally true, logs and stumps provide sufficient insulation to protect colonies.

The territoriality of a colony, or the autonomy of a nest may be questioned. Although most social insects maintain colony independence in this species, no antagonism has been observed when members of different colonies are mixed. When a year-old incipient colony was placed at one end of an observation box supplied with suitable wood and moisture and a year-old reproducing colony derived by fragmentation was similarly placed in the other end of the same box, both groups accepted their facilities. But within 2 days, the fragmented colony moved in with the incipient colony and the groups continued activity with complete compatibility. With such a possibility of colony admixture occurring in field conditions, a colony cannot be defined so much by its developmental history as by its communicating membership.

### Feeding Behavior

Foraging termites are almost exclusively larval forms. Soldiers sometimes accompany foragers, as they do builders of shelter-tubes, but they do not share such work and are dependent upon larvae for food. Primary reproductives can feed themselves and must provide proctodeal food to supply young larvae with required symbiotic protozoa. Later, primary reproductives and replacement reproductives come to be dependent upon larvae. Nymphs can feed themselves and can survive isolated from larvae as was shown above. But nymphs do not consume so much food material as larvae, and probably have no role in supplying nutrients to other members of the colony.

Observation of feeding behavior can be facilitated by the use of colored filter paper and of radioisotopes. Neutral red and Nile blue sulfate absorbed on filter paper and fed to termites can be seen in the gut but later appear in the urate cells and fat body to "color code" termites for many months. Filter paper colored with black India ink or black filter paper (Whatmans No. 29) can serve only as a temporary index of feeding, because it is not absorbed.

Mutual grooming, trophallaxis, and cannibalism are common within termite colonies (McMahan 1969). The extent of trophallaxis in *K. flavicollis* was evaluated by Alibert (1959) who fed termites upon filter paper soaked

with  $^{32}\text{P}$  solution without external contamination. Upon reintroducing labelled termites into the parent colony in the ratio of 1:10, she found that 40% of the total individuals were radioactive after 12 hr.; the percentage increased to 70% after 20 hr. and to 100% after 35 hr.

McMahan, (1966) using small colonies (25-200) of *Cryptotermes brevis* (Walker), introduced single individuals labelled with  $^{57}\text{Co}$  into each colony. Spread of radioactivity diminished with size of colony, but it was 100% with 25 members, and 50% with 200 members after 96 hr.

A preliminary experiment with *R. flavipes* gave evidence that trophallaxis was less prompt and less complete than reported for *K. flavicollis* or *C. brevis*. A further test was conducted as follows: To distinguish between donor and recipient termites, the group to be labelled was first fed filter paper colored with neutral red. The red-dyed termites were then fed black filter paper moistened with a solution of  $^{14}\text{C}$  labelled protein hydrolysate. Seventy red termites with black gut contents showing that feeding of labelled material had occurred, were reintroduced into the field-collected colony from which they had been taken. The colony numbered 259 larvae, 53 nymphs, 5 soldiers, and the 70 labelled larvae, or a ratio of 10 labelled to 55 unlabelled. At 24 hr. intervals samples of termites were individually smeared on planchets and evaluated for radioactivity with a gas-flow G-M counter. Only those beyond the extreme background sample were considered radioactive. Donor (colored) termites consistently showed high radioactivity. Recipient termite radioactivity is as indicated in Table 3. This experiment, confirmed by a

Table 3. Number of radioactive\* recipient termites

Recipient caste	24 hr.	48 hr.	72 hr.	96 hr.
	No. *	No. *	No. *	No. *
Larvae	10 5	10 4	10 4	10 3
Non-feeding larvae	5 0	3 0	3 2	
Nymphs	10 4	10 5	10 1	10 2
Soldiers		2 0	1 0	2 1
Total	25 9	25 9	24 7	22 6

further similar experiment, indicates that exchange of materials among the colony is not complete, and there is no essential increase in radioactive recipients after 24 hr. Metabolism and excretion of the labelled hydrolysate would limit the time for distribution by feeding, but external contamination should continue. In Table 3 a category of non-feeding larvae was indicated. Such larvae have recently molted, have empty guts, and do not ingest filter paper, either directly or by trophallaxis from donor larvae. In *K. flavicollis*, Gosswald and Kloft (1959) found that larvae do not feed, or are not fed, 2 days before and 2 days after molting. In *R. flavipes* the duration of the pre-molt fast has not been determined, but the non-feeding period may be 7 days or longer after molting.

### Foraging

Characteristics of foraging are easier to recognize than the conditions prompting it. Incipient colonies show no foraging activity, but otherwise size of colony is not a condition for foraging. Even small groups of larvae enclosed in small vials may demonstrate foraging behavior. Any size colony may forage even if it exists within a great abundance of food and has access to adequate moisture.

Foraging has two manifestations. One is subterranean tunnelling from the colony site to outlying areas in search of resources. The second is building above-ground shelter-tubes from the colony site or exposed extensions of subterranean tunnels. At the time of swarming, shelter-tubes may serve as emergence routes for winged forms. It is not known if such tubes are built specifically for emergence or relate to foraging as well.

Division of labor among larvae has not been described. It has not been demonstrated that some larvae are programmed to tunnel and build shelter-tubes while others gather food and moisture, or tend the young. If a tube sheltering food-gatherers is broken, no obvious shift in workers to repair the damage is noticeable; the same foragers seem to do both jobs. A more critical examination of division of labor of this kind needs to be made.

Subterranean foraging is difficult to study. LaFage *et al.* (1973) compared activity of two species of termite by placing a grid of toilet paper rolls, which were more effective as bait than wooden blocks, in an infested area. One species, *Gnathamitermes perplexus* (Banks) foraged widely, but superficially, whereas *Heterotermes aureus* (Snyder) foraged intensively at few sites.

A preliminary experiment on termite foraging employed a heavily infested log placed on soil at one end of a greenhouse bench. Thin (3 mm) pieces of wood 6.25, 25, and 100 cm<sup>2</sup> were placed at distances of 30, 60, 120, and 240 cm from the log. Two replicates of wood samples were placed horizontally on the surface of the soil and two replicates were embedded vertically in the soil. Placement of wood samples was random both as to size and position. Seven of the 12 samples came to be infested, but the sequence of attack showed no pattern. Only random foraging and chance finding were indicated.

In a more elaborate experiment, a large pile of old logs known to be infested was moved and the area cleaned of wood that might harbor termites. Several logs containing termites were placed as compactly as possible at one point. A quadrant of 9 radii, spaced by equal angles, was laid with wooden blocks, 1 m apart along each radius, outward for 8 m from the point source of termites. It was reasoned that prompt occupation of wooden blocks would be made by termites residing in the soil nearby, and that delayed occupation would represent foraging termites originating from the occupied blocks or the apical point source. The blocks were examined for termites at 7 to 10 day intervals from May 20 to August 29 and on two occasions thereafter. The general pattern of infestation was as illustrated in Fig. 5. The absence of a consistent pattern confirms that much

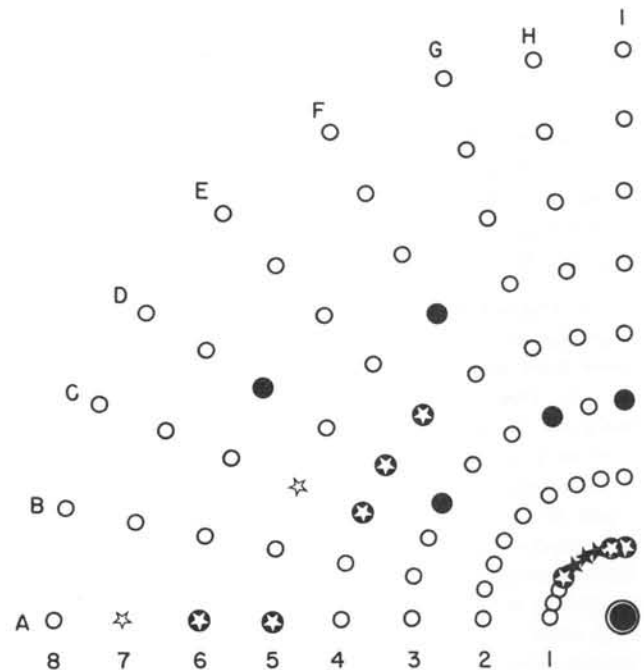


Fig. 5 Termite occupation of bait-blocks placed 1 m apart along radii diverging from point reservoir of termites

Blocks represented by:

- black circles—occupied early and consistently
- white star on black circle—occupied late, but consistently thereafter
- white star alone—occupied early, but temporarily
- black star alone—occupied late and temporarily

foraging is random. The scattered initial occupation may reflect the disturbance and dispersion when the originally infested logs were removed from the site. It is not clear whether several colonies were present or whether a single colony occupied several loci. It might be assumed that the six occupations at meter 1, all of which were delayed, represented migrants from the point source. However, the observation was made that 3 wk. after block G3 was dyed with neutral red, marked termites from there were found at F1, G1, and questionably at I1, in addition to D3. This demonstrates considerable movement by termites and emphasizes that a persistently occupied site does not represent a fixed population. Temporary occupancy of a site could mean that small groups of foragers are destroyed, find the site unacceptable, or are not joined by their colony mates.

Another similar site was prepared as above but in the form of a rectangular grid 5 x 9 m. The logs removed from the site harbored only a small population of termites and no point concentration was provided. Only 1 block out of 45 became infested, and this infestation survived only a few weeks before it was destroyed by ants.

Studies on shelter-tube building by *R. flavipes* have been few and descriptive rather than analytical (Holway 1941).



Shelter-tubes may be built buttressed and free-standing upward, free-hanging downward, and in any direction on a horizontal or vertical surface. Holway (1941) concluded that the majority of tubes were built down rather than up over foundations, but this is doubtless determined by the locus of the main colony, the environment, and the propensity of the colony to build tunnels. Certainly it is agreed that termites choose to build along edges, borders, or angles, possibly because construction is easier.

Foraging (either tube building or subterranean tunnelling) is activated by cues that are not evident to us. It occurs when there is seemingly no need, as for example away from an old tree stump that provides adequate food and moisture. It occurs when it serves no apparent purpose as seen in tube building around the edge of a pan leading nowhere even if resources are in the area. Once triggered, it seems to be a compulsive activity, somewhat directed by the physical substrate (or gravity in the case of free-standing and free-hanging tubes), and becomes rewarding only if chance or some guidance system leads to new resources. Active tube building comes to an abrupt stop at times as if the triggering cues were turned off.

It is important to know if there is a guidance system, and how it works. It is well established that termites follow trail substances secreted by the sternal gland (Stuart 1969). *R. flavipes* is no exception (Smythe and Coppel 1966a, 1966b). Holway (1941) cited the unusual instance of a colony of termites building a shelter-tube downwards over a foundation from infested timber when some of the termites moved down to the soil and built a tube upwards to join the other tube. Guidance could easily be explained by the use of trail substance.

A critical question is whether the termites sense attractive substances at a distance and can orientate to resources, or whether their search is indeed random leading to chance encounter, finding and exploitation of resources giving the appearance of "attraction". Matsumura *et al.* (1969) determined the trail substance (sternal gland secretion) of *R. flavipes* to be n-cis-3, cis-6-trans-8-dodecatriene-1-ol and that this was identical with a biologically active extract of wood partially decayed by *Gloeophyllum (=Lenzites) trabea* (Pers) Fr.). This had earlier been shown to be "attractive" to termites (Esenther *et al.* 1961). Stuart (1969) questioned the conclusion of Esenther *et al.* (1961) and Smythe and Coppel (1966b) that true attraction had been demonstrated. A few simple experiments indicate that *R. flavipes* probably does not sense "attractive" chemicals at a distance (i.e. follow a chemical gradient) other than the trail substance.

If a block of wood partially decayed by *G. trabea* is suspended over an advancing shelter-tube just out of reach of the working termites (ca 1 cm.), no vertical shelter-tube is built up to the block, although this would be no difficulty for the termites. If such a bait-block is supported at the same level in front of an advancing shelter-tube, but separated by 1 cm of air space, termites will build downward or laterally and by-pass the block even though a horizontal tube 1 cm long could easily bridge the gap. If the

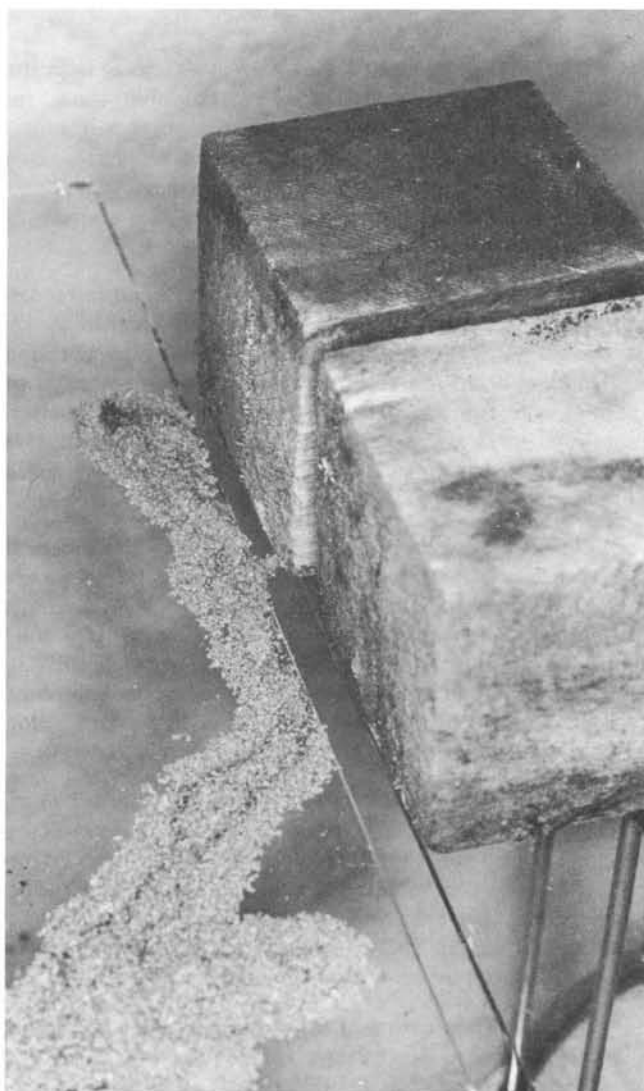


Fig. 6 Bait-blocks on glass plate at same level as glass plate supporting colony of termites building shelter-tube. Tube-building by-passes block separated by 1 cm but bridges gap of 0.5 cm

air separation between tube and block is no more than 0.5 cm, which permits termites to reach it, the tube is built directly to the block. Once an acceptable resource is found, foragers assemble and utilize the site.

Variations of these experiments and observations on shelter-tube building confirm that physical contact with the "attractant" is required, but trail laying can guide other termites to establish the site thereafter. Termites reach out to probe ahead from the end of a shelter-tube. Sometimes they reach only the length of their bodies, but they can fan out to scout the area. If a resource is found, guidance is given for changing direction of tube building if such is called for. The distance a termite can scout may be a function of the durability of the trail it can lay to insure its return to the shelter-tube. This has not been established.

Becker (1966) observed that *R. flavipes* and some other termites would follow traces made by certain ball-point

pens, and concluded that certain ink solvents, notably 2-(2-butoxyethoxy) ethanol and 2-(2-ethoxyethoxy) ethanol, mimicked the trail-following substance. I have confirmed this observation, but found only 2-(2-butoxyethoxy) ethanol to be effective. Concentration of the presented stimulus seems critical. The failure of some inks to induce trail following may be due to some interfering substance or the absence of a necessary component. This warrants further study as a simple trail-following inducing agent could be useful.

Bait-blocks do appear to attract adult termites from a distance. Concentrations of swarming termites have been found at bait-blocks embedded in the soil. Bait-blocks indoors on a tile floor near the point of emergence of winged forms harbored hundreds of termites. The termites kept to the blocks so much that they did not expose themselves in normal flight but died in place. Their death was hastened by the presence of mirex on some of the blocks. In a simple laboratory test a group of adult termites was placed with moist paper in a container that was connected to two boxes by plastic tubes. In one box a dry, partially decayed block was placed; in the other a dry, undecayed block was placed. After about 18 hr., 40 termites were found with the partially decayed block, and none with the other block. This difference is too great to be explained by random search.

#### Parasites and Predators as Natural Control Agents

**Bacteria.** *R. flavipes* does not seem to be especially vulnerable to bacterial infections.

Smythe and Coppel (1965) reported that this and other termites were questionably susceptible to infection by *Bacillus thuringiensis* Berliner, but are vulnerable to toxins produced by this bacterium.

DeBach and McOmie (1939) found *Zootermopsis angusticollis* (Hagen) moderately susceptible to infection by an unidentified bacterium and more susceptible to *Serratia marcescens* (Bizio). I have found *R. flavipes* to be naturally infected with *S. marcescens* on occasion, but usually in association with unidentified fungi.

**Fungi.** The environment of termites is favorable for fungi. They play an important nutritional role either as a direct source of food or by modifying wood to favor termite feeding.

Thaxter (1920) described *Termitaria snyderi* as a fungal parasite on *R. flavipes*, but it seemed to do no harm. *Entomophthora aphilis* and *Beauveria* (= *Sporotrichum*) *globuliferum* (Speg.) were observed by Forbes (1895) to kill *R. flavipes*. Gouger and Kimbrough (1969) found *Antennopsis gallica* Heim and Buchli on *R. flavipes* in Florida. This was apparently nonpathogenic, and so far has not been encountered in Connecticut. Smythe and Coppel (1966c) isolated externally from *R. flavipes* 7 pathogenic species of fungi. *Absidia coerulea* Bain was reported as a possible pathogen of *R. flavipes* on the basis that termites placed on culture plates of the fungus died sooner than

otherwise would have been expected (Lund and Engelhardt 1962).

Beal and Kais (1962) experimentally infected *R. flavipes* and *R. virginicus* (Banks) with *Aspergillus flavus* Link and observed 80% mortality. This fungus (and others) was found by Lenz (1969) to produce toxins detrimental to other species of termites, but the toxins of *A. flavus* reported by Beard and Walton (1971) showed no effect on *R. flavipes*.

Yendol and Paschke (1965) reported that *Entomophthora coronata* (Cost.), but not *E. virulenta* Hall and Dunn, was highly pathogenic to *R. flavipes*, causing 97% mortality 84 hr. after inoculation. Germ tubes from applied conidia readily penetrated the integument and invaded the fat body and musculature primarily, thereafter destroying other tissues.

Laboratory cultures of termites frequently succumb to fungal infections in spite of utilization of fungi and practice of nest sanitation. Fungi as primary pathogens rather than secondary invaders and their role in natural control of termites need to be more critically studied.

**Nematodes.** Banks and Snyder (1920) commonly found nematodes, determined to be *Rhabditis janeti* Lazari Duthier, *Diplogaster* (= *Mikoletzkyia*) *aerivora* Cobb., and an undetermined species, in artificial colonies of *R. flavipes*. Juvenile forms were present in the heads of apparently healthy termites, and adults were only present in sick or dead termites. Massey (1971) described two species of nematode (*Termitrhabditis fastidiosus* and *Rhabpanus ossiculum*) from *R. flavipes*. The former species was found in the gut, the latter in the head. Only immature forms were stated to be parasitic, but the biology of these nematodes was not studied.

Head-dwelling nematodes are consistently found in Connecticut termites, but site may determine incidence. From each of 17 sites, 10 termites were examined for nematodes by macerating the heads in saline solution. Although small, the nematodes are readily seen under a dissecting microscope. Of the 170 termites, 90 harbored nematodes. But a conspicuous difference was noted between termites coming from woodlands and from buildings in suburban or urban settings. Of 50 termites from buildings, only 2 contained nematodes; of 80 termites from woodland logs or stumps, 66 contained nematodes. Fifty other termites from laboratory colonies, the origins of which were not recorded, included 22 with nematodes. Termite cultures maintained in the laboratory showed evidence of losing their nematode parasites.

As discussed by Poinar (1969) these nematodes are probably not primary pathogens. Presumably the dauer stage parasite is well adapted to its host, which serves a phoretic function, and continues its life cycle only when the termite dies. Occasionally a termite, dead from causes not apparent, yields nematodes in larger numbers than usual. This suggests that accidentally or because of a larger infection, the nematode may have been the cause of death. At times the nematodes reproduce abundantly, and large numbers in the juvenile, dauer stage wave over the surface of the substrate to seek attachment to passing hosts.

*Mites.* Mite attack on termites such as by *Pyemotes* described by Weiser and Hrdy (1962) has not been observed on *R. flavipes*.

Banks and Snyder (1920) noted mite hypopi of undetermined species on heads and legs of *R. flavipes*, and other writers have commented in general on termites as phoretic agents of mite hypopi. The hypopus is a non-feeding, dispersal stage of a mite, and would not be expected to damage its carrier. On the other hand, Metcalf, Flint and Metcalf (1951) illustrated mite-carrying termites (*R. flavipes*) and commented, without stating evidence nor the species involved, that the mites killed termites.

Mites found here on *R. flavipes* were determined by R. L. Smiley, ARS, to be *Caloglyphus* sp. Hypopi are frequently found on field-collected termites, but usually in fewer numbers than can build up in laboratory cultures. If clean termites are added to culture media containing hypopi, the hypopi are stimulated to activity and promptly attach themselves to passing termites. Attachment is primarily to the head, less so to the legs, and uncommonly on the rest of the body. The hypopi may cling to the termite for weeks or even months. Molting removes the mites, but grooming and movement in narrow channels does not. Newly molted termite larvae may not immediately become infested again, but this may be a function of exposure to unattached hypopi rather than lack of attraction or possession of repellency. Although termites seem unaffected by the hypopi for long periods, there may come a time when they become less active, their mouthparts appear immobile, and after a day or two of obvious abnormality, die. Within two days, the hypopi begin to molt and continue their life cycle. The symptoms, the apparent absence of other causal agents, and the frequency of colony demise when mites are abundant all point to the mites as the cause of death. But just how the hypopi could kill is not suggested. Death of the termite doubtless provides the stimulus for mite development. Further development of attached mites can also be initiated on termites killed by pinching or poison. A degree of host specificity is likely. *Plodia* larvae, for example, do not attract the hypopi.

*Centipedes.* Centipedes are extremely frequent inhabitants of sites actually or formerly occupied by termites. As centipedes are carnivorous, and especially insectivorous, they are candidate biological control agents. They might explain the absence of termites in tunnels that had once contained them. Centipedes confined with termites can be seen attacking them. One centipede was observed killing as many as 25 in one day, but most are less aggressive. On the other hand, observations indicate that termite colonies can thrive in the presence of centipedes and suggest that centipedes are not a serious threat.

One centipede of undetermined species was placed in each of 4 small jars (30 ml) containing incipient colonies, 7 mo. old (mated pair, eggs, and 30 or fewer larvae). In all cases the colonies continued to develop while the centipedes died after 6 wk. to 5 mo.

*Ants.* As has already been reported (Beard 1973), some

ants live compatibly with termites, but at least 3 species of ants—*Lasius alienus* (Foerster), *L. umbratus* (Nylander) and *Tetramorium caespitum* (L.)—can be effective predators of *R. flavipes* and are capable of destroying incipient and established colonies. Further observations have confirmed this, and the following experiment adds supportive data.

In each of 24 experimental cells were placed 125 termites that potentially could develop into independent colonies. Twelve units were placed at random just under the surface of the soil in a woodland. The other 12 were similarly placed except that a chemical barrier of chlordane dust was applied a few in. below and around the cell. After 1 mo. the cells were examined. Of the 12 units protected by chlordane, 10 showed still thriving termites. Of the 12 unprotected units, only 1 contained living termites. Ants are the most likely factor for the failure of the unprotected "colonies".

# Bait-block Method of Control

Use of persistent chemical barriers to control termites has ecological and practical limitations.

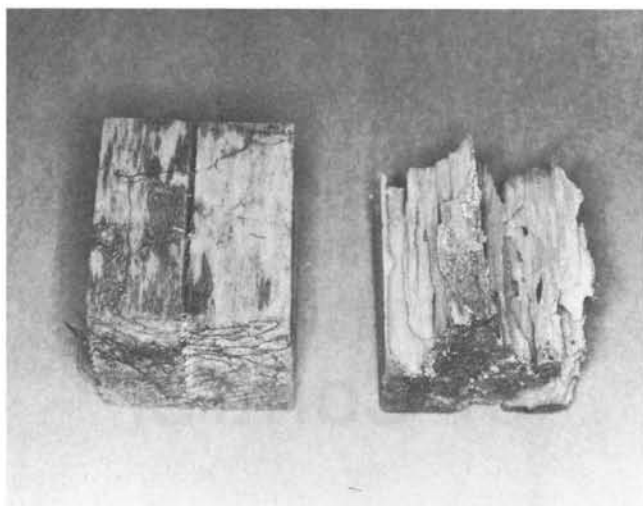
A new approach to termite control, introduced by Esenther and Gray (1968) and Esenther and Beal (1974), employs poisoned blocks of wood acceptable to the termites. Their basic technique was to place a grid of wooden blocks, partially decayed by *G. trabea* and impregnated with mirex (Allied Chemical), at 5 ft. intervals in termite-infested ground. Suppression of termites was accomplished in several months.

Esenther and his co-workers have emphasized the importance of the attractive properties of wood partially decayed by *G. trabea* on the basis that this fungus produces the same metabolite as the termite trail following substance. This is a remarkable coincidence, but as has been shown, termite foraging is largely at random and such decayed wood does not attract larval termites at a distance. This is not surprising because trail substance perception is only at close range. This means that the *G. trabea*-infected wood is not really an attractive bait. It is highly acceptable once the termites find it, but aged wood and wood decayed by other fungi may likewise serve the same purpose.

In these studies the tulip tree wooden blocks were exposed to *G. trabea* inocula, but little effort was made to limit decay to this fungus. The blocks used were, nonetheless, fully acceptable to termites. Those without poison are referred to as bait-blocks. Poisoned blocks were prepared by immersing blocks in a 0.5% acetone solution of mirex for 1 min. and allowing the solvent to evaporate. Alternatively 15 blocks were placed in a tray 16 x 26 cm, 200 ml of 0.5% mirex in acetone were added, the blocks allowed to absorb all the solution and the solvent allowed to evaporate. This is a heavier treatment than may be required, but it proved satisfactory.

Although termite colonies and their sites have elements in common, each situation is unique. This means experimental controls may be impractical or meaningless, and so

Fig. 7 Left: partially decayed tulip tree wood bait-block; right: similar block fed upon by termites



effectiveness of treatment must be judged on other than a comparative basis. Hence each test is considered independently.

- Test 1 Laboratory. A mirex-treated block was placed on top of media occupied by a field-collected colony of termites. Termites were dead or dying within a few days. Subsequent examination showed no living termites.
- Test 2 Laboratory. A bait-block was placed in a container together, but not in contact, with wood harboring a field-collected colony of termites. After the block was frequented by foraging termites, it was replaced by a mirex-treated block. Most termites were killed in a few days; all were dead within a month.
- Test 3 Laboratory. Repetition of Test 2 with similar results.
- Test 4 Laboratory. An open-ended cylinder was placed vertically on a glass plate, filled with termite-infested wood and debris, and covered with a glass plate. Termites built a shelter-tube out from the bottom of the cylinder onto the surface of the supporting plate. When the shelter-tube had extended some 20 or more cm, a bait-block was placed at the advancing front. Foraging termites established the block as a feeding site, after which a mirex-block was substituted for the bait-block. Within 3 days most termites were dead, but a group of survivors appeared unaffected. These were isolated for observation; they slowly sickened and died within 3 wk.
- Test 5 Laboratory. A repetition of Test 4, with essentially the same results. Tests 4 and 5 are analyzed in more detail below.
- Test 6 Field. A blueberry stump known to have been infested with termites for at least 2 yr. was surrounded by a ring of 11 bait-blocks which were partially embedded in the soil and placed 50 cm

from the stump. The blocks were examined at intervals, and when three blocks were occupied by foraging termites, mirex-blocks were substituted. Within a few days no termites were evident in any block. Blocks were left in place for several weeks, during which no termites were seen. After the stump was dug up and dissected, no termites were found.

- Test 7 Field. A decayed double stump of an ash and a maple which had grown in contact with each other was heavily infested with termites. Several bait-blocks were placed on the surface of the soil about 30 cm from the base of the stump. Three blocks that were attacked by foraging termites were replaced by mirex-blocks. After a few days no termites were to be found in any blocks. Examination of the stump disclosed a residual pocket of termites, but these were gone within 2 wk.
- Test 8 Field. A decomposing oak log in contact with the ground was infested with termites. Three bait-blocks were placed on the surface of the soil adjacent to the log. Foragers were slow to find the blocks; only one was attacked after several weeks. This was replaced by a mirex-block. Termites disappeared from the site. No termites were found when the log was dissected 1 mo. later.
- Test 9 Field. In a garden-turf area where termites were known to exist and where garden stakes had been severely damaged, 25 bait-blocks were embedded in the soil 1 m apart in a 5 x 5 grid. These were set in the fall of 1972. In the spring of 1973 the blocks were examined several times. Five blocks became infested with termites and were replaced by mirex-blocks. After 2 wk. no more termites were seen until fall, when two plant stakes at the margin of the grid were found to be infested. Obviously the grid was not extensive enough to include all the termites in the area or a more distant colony had moved into the territory.
- Test 10 Greenhouse. A wooden flat of pachysandra resting on the gravel floor of a greenhouse was found heavily infested with termites. The flat was moved and 10 bait-blocks were placed where the flat had been. Termites accepted three of the blocks and within a week had fed extensively. Mirex-blocks were substituted for these blocks. No termites were evident after 3 days and none appeared during the next 10 mo.
- Test 11 Greenhouse. Similar to Test 10. Boards on a gravel floor infested with termites were removed and bait-blocks were placed there. Five blocks were soon occupied, but only two were replaced by mirex-blocks. With escape from poisoning possible, complete mortality was slower than in Test 10, but within 2 to 3 wk., all termite activity stopped.
- Test 12 Residential. In a suburban residence termites

gained access to stored lumber in a crawl-space with concrete floor by way of a soil pipe through the floor. At time of test, lumber had been removed and shelter-tubes had been destroyed. Under these circumstances, bait-blocks failed to "attract" foragers.

- Test 13 Residential. A relatively new invasion of termites started at the base of a vertical 2 x 8 board serving as the side of a garage door frame. Little damage had been done, but termites built shelter-tubes between the 2 x 8 and the cinder-block wall. The shelter-tube was divided and 3 side branches were being built upwards across the face of the cinder-blocks. A mirex-block was held against the wall surface about 1 cm ahead of one of the advancing tubes. In a day the tube was built up to and around the block, indicating that the block was accepted by the termites. All tube construction halted in 2 days and termites disappeared. No further signs of activity have developed.
- Test 14 Residential. Termites swarmed inside a house, signalling an infestation in wood trim of a door frame, in a wooden baseboard, and probably in hidden studs and other woodwork in the spring of 1973. No ready access to active sites was possible without further damage to the woodwork. Termites were found in boards resting on the ground outside the infested room. Bait-blocks placed adjacent to these boards were readily accepted. Substitution of mirex-blocks resulted in the prompt disappearance of termites. In the spring of 1974 a few adult termites appeared indoors. This may mean that the outdoor termites were not in contact with the indoor termites, or that a small residue of the outdoor colony did not receive adequate dosages of mirex to succumb.
- Test 15 Residential. Severe termite damage was encountered in kitchen cabinetry and in heavy wood panelling of a house built on a slab. Two pest control operators properly refused to consider treatment with chlordane because of probable contamination of a water supply well under the slab. Shelter-tube construction was present in the kitchen cabinet area. Bait-blocks placed there and also against the damaged wood panelling were found and occupied by foraging termites. Replacement with mirex-blocks led to the disappearance of termites. During the following spring, a small swarm (probably less than 100 individuals) emerged in a nearby area. Removal of shelving and panelling disclosed further extensive damage to studs in a wall adjacent to the previously observed damaged area. Three bait-blocks placed adjacent to the exposed damaged wood were occupied, and mirex-blocks were substituted, terminating activity. Even if further treatment may be required at a new site it seems certain that the mirex-blocks terminated activity in three areas.
- Test 16 Residential. Numerous shelter-tubes were discovered being built upward over the concrete foundation of a house. The tubes were broken down and bait-blocks were placed at the points of origin at the soil surface. Four blocks that were accepted were replaced with mirex-blocks. When examined after a week, no termites were found in either treated or untreated blocks; no shelter-tubes have appeared since.
- Tests 17-21 Residential. In five houses the situations were similar enough to be considered as a group. In each case termite damage was localized in structural wood at an outside wall. Bait-blocks placed in the soil outside the areas of infestation were occupied within a reasonable time. Substitution of mirex-blocks led to suppression of all observable termite activity. In these instances sufficient feeding occurred at the mirex-blocks to assure colony destruction.
- Test 22 Residential. Swarming termites emerged in the central part of a house built on a slab where no direct access to the infestation was evident. Foraging termites found bait-blocks placed in soil around the foundation. Mirex-blocks terminated their activity. In this case only the absence of further swarming will give assurance of success.
- Test 23 Residential. In a house similar to that in Test 22, except much smaller, bait-blocks placed around the foundation were found by foragers only after 2 mo. had elapsed. As in Test 15, this house could not be treated with chlordane because of a well beneath the house. Mirex-blocks stopped termite activity at the feeding site.
- Test 24 Residential. In a house having annual swarms for 7 yr., the size of the 1974 swarm suggested a very high termite population. Damage seemed limited to one corner of the house adjacent to a concrete patio, but it extended from the basement to the peak of the gable end. Obviously the termites were well-protected by the patio. Mirex-blocks were placed at two shelter-tube sites where termites were active. Extensive feeding at the mirex-blocks led to cessation of activity there. Four bait-blocks occupied in the soil outside the patio were replaced with mirex-blocks. Although six contaminated feeding sites could account for high mortality among the termites, complete control should not be expected in such an extensive infestation. When structural repairs are carried out further opportunity for mirex treatment may be exposed.
- Test 25 Church. Termites swarmed in a church kitchen, emerging from around the base of a water heater in the spring of 1973. Shelter-tube construction was present under the heater. Bait-blocks at the base of the heater attracted no termites, but blocks in soil around the outside foundation near the kitchen became infested. Replacement with

mirex-blocks resulted in disappearance of termites and no further bait-blocks were attacked. Another swarm emerged from around the water heater in April, 1974. This time adult termites were attracted to the bait-blocks left in the kitchen the previous season. They kept to the blocks in large numbers, hiding beneath and in the kerf, and did not fly. These blocks were also found by worker termites. After six blocks were replaced by mirex-blocks, activity continued. Adults kept to the blocks until they died. Workers built shelter-tubes over and around the blocks. In about 10 days all termite activity ceased; mirex exposure was adequate to kill a large colony.

In some of the above tests (1-8) the technique appeared remarkably simple and effective. In others (10, 11, 13, 16, 17, 18, 19, 20, 21, 22, 23, 25) the final outcome could not be known for certain, although the technique was apparently successful. Even the chemical barrier method now commonly used for termite control depends upon the absence of future swarms and lack of further damage to confirm success. In other tests (9, 14, 15, 24) success was possible, but feeding on mirex-blocks may have been inadequate. Termites did not find the bait-blocks in Test 12, thus the technique was terminated without success.

The technique is based on (1) the foraging behavior that brings the termites to the blocks of wood (2) the feeding, without being repelled, on the mirex-treated wood (3) the rate of intoxication (4) the rate of termite traffic that transports the toxicant to the colony (5) the exchange of food and contaminants that distribute the toxicant among colony members (6) the sensitivity of the colony members to the toxicant and (7) the improbability of any survivors rejuvenating the colony.

As long as worker termites cannot be attracted from a distance, bait placement must be opportunistic, taking advantage of the foraging behavior of the insect. It is noteworthy that even if termite colonies seem adequately supplied with resources (large stumps, logs or even wooden houses) foraging may still provide the opportunity for "baiting."

Especially important to bait-block placement is the recognition of termite territories. This may be facilitated by acquired experience, but improved detection methods would be highly desirable.

Possible repellency and the traffic of foraging termites that might adequately account for transport of toxicant were examined in Laboratory Tests 4 and 5. In these tests termites passed from colony site to food source (bait-block), and back, through shelter-tubes that could be observed with a mirror and suitable light through the bottom plate. Termites passing a given point were counted. In the traffic pattern, food foragers, tube rebuilders, or purposeless travellers could not be distinguished, nor could the time spent by individuals in feeding be determined. When the bait-block was replaced by poisoned block, some of the shelter-tubing was disturbed but termites quickly repaired the breaks. The traffic rates are given in Table 4.

Table 4.

		Number termites passing point/hr.	
		Outbound	Inbound
<b>Lab. Test 4</b>			
Bait-block	8/24/73 AM	395	338
	8/24/73 PM	356	369
	8/27/73 AM	570	462
Mirex-block	8/27/73 AM	373	343
	8/27/73 PM	409	421
	8/28/73 AM	46	52
	8/28/73 PM	0	0
	8/29/73 AM	0	0
<b>Lab. Test 5</b>			
Bait-block	10/16/73 AM	504	467
	10/17/73 AM	445	478
	10/18/73 AM	326	438
Mirex-block	10/18/73 AM	407	382
	10/18/73 PM	368	337
	10/19/73 AM	224	247
	10/22/73 AM	22	22
	10/23/73 AM	0	0

The normal traffic was essentially the same, approximately 400 trips each way per hour, in both tests. This rate suggests an extensive transport, adequate to account for effective food exchange. The drop in traffic when blocks were switched is no greater than can be explained by shelter-tube repair. Repellency clearly is lacking.

Even though traffic was similar in both cases, showing a decline to zero after poisoning, the decline in Test 4 took about 30 hr. as compared with 5 days in Test 5. This may reflect unknown differences in colony sizes.

The decline in traffic paralleled death of the foragers. Their corpses accumulated at the bottom of the container housing the colony. It is significant that dead termites were not seen at the poison site. Termites that did not participate in the traffic pattern were present in both tests. These survived varying lengths of time, but all died within 3 wk. In Test 5 these temporary survivors included 0 larvae, 44% nymphs, 49% secondary reproductives, and 7% soldiers.

Soldiers sometimes participate in larval traffic, but would not be expected to get a primary dose of poison except by contact as they do not feed themselves. Nymphs and possibly reproductives feed themselves, but would escape primary poisoning as they do not participate in the traffic. Thus, they survive unpoisoned—which they did not—or acquire by trophallaxis or contamination a secondary, perhaps reduced, dose of poison that kills more slowly.

The sensitivity of termites to mirex was determined by applying a dosage series of acetone solutions of mirex to filter paper. After the acetone evaporated, the paper was moistened with water and offered to termites. Termites were exposed to the treated paper for 2 days, removed to uncontaminated filter paper, and counted 5 days later. The dosage-mortality curve (Fig. 8) suggests a  $LD_{50}$  of 0.7  $\mu\text{g}$  mirex/cm<sup>2</sup>. Extremely high sensitivity is indicated because the amount of filter paper consumed was scarcely detectable.

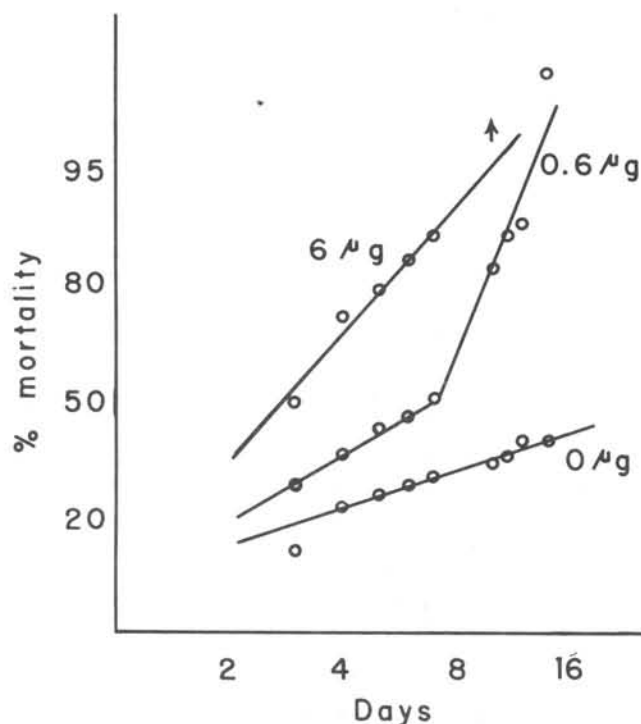


Fig. 8 Time-mortality response of termites exposed for 30 hr. to paper treated with mirex at concentrations of 0, 0.6  $\mu\text{g}$ , and 6  $\mu\text{g}/\text{cm}^2$

The effect of dosage on time of death was determined similarly, using two concentrations of mirex (6.25  $\mu\text{g}/\text{cm}^2$  and 0.625  $\mu\text{g}/\text{cm}^2$ ). Groups of 125 termites were exposed to treated paper for 30 hr., and then transferred to clean paper. Only termites showing no movement were counted

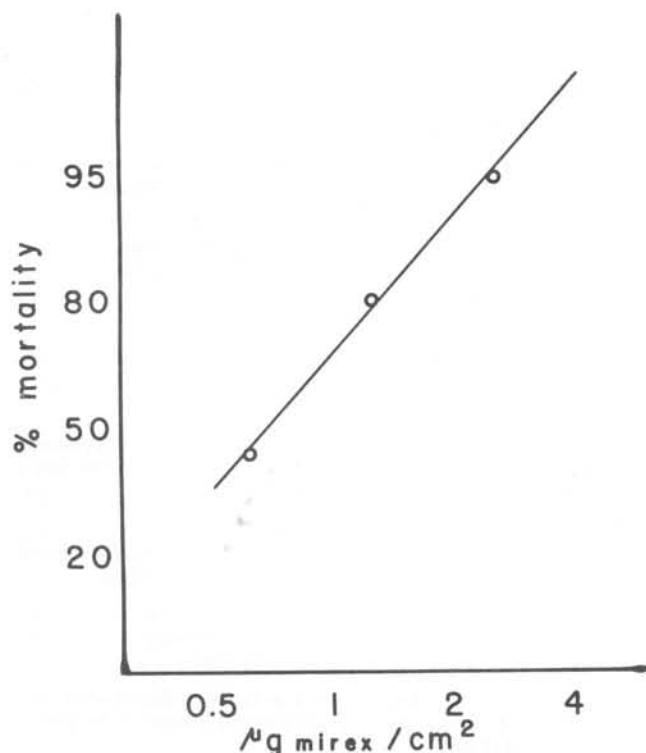


Fig. 9 Mortality of termites after 5 days following 48 hr. exposure to paper treated with mirex

as dead (Fig. 9). Although larvae were used because of availability, the response to the lower dose (bi-modal curve) is consistent with the delayed mortality observed among non-foraging members of colonies in Tests 4, 5, and others. This slow action of mirex allows foraging termites to distribute the toxicant before they die.

On the basis of these data, and the exposed surface areas of wooden blocks used, 1 mg of mirex per block should be adequate to destroy even a large colony of termites. Practicality dictates that heavier concentrations be employed to minimize escape from contact with poisoned surfaces.

The remarkable attractiveness of bait-blocks to adult termites as shown outdoors, experimentally, and in Test 25, raises the question as to adult sensitivity to mirex. Upon exposure to treated paper, treated wood blocks or even treated glass surfaces, adult termites died within 6 days, whereas companions under the same conditions without mirex survived. Numbers of adults available for testing were too limited to permit quantitative determination of their sensitivity as compared with worker termites.

The transport of toxicant from a distance by foragers entails distribution by mutual grooming and feeding among colony mates, by regurgitation and excretion, by physical transport, and by disintegration of poisoned cadavers. A further experiment confirms the exchange of poison in spite of incomplete trophallaxis as measured by radio-labelling. Mortality was compared when different ratios of intoxicated donors and recipients constituted test groups. Intended donors were fed on neutral red-stained paper and then on black filter paper impregnated with mirex (20  $\mu\text{g}/\text{cm}^2$ ). Only red termites with black gut contents after 24 hr. exposure were used as donors. These were added to groups of recipients kept in vials with moist sawdust. Recipient mortality was noted after 3 and 8 days. Death of all donors was assured by the high dosage of mirex made obvious by their feeding. The results are summarized in Table 5.

Table 5

Ratio Donor/recipient	% mortality of recipients	
	3 days	8 days
1:9	53%	91%*
3:7	31%	100%
5:5	60%	100%
7:3	61%	100%
9:1	80%	100%

\*even survivors of this group died a day later

These data suggest that 10% of the members feeding on the primary source of mirex is adequate to destroy the whole colony. Doubtless direct distribution of the poison is principally responsible, but further contamination can persist. Dead termites disintegrate promptly, but the chemically stable mirex can remain after intoxicated foragers are no longer present. This was indicated when, at



the conclusion of the above test, small groups (22) of unexposed termites were added to each of the 3 vials that had the most donors. All termites died within a few days. Here the residual contamination was concentrated, and the termites had little chance to escape lethal doses. Death was not so prompt when groups of ca 200 healthy termites were added to containers used in Laboratory Tests 4 and 5 after the original termites had died. All replacement termites died, but complete kill required 2 to 3 mo.

The possibility of a small group of survivors reconstituting a reproducing colony must be considered. Larvae are the most labile and independent members of the colony, but they are the first to die from mirex poisoning. As far as has been tested, dependent castes survive only temporarily, probably because they receive diluted dosages. Present evidence indicates that even without poisoning, dependent castes are not sufficiently labile to continue a colony in the absence of assisting larvae.

### Conclusions

Advantage can be taken of foraging behavior of termites to locate feeding sites, and to monitor them with unpoisoned bait-blocks. Substituting mirex-treated blocks for bait-blocks results in poison uptake by foraging termites and transport and distribution of lethal doses to other members of a communicating colony. The technique is simple in principle and practice, and succeeds if adequate feeding sites of a discrete colony (communicating group) can be localized. Minimal quantities of poison are used in such a way that natural control agents of termites are not threatened, and the environment is not contaminated with hazardous residues. The system fails if bait-blocks are not found by the termites. Partial success may be achieved if termite colonies overlap in territories inadequately detected. Preventive treatment for termites with mirex blocks is conceivable, but localized application to existing or developing colonies seems most practicable.

### References Cited

- Alibert, J. 1959. Les échanges trophallactiques chez le Termite à cou jaune (*Calotermes flavicollis* Fabr.) étudiés à l'aide du phosphore radio-actif. Acad. Sci. (Paris) C. R. 248: 1040-1042.
- Banks, N. and T. E. Snyder. 1920. A revision of the Nearctic termites . . . with notes on biology and geographic distribution. U. S. Natl. Bus. Bull. 108: 228 pp.
- Beal, R. H. and A. G. Kais. 1962. Apparent infection of subterranean termites with *Aspergillus flavus* Link. J. Insect Pathol. 4: 488-489.
- Beard, R. L. 1973. Ants as predators of *Reticulitermes flavipes*. Environ. Entomol. 2: 397-399.
- Beard, R. L. 1974. Termites in Buildings. Conn. Agric. Exp. Sta. Bull. 695 Rev. 16 p.
- Beard, R. L. and G. S. Walton. 1971. Insecticidal mycotoxins produced by *Aspergillus flavus* var. *columnaris*. Conn. Agric. Exp. Sta. Bull. 725. 26 p.
- Becker, G. 1966. Spurfolge-Reaktion von Termiten auf Glykyl-Verbindungen. Z. Angew. Zool. 53: 495-498.
- Bready, J. K. and S. Friedman. 1963. The nutritional requirements of termites in axenic cultures. 1. Sterilization of eggs of *Reticulitermes flavipes* and the requirements of first-instar nymphs. Ann. Entomol. Soc. Amer. 56: 703-706.
- DeBach, P. H. and W. A. McOmie. 1939. New diseases of termites caused by bacteria. Ann. Entomol. Soc. Amer. 32: 137-146.
- Esenther, G. R. 1969. Termites in Wisconsin. Ann. Entomol. Soc. Amer. 62: 1274-1284.
- Esenther, G. R., T. C. Allen, J. E. Casida, and R. D. Shenefelt. 1961. Termite attractant from fungus-infested wood. Science 134: 50.
- Esenther, G. R. and R. H. Beal. 1974. Attractant-mirex bait suppresses activity of *Reticulitermes* spp. J. Econ. Entomol. 67: 85-88.
- Esenther, G. R. and D. E. Gray. 1968. Subterranean termite studies in southern Ontario. Can. Entomol. 100: 827-834.
- Forbes, S. A. 1895. The white ant in Illinois (*Termes flavipes* Kollar). Ill. State Entomol. Rep. 1893-94; pp. 190-204.
- Gosswald, K. and W. Kloft. 1959. Zur Laboratoriumsprüfung von Textilien auf Termitenfestigkeit mit *Kalotermes flavicollis* Fabr. Entomol. Exp. Appl. 2: 268-278.
- Gouger, R. J. and J. W. Kimbrough. 1969. *Antennopsis gallica* Heim and Buchli (Hyphomycetes: Gloeohaustoriales) an entomogenous fungus on subterranean termites in Florida. J. Invertebr. Pathol. 13: 223-228.
- Harris, W. V. 1958. Colony formation in the Isoptera. Proc. 10th Int. Congr. Entomol., Montreal, 1956. 2: 435-439.
- Holway, R. T. 1941. Tube-building habits of the eastern subterranean termite. J. Econ. Entomol. 34: 389-394.
- King, G. B. 1897. *Termes flavipes* Kollar and its association with ants. Entomol. News 8: 193-196.
- LaFage, J. P., W. L. Nutting, and M. I. Haverty. 1973. Desert subterranean termites: a method for studying foraging behavior. Environ. Entomol. 2: 954-956.
- Lenz, M. 1969. Zur schädigenden Wirkung einiger Schimmelpilze auf Termiten. Mater. Org. (Berl.) 4: 109-122.
- Lund, A. E. and N. T. Engelhardt. 1962. Subterranean termites and *Absidia coerulea* Bain. (Mucorales). J. Insect Pathol. 4: 131-132.
- Luscher, M. 1953. The termite and the cell. Sci. Am. 188: 74-78.
- Massey, C. L. 1971. Two new genera of nematodes parasitic in the eastern subterranean termite, *Reticulitermes flavipes*. J. Invertebr. Pathol. 17: 238-242.
- Matsumura, F., Akira Tai, and H. C. Coppel. 1969. Termite trail-following substance, isolation and purification from *Reticulitermes virginicus* and fungus-infected wood. J. Econ. Entomol. 62: 599-603.
- McMahan, E. A. 1966. Food transmission within the *Cryptotermes brevis* colony (Isoptera: Kalotermitidae). Ann. Entomol. Soc. Amer. 59: 1131-1137.
- McMahan, E. A. 1969. Feeding relationships and radioisotope techniques. Chap. 12 in Krishna, K. and F. M. Weesner (eds.) Biology of Termites. Academic Press, New York, v. 1, pp. 387-406.
- Metcalf, C. L., W. P. Flint, and R. L. Metcalf. 1951. Destructive and Useful Insects. McGraw-Hill, New York. fig. 512, p. 856.
- Miller, E. M. 1969. Caste differentiation in the lower termites. Chap. 9 in Krishna, K. and F. M. Weesner (eds.) Biology of Termites. Academic Press, New York. v. 1, pp. 283-310.
- Poinar, G. O., Jr. 1969. Diplogasterid nematodes (Diplogasteridae: Rhabditia) and their relationship to insect disease. J. Invertebr. Pathol. 13: 447-454.
- Smythe, R. V. and H. C. Coppel. 1965. The susceptibility of *Reticulitermes flavipes* (Kollar) and other termite species to an

- experimental preparation of *Bacillus thuringiensis* Berliner. J. Invertebr. Pathol. 7: 423-426.
- Smythe, R. V. and H. C. Coppel. 1966a. A preliminary study of the sternal gland of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Amer. 59: 1008-1010.
- Smythe, R. V. and H. C. Coppel. 1966b. Some termites may secrete trail blazing attractants to lead others to food sources. Pest Control 34(10): 73-78.
- Smythe, R. V. and H. C. Coppel. 1966c. Pathogenicity of externally occurring fungi to *Reticulitermes flavipes*. J. Invertebr. Pathol. 8: 266-267.
- Snyder, T. E. 1915. Insects injurious to forests and forest products. Biology of the termites of the eastern United States with preventive and remedial measures. U. S. Dept. Agric. Bur. Entomol. Bull. 94 pt. II: 13-85.
- Snyder, T. E. 1935. Our Enemy the Termites. Cornell Univ. Press, Ithaca: 196 pp.
- Snyder, T. E. 1956. Annotated, subject-heading bibliography of termites 1350 B.C. to A.D. 1954. Smithson. Misc. Collect. 130: 1-305.
- Snyder, T. E. 1961. Supplement to the annotated, subject-heading bibliography of termites, 1955 to 1960. Smithson. Misc. Collect. 143: 1-137.
- Snyder, T. E. 1968. Second supplement to the annotated, subject-heading bibliography of termites 1961-1965. Smithson. Misc. Collect. 152: 188 p.
- Stuart, A. M. 1969. Social behavior and communication. Chap. 7 in Krishna, K. and F. M. Weesner (eds.) Biology of Termites. Academic Press, New York, v. 1, pp. 193-232.
- Thaxter, R. 1920. Second note on certain peculiar fungus parasites of living insects. Bot. Gaz. 69: 3-9.
- Thompson, C. B. 1917. Origin of the castes of the common termite, *Leucotermes flavipes* K 1. J. Morphol. 30: 83-153.
- Turner, N. 1949. Control of termites in buildings. Conn. Agric. Exp. Sta. Circ. 172: 8 p.
- Turner, N. 1961. Termites in buildings. Conn. Agric. Exp. Sta. Circ. 218:12p.
- Turner, N. 1968. Termites in buildings. Conn. Agric. Exp. Sta. Bull. 695:14p.
- Turner, N. and J. F. Townsend. 1936. Termite control in buildings in Connecticut. Conn. Agric. Exp. Sta. Bull. 382: 207-242.
- Turner, N. and J. F. Townsend. 1939. Control of termites in buildings. Conn. Agric. Expt. Sta. Circ. 134:14p.
- Weiser, J. and I. Hrdy. 1962. Pyemotes-mites as parasites of termites. Z. Angew. Entomol. 51: 94-97.
- Wilson, E. O. 1971. The Insect Societies. Belknap Press, Cambridge, Mass. 548 p.
- Yendol, W. G. and J. D. Paschke. 1965. Pathology of an *Entomophthora* infection in the eastern subterranean termite, *Reticulitermes flavipes* (Kollar). J. Invertebr. Pathol. 7: 414-422.