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TERMITE DISTRIBUTION, COLONY SIZE, AND POTENTIAL FOR DAMAGE

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ABSTRACT *Coptotermes formosanus* Shiraki, *Heterotermes aureus* (Snyder), and *Reticulitermes flavipes* (Kollar) are extremely important economic pests in North America and Hawaii. In the past decade, mark-release-recapture studies using dye markers have resulted in much larger estimates of the foraging populations in colonies of these termite species than had been suggested by earlier studies using direct sampling methods. Colonies containing from several hundred thousand to several million termites can forage over an area exceeding 3,000 m^2. Foraging worker biomasses up to 34 kg have been reported, and a colony of this size would consume approximately 1 kg of wood each day. The results of these studies indicate that many structures within the vicinity of a discovered subterranean termite infestation are likely to be at risk, and confirm that localized spot treatment with soil termiticides within infested structures is not appropriate for subterranean termite control. Baiting systems could effectively reduce colony populations, but will require monitoring of colony foraging activity after treatment.

Keywords - *Coptotermes formosanus*, *Heterotermes aureus*, *Reticulitermes flavipes*, subterranean termites, Rhinotermitidae, baits

There are approximately 2,200 known species of termites (Isoptera), most of which are found only in the tropics (Wood and Johnson 1986). In Hawaii and North America, although drywood termites (Kalotermitidae) are serious structural pests, the most economically important pests are the subterranean termites *Coptotermes formosanus* Shiraki, *Heterotermes aureus* (Snyder) and *Reticulitermes* spp. (Rhinotermitidae) (Weesner 1965; Mauldin 1986). The Formosan subterranean termite, *C. formosanus* is a worldwide problem in the tropics and subtropics, and is found in Hawaii, portions of the southeastern United States (Su and Scheffrahn 1990), and (very recently) the southern California coast (M. K. Rust, pers. commun.). *Heterotermes aureus* is limited to the desert regions of southern Arizona, California, and Mexico, while *Reticulitermes* spp. represent the most broadly distributed termite genus in North America (Weesner 1965). The eastern subterranean termite, *Reticulitermes flavipes* (Kollar), is found

throughout the southeastern United States, north along the Atlantic coast into Maine, and west along the shores of the great lakes into Ontario, Canada (Weesner 1970). Transported infestations of this species have become established as far north as Winnipeg, Manitoba (Anonymous 1989).

These North American subterranean termites nest in the soil, and their galleries do not incorporate mounds or other nest structures that are separable from the surrounding soil matrix. This presents obvious difficulties in studying colony demographics and foraging dynamics. In the past decade mark-release-recapture (or capture-recapture) methods using a fat-soluble dye, have proven extremely useful in studying colony population sizes and foraging territories of the three principal North American subterranean termite genera.

DIRECT METHODS OF POPULATION ESTIMATION

Direct, destructive sampling has been used to measure the population of mound-building termite colonies (e.g., Darlington 1984). Howard *et al.* (1982) used excavation, followed by exhaustive trapping with corrugated cardboard, to census *R. flavipes* colonies living in stumps in rural Mississippi. Their estimate of an average *R. flavipes* colony population of ca. 245,000 termites was, until very recently, the most authoritative and frequently cited estimate available for this serious structural pest. However, since the common North American subterranean termites generally do not have a well-defined nest structure, total gallery excavation is a formidable task, and certainly not possible in densely inhabited urban areas. Loss of insects in the process of collecting and processing such large quantities of soil is also a problem.

In open range-land, extraction of termites from soil cores has been used to estimate population density (Uekert *et al.* 1976), although not discreet colony populations. This method is impractical in urban situations, since neither subterranean galleries nor the insects themselves are likely to be distributed homogeneously over a given area.

Sequential removal of termites in cardboard baits was used by Ewart (1988) to estimate the populations of *Coptotermes lacteus* (Froggatt) mounds in Australia. Although less intrusive than excavation or soil cores, this is also a destructive sampling method, and best suited to fairly small populations where the number of foragers captured will decline rapidly in sequential captures.

Foraging intensity, or the amount of cellulosic food material removed per unit of time by termites in a given area, offers a simple method of estimating the change in size of a foraging termite population, after a bait application for example (e.g., Ostaff and Gray 1975; Jones 1988). However, estimation of true population size is not practical, unless one is actually able to measure termite feeding on all the available food resources. In all likelihood, though, this is the method that will be adopted by pest control operators to determine the success of termite baiting operations, because of the speed and simplicity of placing and monitoring wooden stakes or baits at a given site. The responsibility will lie with researchers to supply the pest control industry with at least "rule of thumb" correlations between feeding intensity and forager numbers.

A difficulty in applying any of these direct methods of population estimation to North American subterranean termite colonies is that one must either have prior knowledge of the distribution of individual colonies in the study area, or make critical (and untestable) assumptions about that distribution.

DIRECT METHODS OF TERRITORY MEASUREMENT

Methods of measuring subterranean termite foraging territories were discussed by Jones (1988a) in an address to the second National Conference on Urban Entomology. Excavation of termite galleries, spatial patterns of attack on natural vegetation or bait grids, and bioassays of agonistic interactions among conspecifics from different sites have all been used to estimate territory sizes. King and Spink (1969) excavated a *C. formosanus* colony in Louisiana and determined that the galleries extended throughout an area of approximately 5,650 m^2, a figure that has been supported by later mark-release-recapture studies. Haverty *et al.* (1975) estimated the average size of *H. aureus* foraging territories as 12.5 m^2 from the patterns of attack on baits placed in a large grid, but later mark-release-recapture studies by Jones (1990b) demonstrated that this type of analysis greatly underestimated actual territory sizes.

MARK-RELEASE-RECAPTURE STUDIES

Radioisotopes have been used in several studies to measure subterranean termite foraging territories (e.g., Li *et al.* 1976; Spragg and Paton 1980). However, histological dyes have proven to be the most useful and popular tools for marking termites. Studies using these dyes to mark *C. formosanus*, *R. flavipes*, and *H. aureus* have, in the past decade, generated dramatically different sociometric data than had been previously assumed, or suggested by direct sampling methods.

The use of dyes to mark subterranean termites appears to have originated independently during the early 1970's with two well-known termite researchers: Frances M. (Weesner) Lechleitner at the University of Colorado, and Minoru Tamashiro at the University of Hawaii. To date, the record of Lechleitner's work with dyes is limited to unpublished reports (c.f., footnote in Esenther 1980). Tamashiro's work in this area had greater impact through his publications with his students, and the independent contributions of those students.

A prerequisite to the use of dyes is an efficient and nondestructive method of collecting (and recollecting) termites from the soil. In the dry southwest, grids of toilet paper rolls placed on the soil surface proved effective with *H. aureus* and other desert termites (La Fage *et al.* 1973), while small wooden boxes, each placed over a stake and contained within a metal can placed on the soil with the bottom cut out, were used in Hawaii to collect *C. formosanus* (Tamashiro *et al.* 1973). Su and Scheffrahn (1986) modified the Hawaiian trap design so that traps could be hidden from sight in public areas of urban Florida. Grace (1989a) further modified this design to improve captures of *R. flavipes* in Ontario, Canada, and this design has also proved effective for collecting large numbers of *Reticulitermes hesperus* Banks workers in California (J. Smith, pers. commun.). In addition to wood, these later designs incorporated the use of corrugated cardboard, which had been described by Esenther (1980) and La Fage *et al.* (1983) as an excellent substrate for collecting subterranean termite foragers. Recently, Ewart *et al.* (1992) recommended a simple modification (a drill hole) of the wooden stakes usually used

to locate termite field sites, in order to facilitate subsequent installation of collection traps without disrupting the termites' foraging galleries.

Dyes were first used in Hawaii to measure the distance travelled by *C. formosanus* workers, fed filter paper impregnated with Fast Green, between interconnected traps (Fujii 1975). The maximum distance thus measured of 160 feet (Fujii 1975) was very close to the distances of 165 feet (Ehrhorn 1934) and ca. 200 feet (King and Spink 1969) reported from destructive excavations of Formosan subterranean termite galleries. Subsequently, Lai (1977) and Lai *et al.* (1983) screened nine histological dyes and identified Sudan Red 7B as the most persistent and least toxic dietary dye marker for *C. formosanus*. In addition to measuring termite foraging distances (110 m), Lai (1977) was the first researcher to use the simple Lincoln (1930) index, based on the ratio of marked to unmarked workers in the recaptured sample, to estimate the foraging population of three *C. formosanus* colonies at 1.3-1.6 million. Su (1982) and Su *et al.* (1984) applied Lai's (1977) technique to estimate *C. formosanus* colony populations as high as 4.4 million, and, more importantly for the validity of the method, demonstrated that foraging termite workers did not show fidelity to any particular feeding site. Su *et al.* (1983a, 1983b) also refined Lai's (1977) application dosage and demonstrated that Sudan Red 7B was not passed in detectable quantities by trophallaxis.

As is illustrated by the citations above, Sudan Red 7B has been the subject of a fairly large number of methodological papers. Su *et al.* (1988) further refined the dose/time relationship for effective marking of *C. formosanus*, and found that this dye was not appropriate for marking *R. flavipes* with the 41-day release-recapture cycle used by these authors (Su and Scheffrahn 1988a, 1988b). However, Grace and Abdallay (1989) demonstrated that Sudan Red 7B could safely be used with shorter (ca. 3 week) release-recapture cycles with *R. flavipes* (Grace 1989, 1990; Grace *et al.* 1989). Sublethal effects of Sudan Red 7B on *C. formosanus* were found by Delaplane *et al.* (1988) and Delaplane and La Fage (1989), who confirmed Lai's (1977) observation of reduced gut protozoan populations, and also attributed a slight but significant decrease in termite feeding to dye exposure.

The dye Neutral Red was used by Esenther (1980), who attributed the dye method to Lechleitner, to mark *R. flavipes* workers and estimate the size of termite colonies in Wisconsin. Although these were the first such estimates for *R. flavipes* colonies, they had little impact due to the large standard errors of the estimates, and limited distribution of his report (Esenther 1980). Grace *et al.* (1989) subsequently confirmed Esenther's (1980) observation that *R. flavipes* colony populations could number into the millions, with lower standard errors associated with these authors' estimates.

Neutral Red was also identified by Salih and Logan (1990) as the most promising of 30 dyes tested as markers for *Microtermes lepidus* Sjostedt. The search continues for additional dye markers, to use either singly or in combination (e.g., Grace and Abdallay 1990). Recently, Su *et al.* (1991) identified Nile Blue as a safe and persistent marker for *R. flavipes*.

So long as the dye marker is readily recognized, mark-release-recapture methods provide a definitive measurement of subterranean termite foraging distances (the distance between release and recapture trap sites) and, with an adequate distribution of traps throughout the site, foraging territory areas. In urban areas where field sites are always constrained by pavement, buildings, fences, and other obstructions, these distances and territory sizes generally represent minimum values since the actual territories may well extend beyond the boundaries of the site.

Population estimates from mark-release-recapture studies are somewhat less definitive, since the validity of the Lincoln index estimate is contingent upon certain assumptions (Southwood 1978): (1) marked animals are not affected in behavior and life expectancy, and marks will not be lost or transferred; (2) marked animals become completely mixed in the population; (3) the probability of capturing a marked animal is the same as that of capturing any member of the population; (4) sampling must be at discrete time intervals; (5) the population is closed; (6) there are no births or deaths in the period between sampling. Although Su *et al.* (1984) established that *C. formosanus* foragers show no allegiance to specific foraging sites, assumptions (2) and (3) are difficult to demonstrate in practice and are usually dealt with simply by placing a large number of traps throughout the study area.

COLONY POPULATIONS AND FORAGING TERRITORIES

Prior to the use of mark-release-recapture methods, the best estimates of North American subterranean termite colony populations derived from direct sampling methods were as follows: *C. formosanus*, 450,000 (Nakajima and Mori 1961, cited in Su and Tamashiro 1987); *H. aureus*, 22,632 (Haverty *et al.* 1975); *R. flavipes*, 244,445 average with a range of 51,505 - 363,512 (Howard *et al.* 1982).

Mark-release-recapture studies have revised all of these estimates to reflect much larger colony sizes: *C. formosanus*, 1.4 - 6.9 million (Su and Scheffrahn 1988); *H. aureus*, 45,000 - 300,000 (Jones 1987, 1990a); *R. flavipes*, 0.72 - 3.2 million (Grace *et al.* 1989; Grace 1989, 1990). Very large foraging territories have also been measured in these studies: *C. formosanus*, 3,571 m^2 (Su and Scheffrahn 1988); *H. aureus*, 3,316 m^2 (Jones 1987, 1990b); *R. flavipes*, 1,091 m^2 (Grace *et al.* 1989). These revised estimates do not, of course, mean that all termite colony populations or territories are these sizes, but they certainly demonstrate a greater potential for colony growth than had been considered possible based upon the earlier estimates.

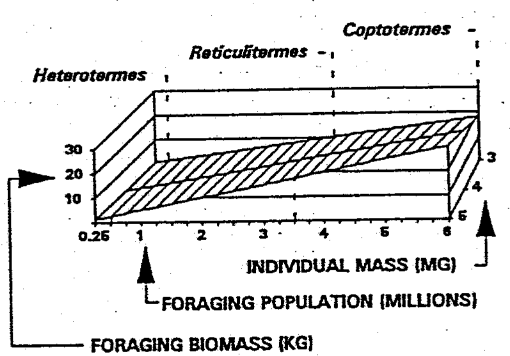

FIGURE 1. Estimated foraging biomass of colonies of *Heterotermes aureus*, *Reticulitermes flavipes*, and *Coptotermes formosanus*, based on the weight of individual workers and current published estimates of the size of colony foraging populations (see text). Dotted lines indicate the approximate range for each termite species.

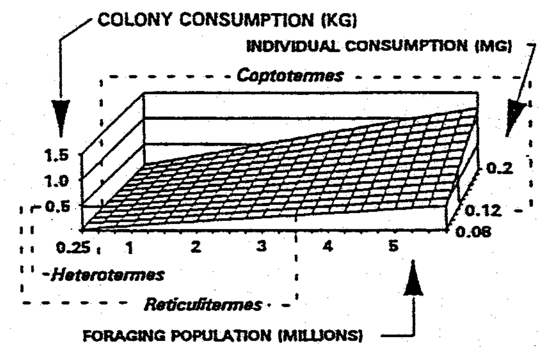

FIGURE 2. Estimated daily wood consumption by active colonies of *Heterotermes aureus*, *Coptotermes formosanus*, and *Reticulitermes flavipes*, as a function of the daily consumption of individual workers and the estimated foraging population. Dotted lines indicate approximate consumption range for each termite species.

POTENTIAL FOR DAMAGE AND IMPLICATIONS FOR CONTROL

With termite colony populations extending into the millions, the foraging biomass of an individual colony (superorganism) can be considered equivalent to a large grazing animal. The *R. flavipes* colony foraging populations measured by Grace *et al.* (1989) represented foraging biomasses of 7 -10 kg, and the *C. formosanus* colonies studied by Su and Scheffrahn (1988) were between 4 - 34 kg. Figure 1 represents termite foraging biomass as a function of the foraging population and the average weight of individual workers, with the approximate cut-off points for each termite genus based upon current mark-release-recapture information.

Although feeding may be spread over several thousand square meters, a large *R. flavipes* colony will ingest almost 0.5 kg of wood each day, while a large *C. formosanus* colony could consume twice that amount (Figure 2). Individual subterranean termite colonies thus present a grave threat to wooden structures within their foraging territory. From the point of view of termite control, the large size of these foraging territories certainly confirms that spot-treatment (application of soil termiticide in a localized portion of the infested structure) for these subterranean termites is not practical. Moreover, structures (or other wood in service) in the vicinity of an infested building should be considered at risk, and a pest control operator would be quite justified in promoting inspection of such buildings.

Baiting systems using baits, dusts, or microbial pest control agents for subterranean termite control may well be implemented in the near future, and mark-release-recapture studies are absolutely essential in bait development to demonstrate efficacy and refine application methods (e.g., Su 1991). Because bait placement will be critical to the success of this method, pest control operators will have to monitor the site after bait application much more rigorously than has been the case with soil treatments. However, it is unrealistic to expect that pest control operators will be prepared to conduct mark-release-recapture studies in conjunction with bait applications. Pest control operators will likely place small wooden stakes or their equivalent, and monitor termite population suppression by the decline in feeding on these stakes.

Practical application by pest control operators of baiting systems for subterranean termite control will probably follow this sequence:

(i) Pre-bait to identify locations for bait application. This may be less necessary in or around structures where infestation is quite visible. However, pre-baiting techniques such as hollow stakes (Ewart *et al.* 1992) may also be very useful in applying baits without interfering unduly with termite foraging galleries.

(ii) Apply baiting system. Bait stations may contain an oral toxicant, a toxic dust or other topical formulation, or a microbial agent. Aggregation traps for mass trapping, followed by treatment with a toxicant and release of the treated individuals, might also be effective (although labor-intensive) in some situations (Grace and Abdallay 1990; Myles and Grace 1991).

(iii) Monitor termite foraging intensity during and after treatment with stakes or other monitoring technique.

(iv) Continue to use a monitoring method (stakes) along with periodic property inspections as part of a continuing service contract.

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