# Seasonal Foraging and Feeding Behavior of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a Wildland and a Residential Location in Northern California

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**ABSTRACT** Seasonal activity of *Reticulitermes* was observed at 2 sites using ABS pipe monitoring stations. At a wildland site, 68 of the monitoring stations were occupied by termites during the study; 53, 10, and 5 for hydrocarbon phenotypes A, B, and C, respectively. At the residential site, 26 monitoring stations were occupied; 14 and 12, for hydrocarbon phenotypes A′ and D, respectively. Live body weights of workers averaged 2.28, 1.46, and 1.66 mg for phenotypes A, B, and C, respectively, at the wildland site. The workers had similar live body weights at the residential site; phenotype D averaged 2.40 mg, slightly more than the 2.26 mg for phenotype A′. There were no discernible seasonal or monthly trends in live body weights. The percentage of the monitoring stations occupied ranged from 76.7–89.3% and 81.2–93.5% at the wildland and residential sites, respectively. The estimated number of termites was low in the late fall through the early spring and peaked from June to October at the wildland site and peaked from June to November or December at the residential site. Wood consumption by *Reticulitermes* followed similar trends at both sites. Wood consumption was minimal during the winter, increased slightly in the spring and early summer, peaked in the summer and early fall, then declined in the late fall. Wood consumption reached 1.1–1.3 g per day per monitoring station at the wildland site and 0.8 g per day per monitoring station at the residential site.

**KEY WORDS** subterranean termites, feeding behavior, foraging behavior, wood consumption

TERMITES CAUSE SIGNIFICANT economic impact to wooden structures throughout the United States, including California (Brier et al. 1988, Su and Scheffrahn 1990). Subterranean termites (primarily *Reticulitermes* spp. and *Coptotermes formosanus* Shiraki) account for ≈90% of the damage and control costs. From the late 1940s until recently the pest control industry relied primarily on chemicals applied to the soil for control of subterranean termites. These pesticides are intended to form a long-lived toxic or repellent barrier between the structure and termites in the soil. They do not necessarily reduce or eliminate termite populations; they simply exclude termites from the structure. This strategy of placing an impenetrable chemical barrier in the soil remains the mainstay of termite prevention and control in the United States today (Su and Scheffrahn 1998).

A substitute or supplementary control strategy, involving use of baits, was originally developed for control of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Beard 1974; Esenther and Beal 1974, 1978). This technique employed the now-banned insecticide mirex, deployed in decayed wooden blocks. There is a renewed interest in commercial development of baits for subterranean termite control (Potter 1997, Forschler 1998, Su and Scheffrahn 1998). The goal of this approach is to reduce, suppress, or eliminate subterranean termite colonies or foraging populations. An improved understanding of the foraging or feeding dynamics of *Reticulitermes* is necessary to provide a basis for assessment of baits for termite control.

There have been relatively few studies of the foraging and feeding characteristics of *Reticulitermes* species (Su and Scheffrahn 1994, Haagsma and Rust 1995). Equivalent information has been gathered for 2 subterranean termite species (*Heterotermes aureus* (Snyder) and *Gnathamitermes perplexus* (Banks) in the desert Southwest (Haverty et al. 1974, La Fage et al. 1976, Jones and Nutting 1989). However, similar information for *Reticulitermes* in northern California simply does not exist.

The research reported here provides essential background for development of bait-toxicant delivery systems for control of *Reticulitermes* spp. in northern California. The specific objectives of this study were to demonstrate a mix of *Reticulitermes* taxa present and

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to describe the seasonal cycles of abundance of termites in monitoring devices and wood consumption by subterranean termites in a wildland and a residential site.

## Materials and Methods

**Study Areas.** *Reticulitermes* was studied in a wildland setting without the interference of buildings, as well as in a residential location. The residential site was used to develop an understanding of the ecology and behavior of *Reticulitermes* under situations where suppression or elimination of subterranean termites may be desirable.

Wildland studies were conducted in the Eddy Arboretum in the western portion of the Pacific Southwest Research Station's Institute of Forest Genetics near Placerville, CA, at an elevation of ≈775 m. The site had an area of ≈4 ha and was composed of a 70-yr-old plantation of mixed native and exotic *Pinus* species spaced at 4-m intervals. The canopy was partially closed with numerous open patches created by tree mortality.

The residential location was in Novato in Marin County ≈40 km north of San Francisco, CA, and consisted of a single family dwelling, a church, and extensive gardens on a 1-ha lot. The house and adjacent garden area had a history of infestation by *Reticulitermes*. No remedial control with soil termiticides was initiated to terminate infestation of the structures at the residential site before, or during the course of our study. However, a sand barrier had been placed inside the foundation to prevent termites access to the structure (Lewis et al. 1996).

**Monitoring Stations.** Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) stakes were driven into the soil in a 2 × 2-m grid at the wildland site or at ≈1-m intervals around structures and fences at the residential site. Stakes were checked quarterly for signs of termite activity. Stakes with termites present and signs of feeding served as foci for placement of a monitoring station (Lewis et al. 1998). Sixty-five monitoring stations were initially installed at the wildland site and 39 at the residential site.

The monitoring substrate used was a bundle of 11–13 pieces of 30 by 3 by 1-cm, aged ponderosa pine (dry weight ≈400–500 g) held together with 3 rubber bands. The wood bundles were thoroughly soaked in water 24 h before being placed into a monitoring station. Bundles were inserted into the monitoring station so that the cut ends of all pieces of wood were in contact with the soil. The monitoring stations were then sealed. Monitoring stations were examined approximately every 28 d for 3 yr at the wildland site and 2 yr at the residential site (Lewis et al. 1998).

**Termites.** According to accepted biogeographical information, only *R. hesperus* should occur on our wildland and residential sites (Weesner 1970, Nutting 1990). Available keys to soldiers were not helpful in identifying our samples to species. Alates are found only seasonally, thus could not be used for species determination of termites in each monitoring station. In recent years, cuticular hydrocarbon characterization has proven useful as a method for identifying termites and allowed us to use the more abundant worker caste for determination of *Reticulitermes* taxa (Haverty and Nelson 1997).

A sample of 200 live workers was collected from each monitoring station each month, weighed, then placed in a −20°C freezer for later characterization of the cuticular hydrocarbons. These cuticular hydrocarbon profiles were primarily used to determine the hydrocarbon phenotype of *Reticulitermes* collected from each monitoring station on a given date (Haverty and Nelson 1997). Samples of soldiers from each monitoring station were placed in 70% ethanol, and these vouchers were deposited in the Essig Museum of the University of California, Berkeley.

Live body weights were collected to compliment the cuticular hydrocarbon information for characterization of taxa. Each sample of 200 termites (we weighed only undifferentiated pseudergates beyond the 3rd instar; nymphs, larvae, and soldiers were not included in the sample) was aspirated from a tray containing termites and debris. Clean samples of 200 termites were then weighed, as a group, in the collection cup, and the average weight of these worker termites was the data point.

We assumed the true variances for each sample date were the same. The number of individual 200-worker samples used for each phenotype were as follows: 1,030 for phenotype A, 154 for phenotype B, 77 for phenotype C, 129 for phenotype A′, and 123 for phenotype D. Overall means for each phenotype were calculated by averaging the mean weight for each monitoring station for all collection dates; individual collection date means were not weighted by the number of samples for that date. Box plots were drawn to compare and contrast cuticular hydrocarbon phenotypes of *Reticulitermes* and corroborate the existence of >1 taxon on both sites.

**Seasonal Trends in Foraging.** Each monitoring station was visited monthly after installation. Wood bundles were removed and replaced with another preweighed, water-soaked bundle. Presence or absence of termites or termite activity was noted. Each wood bundle containing termites was placed in a separate plastic bag and moved to a shaded location on site for removal of the termites. All termites contained within the wood bundle were tapped onto a tray and the number of termites visually estimated (size classes were as follows: 0 = 0, 1 = 1–100, 2 = 101–300, 3 = 301–1,000, and 4 = >1,000). Termites were then placed in a labeled 15 by 10 by 10-cm plastic box provisioned with a damp paper towel and returned to the laboratory to be weighed and placed in culture. All pieces in a bundle were bound together with rubber bands and returned to the laboratory to determine the amount of wood removed (see *Seasonal Trends in Feeding* below).

Once a monitoring station was occupied by termites it was considered active; before a monitoring station was occupied it was considered a control for determination of feeding trends (see below). A monitoring

station was considered active even though no termites were present at the time of sampling, provided it had signs of termite activity (soil or cartoning on the bundle boards). An active monitoring station did not revert to the status of a control until there were no signs of activity for at least 5 consecutive months. We established this criterion for active status so that we would not eliminate legitimate "zero" values from the feeding trends or over-estimate activity. Thus, the same monitoring station could change back and forth between active and control status over the course of our study. Most, however, remained active once occupied or in control status once abandoned.

The percentage of monitoring stations active and the total estimated number of termites foraging at the time of each inspection were calculated for each month. The percentage of monitoring stations active each month was calculated by adding the number of monitoring stations with a size class rating of 1–4 (in other words termites were present), dividing by that sum plus the number of vacant monitoring stations (currently unoccupied or with evidence of activity during the previous month) times 100. The total estimated number of termites at each inspection was estimated by summing the total number of monitoring stations in a size class times the midpoint of the size class (0 = 0, 1 = 50, 2 = 200, 3 = 650, and 4 = 5,000), an estimating procedure similar to that used by Haverty et al. (1974) and La Fage et al. (1976).

**Seasonal Trends in Feeding.** Once a month, the wood bundles were removed from each monitoring station at each site. Bundles were returned to the laboratory where the soil and termite carton were removed by brushing lightly with a wire brush and using a dental probe. Bundles were placed in an oven at 105°C, dried for 72 h, and weighed to the nearest 100 mg. Wood consumption for each bundle was determined by subtracting this weight from the dry weight before being placed in the field.

Each monitoring station had 2 different bundles that were exchanged each month. Bundles were labeled with an aluminum tag stapled to one of the boards. While one was being processed, the other was in the monitoring station being used by the termites. Bundles were always placed back into the same monitoring station so that termites were fed the same wood and not wood that had been inhabited by another colony or species. When a piece of wood within the bundle was consumed to the point of being too difficult to use for determination of weights, it was replaced with a new board. New boards were dried for 72 h and weighed with the remainder of the bundle before use in the field.

Wood bundles were also collected from monitoring stations with no termite activity. Wood consumption for monitoring stations that were unoccupied for 5 consecutive months or more were included with the controls to account for the natural decay process and weight loss attributed to cleaning and drying. These data served as a measure of the error in our technique for determining wood consumption. Vacant monitoring stations that were previously active, but were unoccupied for 4 or less consecutive months, were included with the active stations. Thus, the sample size for the number of monitoring stations in the control category varied throughout the study.

Wood consumption was expressed as grams of wood removed per monitoring station per day to equalize wood consumption when intervals between samples were unequal. Feeding rates for each phenotype at each site were compared with the wood weight loss for the control monitoring stations during the same period of time. Satterthwaite's approximation to the $t$-test was used to make these comparisons without assuming that variances were equal (SAS Institute 1996). Mean wood consumption (or weight loss) values were compared at the $\alpha = 0.05$ level.

## Results and Discussion

***Reticulitermes* Taxa.** Five cuticular hydrocarbon phenotypes of *Reticulitermes* were found in these study areas (Haverty and Nelson 1997). Three distinct hydrocarbon phenotypes (A, B, and C) were found at the wildland site. Samples from 53 of our monitoring stations were characterized as phenotype A, 10 as phenotype B, and 5 as phenotype C. Two additional hydrocarbon phenotypes were characterized from our monitoring stations at the residential site: A′ and D (Haverty and Nelson 1997). Phenotype A′ is very similar to A. Fourteen of the monitoring stations sampled at the residential site were characterized as phenotype A′ and 12 as phenotype D. On the basis of cuticular hydrocarbon analysis (Haverty and Nelson 1997) and agonistic behavior (Haverty et al. 1999) we

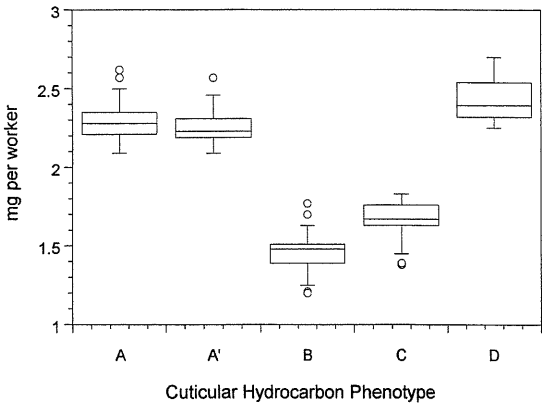


Fig. 1. Box plots of body weights for *Reticulitermes* workers of 3 cuticular hydrocarbon phenotypes (A, B, and C) sampled from monitoring stations at the wildland site near Placerville, CA, and for 2 cuticular hydrocarbon phenotypes (A′ and D) sampled from monitoring stations at the residential site in Novato, CA. Box plots were made to enclose 50% of the data with the median value of the body weight for each phenotype displayed as a horizontal line. The top and bottom of the box mark the limits of ±25% of the body weight measurements. The lines extending from the top and bottom of each box mark the minimum and maximum values that fell within an acceptable range. Values outside of this range, called outliers, are displayed as individual points.

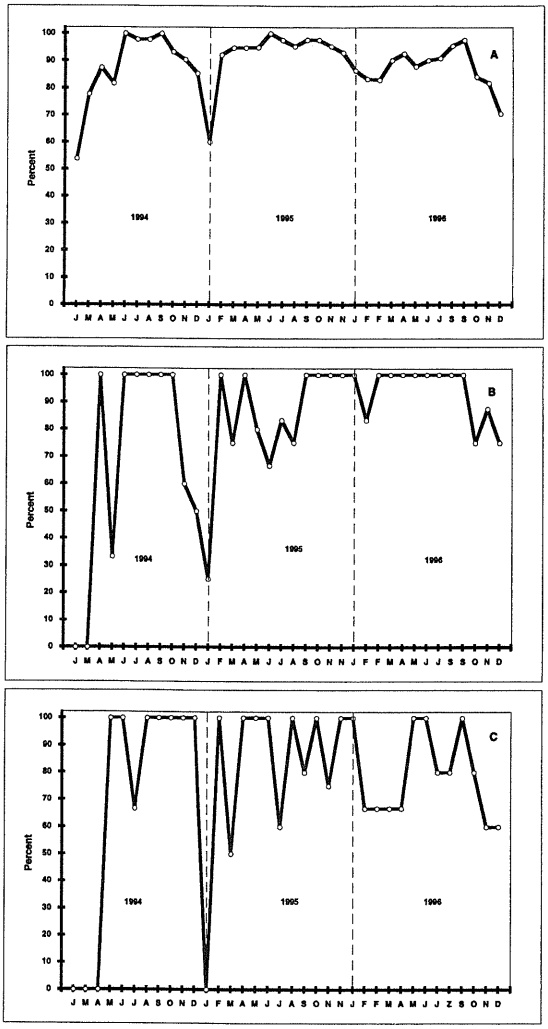


Fig. 2. Percentage of monitoring stations occupied by *Reticulitermes* cuticular hydrocarbon phenotypes A, B, and C at the wildland site near Placerville, CA. Monthly inspections were made from January 1994 through December 1996.

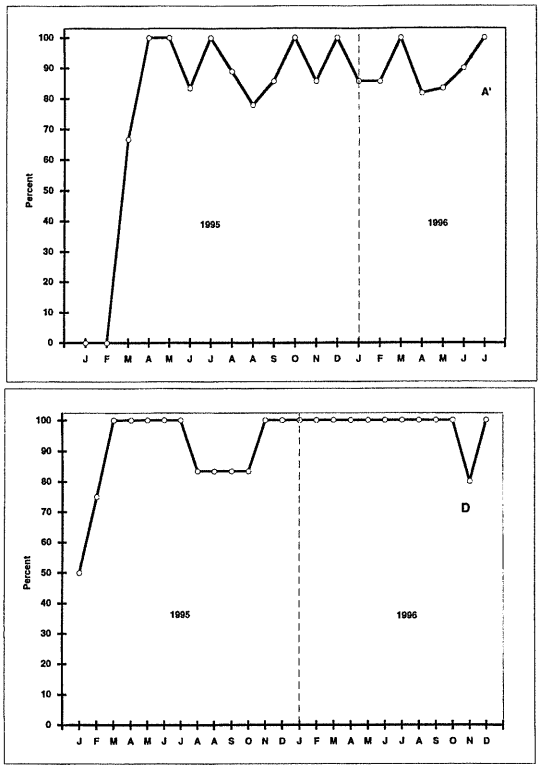


Fig. 3. Percentage of monitoring stations occupied by *Reticulitermes* cuticular hydrocarbon phenotypes A′ and D at the residential site in Novato, CA. Monthly inspections were made from January 1995 through December 1996.

never found 2 phenotypes occupying a monitoring station at the same time. We never observed a cuticular hydrocarbon pattern that had components of >1 phenotype. Furthermore, if mixed phenotypes were placed together on a tray or in a plastic box, we would have observed fighting between phenotypes (Haverty et al. 1999).

Live body weights of workers from each of the 3 cuticular hydrocarbon phenotypes from the wildland site appeared quite different. Phenotype A workers averaged 2.28 mg, phenotype B averaged 1.46 mg, and phenotype C averaged 1.66 mg ($n$ = 1030, 154, and 77 samples of 200 workers, respectively) (Fig. 1). Live body weights of workers from the residential site were also slightly different; phenotype A′ workers averaged 2.26 mg, whereas phenotype D workers were slightly heavier with an average weight of 2.40 mg ($n$ = 129 and 123 samples of 200 workers, respectively) (Fig. 1).

We did not discern any seasonal patterns in live body weights for any phenotype. Live body weight varied from month to month for all cuticular hydrocarbon phenotypes and there was even a slight downward trend over the 3-yr time span for phenotype A at the wildland site. Haagsma and Rust (1995) also observed oscillations in live body weight, but did not attribute this to any seasonal or developmental phenomenon. They did recognize a very obvious difference in both live and dry body weights of *R. hesperus* workers at their 2 research sites, one an urban and the other a wildland. These differences observed by Haagsma and Rust (1995) greatly exceed what we have seen in intraphenotype live body weight differences; they were more akin to the differences between phenotypes A and B from the wildland site (Fig. 1) and suggest to us that the sites they studied may have been inhabited by different *Reticulitermes* taxa.

We are confident that 4 of these hydrocarbon phenotypes, which we identify as A, B, C, and D, represent separate species of *Reticulitermes*. Distinct cuticular hydrocarbon mixtures, morphological differences (both live body weight and soldier head capsule measurements [Haverty and Nelson 1997]), unequivocal agonistic behavior between hydrocarbon phenotypes

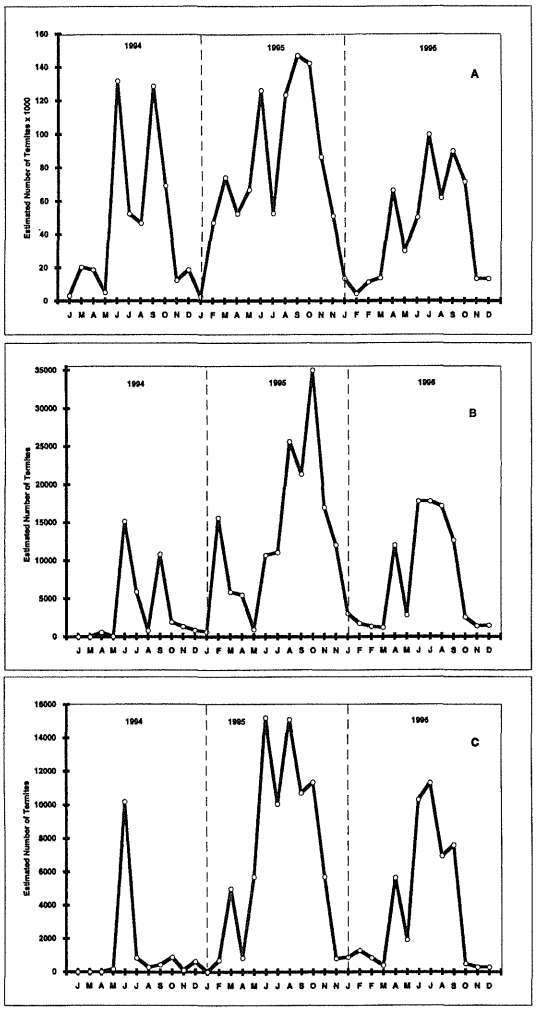


Fig. 4. Total estimated number of termites in cuticular hydrocarbon phenotypes A, B, and C from monitoring stations at the wildland site near Placerville, CA, over 3-yr period.

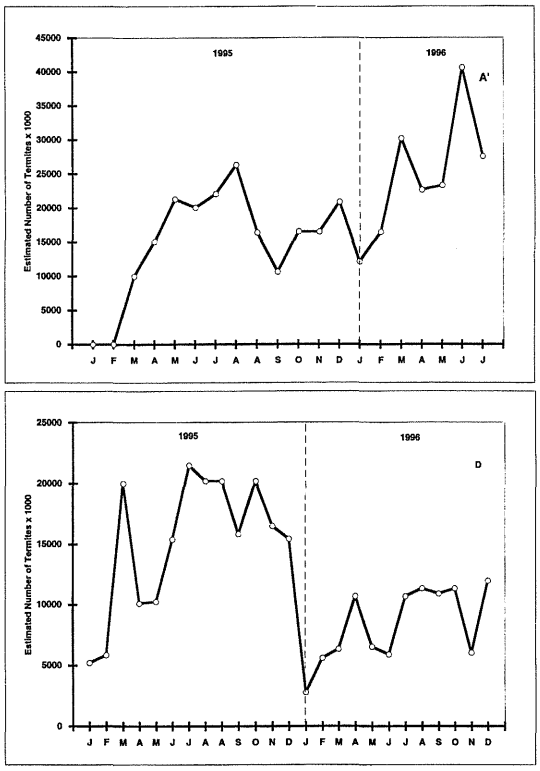


Fig. 5. Total estimated number of termites in cuticular hydrocarbon phenotypes A′ and D from monitoring stations at the residential site in Novato, CA, over 2-yr period.

(Haverty et al. 1999), and soldier defense secretion mixtures (M.I.H., unpublished data) support this conclusion. Phenotypes A and A′ are probably variants of the same species, subspecies, or very closely related species; slight differences in cuticular hydrocarbon mixtures and unequivocal agonistic behavior support status as different taxa. Live body weights of phenotype A and A′ workers were equivalent.

**Seasonal Trends in Foraging.** The proportion of monitoring stations occupied at the time of sampling varied from month to month and between sites. Fluctuation in the percentage of occupied monitoring stations followed the same general pattern for all 3 phenotypes at the wildland site: fewer stations were occupied during the winter months and the greatest number of stations were occupied during the summer and early fall (Fig. 2). Monitoring station occupancy rate was high for phenotype A averaging 89.3% throughout the 3-yr period. Occupancy of monitoring stations by phenotypes B and C displayed greater oscillation with an average occupancy of 82.5% for B and 76.7% for C (Fig. 2). The oscillations for phenotypes B and C were greater because of the fewer number of monitoring stations that they occupied: phenotype C inhabited only 1 monitoring station until June 1994.

Fluctuation in the percentage of monitoring stations occupied at the residential site was much less than at the wildland site. Once monitoring stations became active, they were seldom abandoned. This pattern was followed by both phenotypes (Fig. 3) and there was no apparent seasonal fluctuation in the occupancy at the residential site. Temperature fluctuated much less at the residential site than at the wildland site; the residential site is adjacent to San Francisco Bay and its climate is much less extreme. Furthermore, the monitoring stations were near a structure or in irrigated gardens at the residential site. The occupancy rate of the monitoring stations with phenotype A′ colonies from January 1995 to July 1996 was 81.2%. [Observations from August 1996 to December 1996 are not included because 2 of the 3 phenotype A′ colonies were used in assessment of a commercial subterranean termite bait system.] For phenotype D the mean monitoring station occupancy rate was 93.5% through out the 2-yr period (Fig. 3).

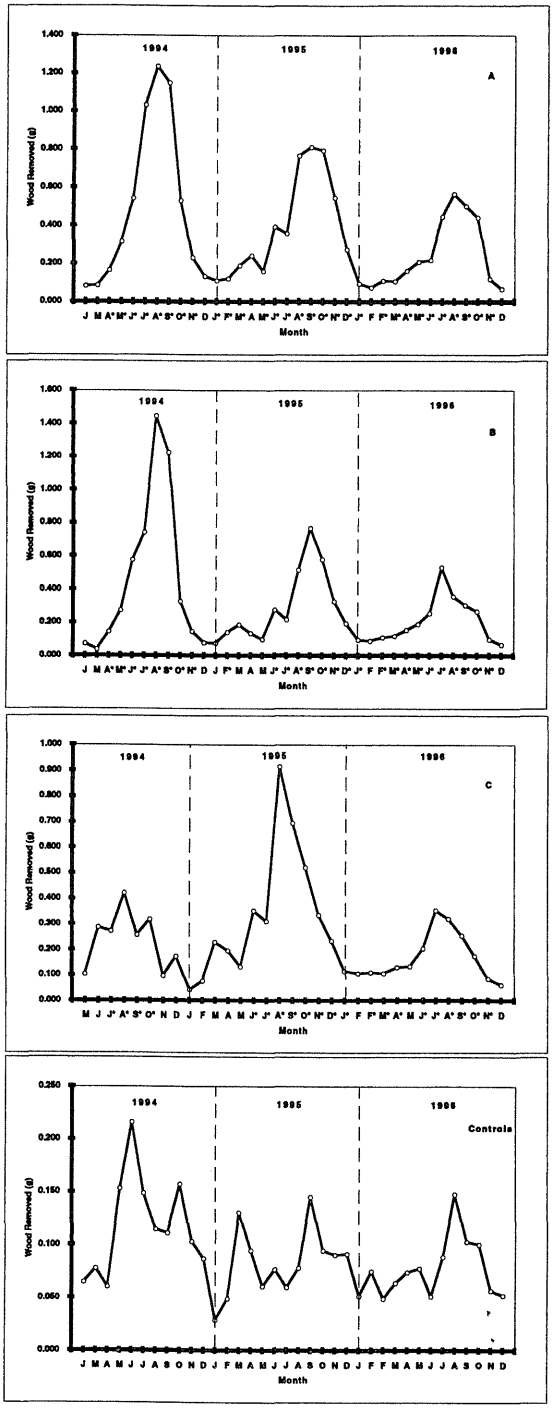


Fig. 6. Wood consumption (grams per monitoring station per day) for 3 cuticular hydrocarbon phenotypes of *Reticulitermes* at the wildland site near Placerville, CA, during 1994, 1995, and 1996. Wood consumption rates for months marked with an asterisk are statistically significant from the control at $\alpha = 0.05$ by Satterthwaite's approximation to the *t*-test (SAS Institute 1996).

The estimated number of termites within the monitoring stations showed seasonal trends at both sites. The total estimated number of termites collected in the monitoring stations varied drastically among the 3 phenotypes at the wildland site, primarily because of the difference in the number of monitoring stations occupied by each (phenotype A, B, and C were in 53, 10, and 5 monitoring stations, respectively). The maximum estimated number of termites collected was 188,750 in October 1995 (Fig. 4). Phenotype A accounted for ≈82% of the total number of termites collected. The estimated number of termites in the monitoring stations at the wildland site showed definite seasonal trends. A pattern of low estimated numbers of termites in the late fall through early spring and high estimated number of termites from early spring to late fall, with a peak from June through October. The exact times of the increases and decreases varied slightly from year to year (Fig. 4).

The estimated number of termites present decreased each summer at the wildland site during the months of June, July, or August (Fig. 4). We routinely made our collections between 1000 and 1200 hours; air and soil temperatures at that time would easily explain this decrease. During the summer at the wildland site, air temperatures at this time of day can reach 35°C. A similar decrease was seen with *H. aureus* in the Sonoran Desert (Haverty et al. 1974); foraging activity was depressed during the hot summer months unless there was significant rainfall to cool the surface layer of soil. Haagsma and Rust (1995) observed a more extreme depression of foraging activity by *R. hesperus* in an arid, wildland location near Riverside, CA; the number of termites recorded during the summer months was much reduced over the number of termites collected in the winter.

The total estimated number of termites collected in the monitoring stations at the residential site was less than at the wildland site. The estimated number of termites of both phenotypes varied as it did at the wildland site, primarily because of the difference in the number of monitoring stations occupied by each phenotype (phenotype A′ and D were in 14 and 12 monitoring stations, respectively). The maximum estimated number of termites collected at the residential site was 46,500 on 2 different occasions: August 1995 and June 1996 (Fig. 5).

The estimated number of termites in the monitoring stations at the residential site did not show an extreme seasonal trend as was seen at the wildland site. The generalized pattern was one of low estimated numbers of termites in the late fall through early spring and high estimated numbers of termites from early spring to late fall, with a peak from June through November or December. Phenotype A′ appeared to have greater estimated numbers of termites in the monitoring stations when the estimated numbers of phenotype D workers were lower. The opposite was also true: when the estimated numbers of phenotype D workers were high, estimated numbers of phenotype A′ workers were low (Fig. 5). The summer decrease in the estimated number of termites present seemed to occur

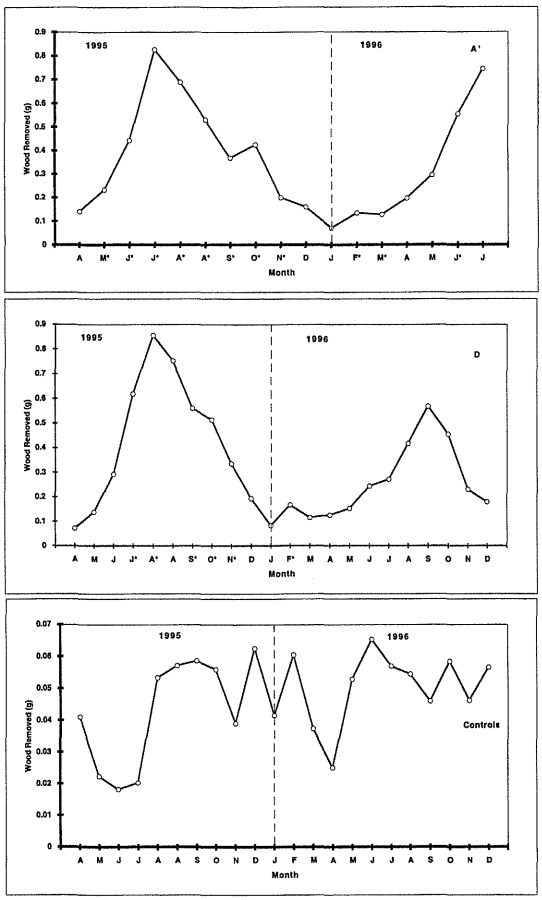


Fig. 7. Wood consumption (grams per monitoring station per day) for 2 cuticular hydrocarbon phenotypes of *Reticulitermes* at the residential site in Novato, CA, for 1995 and 1996. Wood consumption rates for months marked with an asterisk are statistically significant from the control at $\alpha = 0.05$ by Satterthwaite's approximation to the *t*-test (SAS Institute 1996).

earlier at the residential site than at the wildland site; the depression in the estimated number of termites present occurred from April to May or May to June (Fig. 5).

**Seasonal Trends in Feeding.** Feeding by termites at both sites displayed the same general trends. Feeding is minimal or absent during the winter and early spring and peaks in mid to late summer. Feeding activity was measured at the wildland site for 36 mo (Fig. 6). During 1994 feeding at the monitoring stations was minimal until April, peaked in August, and declined to near zero in November for phenotype C and in December for phenotypes A and B (Fig. 6). At the peak, hydrocarbon phenotypes A and B consumed 1.12–1.33 grams per day per station greater than the control, respectively, whereas consumption by phenotype C was 0.31 gram per day per station greater than the control (Fig. 6).

Feeding appeared to be delayed in 1995 until June for all 3 phenotypes (Fig. 6). Feeding peaked in August for phenotype C and in September for phenotypes A and B. At the peak, wood consumption in the monitors was ≈0.55–0.67 gram per day per monitor greater than the controls for all 3 hydrocarbon phenotypes (Fig. 6). Statistically significant feeding continued until January 1996, then approached zero for all 3 phenotypes for most of the month of January (4 January 1996–1 February 1996). In 1995, phenotype C began to use the monitoring stations to a greater degree than in 1994 (Fig. 2).

During 1996, feeding was apparently delayed considerably until mid-June to mid-July (Fig. 6). This may have been because of the extremely heavy precipitation experienced in central California during January to May. Feeding peaked in July for phenotypes B and C and in August for phenotype A. In addition, to being delayed, feeding appears to be much reduced in 1996; at peak feeding activity, consumption exceeded weight loss from the controls by only 0.27–0.44 gram per day per monitor (Fig. 6). We are not certain of the reason for this apparent downward trend from 1994–1996. We routinely remove all termites collected in the monitoring stations without replacing them. This harvesting of foraging termites might have taken a toll on the termite populations. Furthermore, the quality of the wood in the bundles gradually changed from using aged ponderosa pine to using wood cut from recently purchased stakes, and this may have affected any preference for the wood in the monitoring stations.

Measurement of feeding activity at the residential site did not begin until April 1995. Statistically significant feeding occurred in May, peaked in July, and continued into November for phenotype A'. For phenotype D statistically significant feeding did not occur until the June/July interval, peaked in August, and continued into November (Fig. 7). At the peak, termites consumed 0.81–0.83 gram per day per monitor more than the weight loss in the controls.

In 1996, statistically significant feeding occurred as early as February at the residential site and began to increase dramatically for phenotype A' in May; for phenotype D increased feeding was delayed until June (Fig. 7). For phenotype A' feeding peaked in July and in September for phenotype D. At the peak, termites consumed 0.52–0.69 gram per day per monitor more than the weight loss in the controls (Fig. 7).

In summary, the monitoring station that we designed and used in this study (Lewis et al. 1998) appears to be an excellent mechanism for studying seasonal activity of *Reticulitermes* in both wildland and residential localities. The sequence of monitoring with ponderosa pine stakes followed by installation of monitoring stations as described above, proved to be very efficient. We refined this by abandoning locations when monitoring stations were not occupied and moving the equipment to a new, potentially active site. This approach is not unique; it has been used in research studies in Florida (Su and Scheffrahn 1986), Hawaii (Grace 1996), and Georgia (Forschler and Townsend 1996). We feel that assessing the number of termites in a station is not as reliable an indication of termite activity over time as the measurement of wood

consumption. Counting the number of termites collected simply represents the equivalent of a photograph of the activity at the particular time of collection. Measuring wood consumption represents a running average of the activity during the period between collections, but also assumes equivalent feeding at this resource in relation to other feeding sites used by these termites.

Understanding the cycle of feeding is relevant to the installation of baits and when to expect optimal results. It will also help researchers determine when a drop in feeding activity is correlated with the elimination, or severe reduction, of a colony rather than the seasonal aspects of feeding. Knowing when termites are likely to be present and when they are not could simplify the monitoring aspects of a bait/monitoring control program.

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