Size and Dispersion of Colonies of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a Wildland and a Residential Location in Northern California

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ABSTRACT Mark-release-recapture studies were conducted to estimate foraging populations, maximum foraging distances between foraging sites, and minimum total foraging distance for three colonies of two cuticular hydrocarbon phenotypes of *Reticulitermes* at a wildland site near Placerville, CA, in the Sierra Nevada foothills and for six colonies of three phenotypes at two residential sites in Marin County. At Placerville, the hydrocarbon phenotype B colony had the fewest termites, with an estimated foraging population of 4,476–13,602, and occupied only one monitoring station. The two phenotype A colonies had foraging populations estimated to range from 40,809 to 128,597; one inhabited one monitoring station, whereas the other occupied three stations with a maximum distance between monitoring stations of 6.3 m. At the Marin County sites, two phenotype D colonies were estimated to have foraging populations ranging from 9,191 to 194,692; each foraged at a single monitoring station. Estimated foraging populations for the three phenotype A′ colonies ranged from 71,483 to 491,901 with the maximum distance between monitoring stations ranging from 11.7 to 25.3 m. The phenotype A colony was estimated to have 8,747–25,190 foragers, with a maximum distance between monitoring stations of 1.8 m.

KEY WORDS *Reticulitermes* spp., foraging populations, foraging territory, mark-release-recapture

TERMITE DAMAGE HAS a significant economic impact on many wooden structures throughout the United States. *Reticulitermes flavipes* (Kollar), *R. virginicus* (Banks), *R. hesperus* Banks, and *R. tibialis* Banks are among the most economically important pests of structures in the mainland United States (Su and Scheffrahn 1990), yet there have been relatively few studies of their population size and foraging characteristics (Esenther 1980; Howard and Haverty 1980, 1981; Howard et al. 1982; Grace et al. 1989; Grace 1990, 1992; Su et al. 1993; Haagsma and Rust 1995; Forschler and Townsend 1996; Thorne et al. 1996). Equivalent information has been gathered for *Heterotermes aureus* (Snyder) in the desert Southwest (Haverty and Nutting 1975; Haverty et al. 1975; Jones et al. 1987, Jones and Nutting 1989; Jones 1990a, 1990b) and *Coptotermes formosanus* Shiraki in Louisiana, Hawaii, and Florida (King and Spink 1969, Lai 1977, Tamashiro et al. 1980, Su et al. 1983, Su and Scheffrahn 1988, Grace et al. 1996). However, similar information for *Reticulitermes* in northern California does not exist.

We report here estimates of the foraging populations and distances or territories of colonies of *Reticulitermes* from two locations in northern California: a wildland site in the Sierra Nevada and two residential sites in Marin County. This work was conducted to assist the development of baits for control of subterranean termites. An understanding of the size of termite foraging populations and the magnitude of their foraging areas and distances are key to effective deployment of baits, as well as understanding the role *Reticulitermes* plays in natural systems.

Materials and Methods

Study Areas, Termites, and Monitoring Stations. We used one wildland location and two residential locations (Haverty et al. 1999a). The wildland site was in the Eddy Arboretum in the western portion of the Pacific Southwest Research Station's Institute of Forest Genetics (IFG) near Placerville, CA. The wildland site was used to study *Reticulitermes* colonies in a setting without the interference of artificial structures. The residential locations were in Novato and Larkspur. The Novato site (St. Francis Church) consists of a single family dwelling (that serves as the church rectory), the church, and extensive gardens, walks, and large trees on a 1-ha lot. The rectory is heavily infested with *Reticulitermes*. The Larkspur site is a single family dwelling (60 yr old) with a light infes-

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tation of *Reticulitermes*. The residential sites were used to develop an understanding of the ecology and behavior of *Reticulitermes* under situations where suppression or elimination of colonies is desirable.

According to currently accepted biogeographical information, only *R. hesperus* should occur on our Sierra Nevada (IFG) and Marin County (Novato and Larkspur) sites (Weesner 1970, Nutting 1990). Available keys to soldiers were not helpful in identifying our termites to species. Alates are found only seasonally and were extremely rare in foraging groups, thus could not be used for species determination at each monitoring station. Thus, we characterized the cuticular hydrocarbons of the termites collected from each of our monitoring stations (see below), because this allowed us to use the more abundant worker caste to assign a *Reticulitermes* taxon (Haverty and Nelson 1997). Samples of soldiers, workers, and nymphs were placed in 70% ethanol and deposited in the Essig Museum of the University of California, Berkeley.

Stakes of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws, were driven into the soil in a grid (2 × 2m) at (IFG) or at 1-m intervals around structures at residential sites and checked quarterly for signs of termite activity. Those stakes with termites present and revealing signs of significant termite feeding served as foci for placement of a monitoring station adjacent to the stake (Lewis et al. 1998). Sixty-eight monitoring stations were installed at IFG, 38 at the Novato site, and 12 at the Larkspur site.

Mark-Release-Recapture Studies. Size and dispersion of foraging populations were estimated with mark-release-recapture studies. At each site, all termites collected from a single monitoring station with high foraging activity were counted, taken to the laboratory, and fed filter paper impregnated with 0.1% (wt:wt) Nile Blue A (Sigma, St. Louis, MO) for 14 d (Su et al. 1993, Su 1994, Forschler and Townsend 1996). After 14 d, the fat body of nearly all of the workers was blue. Stained workers were counted and returned to the single bait station from which they had been collected (Grace et al. 1989, Su et al. 1993, Haagsma and Rust 1995). All monitoring devices were visited 2 wk after the stained termites were released, and the number of stained and unstained termites in each trap was determined. Termites collected from additional stations containing marked termites were stained (as above) and released to their respective monitoring stations. This mark-release-recapture scheme was repeated three times for each colony examined. This same procedure was done with Sudan Red 7B (Sigma) (Su et al. 1983, Grace and Abdallay 1989) for one colony at IFG and one colony at the Novato site. The Lincoln index and the weighted mean model (Bailey 1951, Su and Scheffrahn 1988, Su et al. 1993, Su 1994, Forschler and Townsend 1996) were used to estimate the foraging population (and standard error of the estimate) for each colony. The Lincoln index was calculated using the data from the first mark-release-recapture cycle.

Using the mark-release-recapture regime, we associated monitoring stations for three colonies at IFG, four colonies at Novato, and two colonies at Larkspur. When marked workers appeared in a nearby monitoring station that had not previously contained marked foragers, we assumed that the foraging groups within these monitoring stations were members of the same colony. For the purposes of this paper we considered a colony to be foraging groups of the same phenotype sharing interconnected galleries (Su and Scheffrahn 1998). Our definition assumes that these foragers also are associated with other conspecifics involved in cooperative rearing of offspring (Wilson 1971). The maximum distance between monitoring stations used by a colony was determined by simply measuring (or calculating) the linear distance between the two connected monitoring stations that are farthest apart. The minimum total distance potentially traveled by members of a colony was computed as the sum of the linear distances between all possible pairs of monitoring stations occupied by the colony. This measurement assumes foraging galleries between monitoring stations are constructed in a straight line, which is highly unlikely, and therefore is a conservative estimate of the distances that could be traveled by foragers in these colonies.

Results and Discussion

***Reticulitermes* Taxa on Site.** One of the first problems we encountered was the inability to identify the *Reticulitermes* foragers to species. By characterizing cuticular hydrocarbons of all foraging groups in the monitoring stations on all of our sites, we identified five phenotypes of *Reticulitermes* in these study areas (Haverty and Nelson 1997). At IFG, we found three very distinct hydrocarbon phenotypes: A, B, and C. Samples from 53 of our monitoring stations were characterized as phenotype A; 10 as phenotype B, and five as phenotype C.

Two additional hydrocarbon phenotypes were characterized from our monitoring stations in Marin County: A′ and D. Phenotype A′ is very similar to A, with the exception of two additional peaks (separate isomers of pentacosatriene) that do not appear in any phenotype A samples (Haverty and Nelson 1997). Phenotype D is qualitatively similar to, but quantitatively very different from, phenotype B from IFG. Sixteen of 34 monitoring stations sampled in Marin County were characterized as phenotype A′, four as phenotype A, and 14 as phenotype D.

We are fairly confident that four of these hydrocarbon phenotypes (A, B, C, and D) represent separate species of *Reticulitermes*. Distinct, consistent, repeatable cuticular hydrocarbon mixtures and soldier head capsule measurements (Haverty and Nelson 1997), consistent body weight differences between phenotypes A, A′, and D versus B versus C (Haverty et al. 1999a), unequivocal agonistic behavior toward individuals of a different phenotype (Haverty et al. 1999b), and distinct, consistent, and repeatable soldier defense secretion mixtures (unpublished data) lead us to 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.

At IFG the occupying phenotype A foragers were replaced by phenotype C foragers in one monitoring station. Foraging groups of phenotypes A and B were collected within 2 m of each other at IFG. At the Novato site, phenotype A′ foragers displaced phenotype D foragers in one monitoring station. Phenotypes A′ and D occupied monitoring stations within 3 m of one another at the Novato site. No phenotype shifts occurred at the Larkspur site, but phenotype A and D consistently foraged at monitoring stations that were within 1 m of one another.

Foraging Populations. Mark-release-recapture studies resulted in forager population estimates that seemed small when compared with early reports of *R. flavipes* colonies having several millions of individuals (Esenther 1980; Grace et al. 1989; Su et al. 1993). Our estimates were, however, similar to colony estimates reported for *R. flavipes* and *R. virginicus* by Forschler and Townsend (1996) and Howard et al. (1982), with a great majority of the colony estimates below 200,000. Thus, far, we have characterized two phenotype A colonies and one phenotype B colony at IFG; three phenotype A′, two phenotype D, and one phenotype A from Marin County. Foraging population estimates range from a low of 4,476 to a high of 491,901 (Table 1).

We agree with Thorne et al. (1996) and Evans et al. (1998) that the forager population estimates generated by mark-release-recapture methods should be interpreted cautiously. Small standard errors relative to the estimate of both the Lincoln index and the weighted mean model imply precision, but the accuracy of one or both methods is questionable. In only one instance (Marin-1 colony) did we have estimates that seemed to agree, based on the Lincoln index and the weighted mean model. In all of the other cases, one of the estimates was 1.6–3.0 times as large as the other (Table 1) and no method was consistently higher than the other (Forschler and Townsend 1996).

There is no practical way to test the accuracy of estimates (by Lincoln index or weighted mean model) of foraging populations of subterranean termites without destroying the colony. Even direct excavations, such as those done by Howard et al. (1982), probably do not account for all of the termites in a colony. Furthermore, the colony and its gallery system are destroyed in the process. The key considerations in using a marker to estimate termite foraging population size are (1) to release as many marked individuals as possible, (2) to allow those marked individuals sufficient time to leave the point of release and mix thoroughly throughout the gallery system, and (3) to collect as many termites as possible during recapture (J. K. Grace, personal communication). The weighted mean model meets these criteria but requires much more time and resources than does using the Lincoln index. It would be helpful if the foraging territory could be determined in advance, using another dye (Su et al. 1991) or fluorescent paint (Forschler 1994) rather than relying on the mark-release-recapture activity to determine foraging territory. This would facilitate marking foragers from multiple monitoring stations at the beginning of the mark-release-recapture cycle (Forschler and Townsend 1996). The decision to use either the Lincoln index or the weighted mean model should be based on the objectives of the study and the resources available for the study.

We did not conduct specific experiments to test the validity of the underlying assumptions of population estimates based on mark-release-recapture studies (Thorne et al. 1996, Evans et al. 1998). We are confident that the mark (fat-soluble dye) persists over the complete mark-release-recapture cycle. We fed collected foragers on stained filter paper for 14 d rather than the 3 d (Su et al. 1993, Thorne et al. 1996) or 1 wk (Forschler and Townsend 1996) in previous studies. The surviving individuals that were returned to their monitoring station were quite blue. We did not test whether these individuals had sufficient stained filter paper in their gut to pass it on to colony mates. Furthermore, we know that the mark is persistent in these colonies because we continued to collect stained foragers months after our mark-release-recapture studies during the course of studies of foraging behavior at these same sites (Haverty et al. 1999a).

We do have suspicions that the survival rate of marked individuals returned to the monitoring stations is slightly reduced. In all but two instances, the number of foragers returned to the monitoring stations after feeding on stained paper in the laboratory for 14 d was an average of 81% of the total number of foragers captured in the previous cycle. This decrease was caused primarily by mortality in the laboratory, not lack of feeding on the stained paper. The third release cycle of IFG-2 was reduced by 96.7% because of excessive mortality, apparently from over-watering the filter paper. The two exceptions (IFG-3 and Marin-6) involved augmentation of the second release with termites from laboratory cultures from the same monitoring station (Table 1). The third release for Marin-1 was terminated because of high mortality during the marking process (Table 1).

Of the nine colonies for which we estimated foraging populations, four were restricted to a single monitoring station (IFG-1, IFG-3, Marin-4, and Marin-5). Of the other five colonies, it appears that marked individuals traveled to other monitoring stations over distances approaching 25 m (Marin-1 and Marin-3). In two instances, foragers temporarily abandoned individual monitoring stations (IFG-2, Yq30; Marin-3, St35 and St40; and Marin-6 and L32). From these observations, we surmise that foragers mix fully with unmarked foragers within the interval of release and recapture. We saw nothing that would imply site fidelity or avoidance of disturbed monitoring stations (Forschler and Townsend 1996, Evans et al. 1998).

We can only assume that the probability of capture of marked and unmarked individuals is the same, provided marked foragers remain healthy. Furthermore, we also must assume the population is closed over the 8-wk term of the mark-release-recapture cycle. The most critical of the assumptions in this study is that

Table 1. Population estimates based on Lincoln Index and Weighted Mean Model and foraging distances for *Reticulitermes* spp. colonies at the Institute of Forest Genetics and 2 locations in Marin County: St. Francis Church, and the Lesneski residence

Location-Colony[a]	Monitor[a]	Taxon[b]	Mark-release-recapture cycle[c]									Lincoln Index (SE)	Weighted mean model (SE)	Max dist. (m)[d]	Min. total dist. (n)[e]
			R1	M1	N1	R2	M2	N2	R3	M3	N3				
IFG-1	Yk32	A	3,312	29	1,126	988	24	179	152	20	208	128,597 (22,047)	73,092 (8,611)	0	0
IFG-2	Yq31	A	1,423	6	266	148	41	1,091	102	18	842	—	—	—	—
	Yq30		0	34	1,136	592	84	2,425	19	0	0	—	—	—	—
	Yr33		0	19	290	193	0	8	0	27	1,267	—	—	—	—
	Total		1,423	59	1,692	933	125	3,524	121[f]	45	2,109	40,809 (5,049)	67,284 (4,456)	6.3	12.8
IFG-3	Yv34	B	698	80	518	1336[g]	114	1,073	976	48	256	4,476 (454)	13,602 (876)	0	0
Marin-1	St18	A′	7,742	190	13,115	11,945	321	7,862	7,210	357	4,702	—	—	—	—
	St25		0	233	13,761	12,467	630	6,461	5,602	1,037	10,171	—	—	—	—
	St12[g]		0	0	0	0	0	0	0	0	0	—	—	—	—
	Total		7,742	423	26,876	24,412	951	14,323	12,812	1,394	14,873	491,901 (23,617)	473,420 (9,000)	13.4	26.4
Marin-2	St57[h]	A′	2,803	100	5,790	4,461	99	4,941	4,624	0	3,215	—	—	—	—
	St87[h]		0	0	0	0	172	3,628	3,758	0	176	—	—	—	—
	Total		2,803	100	5,790	4,461	271	8,569	8,382	0	3,391	162,294 (15,774)	347,420 (18,086)	11.7	11.7
Marin-3	St63	A′	1,879	139	5,055	4,781	15	445	—	—	—	—	—	—	—
	St35		0	7	111	0	0	0	—	—	—	—	—	—	—
	St40		0	4	503	330	0	0	—	—	—	—	—	—	—
	St66		0	0	0	0	43	1,072	—	—	—	—	—	—	—
	St69		0	0	0	0	288	6,279	—	—	—	—	—	—	—
	St71		0	0	0	0	9	382	—	—	—	—	—	—	—
	St78		0	12	494	259	58	906	—	—	—	—	—	—	—
	Total		1,879	162	6,163	5,370	413	9,094	—[i]	—[i]	—[i]	71,483 (5,474)	132,106 (5,514)	25.3	291.6
Marin-4	St21	D	823	561	6,265	5,512	864	3,932	2,798	1,632	6,901	9,191 (369)	26,506 (960)	0	0
Marin-5	L6	D	841	4	926	829	17	841	706	12	301	194,692 (63,482)	84,963 (14,993)	0	0
Marin-6	L34	A	156	13	604	1,268[j]	11	222	204	22	414	—	—	—	—
	L32		0	1	181	158	0	0	0	2	34	—	—	—	—
	Total		156	14	785	1,426	11	222	204	24	448	8,747 (2,024)	25,190 (3,633)	1.8	1.8

[a] Marin County sites are signified by a monitor with St for St. Francis Church in Novato and L for the Lesneski residence.

[b] Hydrocarbon phenotype as described in Haverty and Nelson (1997). The exact species of *Reticulitermes* has not been determined.

[c] Mark-release-recapture cycle: R1, number of marked termites released in the first cycle; M1, number of marked termites recovered in first recapture; N1, number of termites (marked and unmarked) recaptured in first recapture; R2, number of termites released in the second cycle; M2, number of marked termites recovered in second recapture; N2, number of termites (marked and unmarked) recaptured in second recapture; R3, number of termites released in the third cycle; M3, number of marked termites recovered in third recapture; N3, number of termites (marked and unmarked) recaptured in third recapture.

[d] The longest distance between two monitoring stations used by this colony.

[e] The cumulative distance among all of the monitoring stations used by this colony.

[f] A large proportion of the individuals marked in this portion of the cycle died as a result of overwatering of the filter paper. Thus, <10% of the foragers gathered in the second cycle lived to be released in the third cycle.

[g] This monitoring station was not a part of this colony during the mark-release-recapture portion of this study, but data became part of the foraging territory.

[h] The mark-release-recapture work on this colony was done with Sudan Red 7B.

[i] The third portion of the mark-release-recapture cycle was discontinued due to excessive mortality in the foragers feeding on the stained filter paper in the laboratory.

[j] The number of marked (dyed) foragers was augmented in this release cycle by taking individuals that we maintained in culture in the laboratory.

marking with dye affects the survivorship of the returned foragers. Any reduction in survivorship will decrease the probability of recapturing marked individuals and will increase the population estimate.

We accept that our forager population estimates are slightly high. Our general conclusion is that the colonies that we have been working with at all three of our sites are more similar to the situation with *Reticulitermes* in Georgia and southern California and *H. aureus* in southern Arizona: numerous, relatively small colonies coexisting in the same area with populations ranging from (5,000–500,000 foragers (Haverty et al. 1975; Jones 1990a, 1990b; Haagsma and Rust 1995; Forschler and Townsend 1996).

Foraging Area, Territory, Range, Distance. Our attempts at defining foraging territories were frustrating at first. We expected the termites marked in one monitoring station to show up in numerous other stations and cover foraging areas ranging up to ≥3,000 m^2 with maximum foraging distances in excess of 70 m, as has been demonstrated for *R. flavipes* in Florida (Su et al. 1993) and Canada (Grace et al. 1989, Grace 1990), *C. formosanus* in Louisiana (King and Spink 1969), Florida (Su and Scheffrahn 1988), and Hawaii (Lai 1977, Tamashiro et al. 1980), and *H. aureus* in southern Arizona (Jones 1990a).

Our first mark-release-recapture attempt with a phenotype A monitoring station at IFG (IFG-1) re-

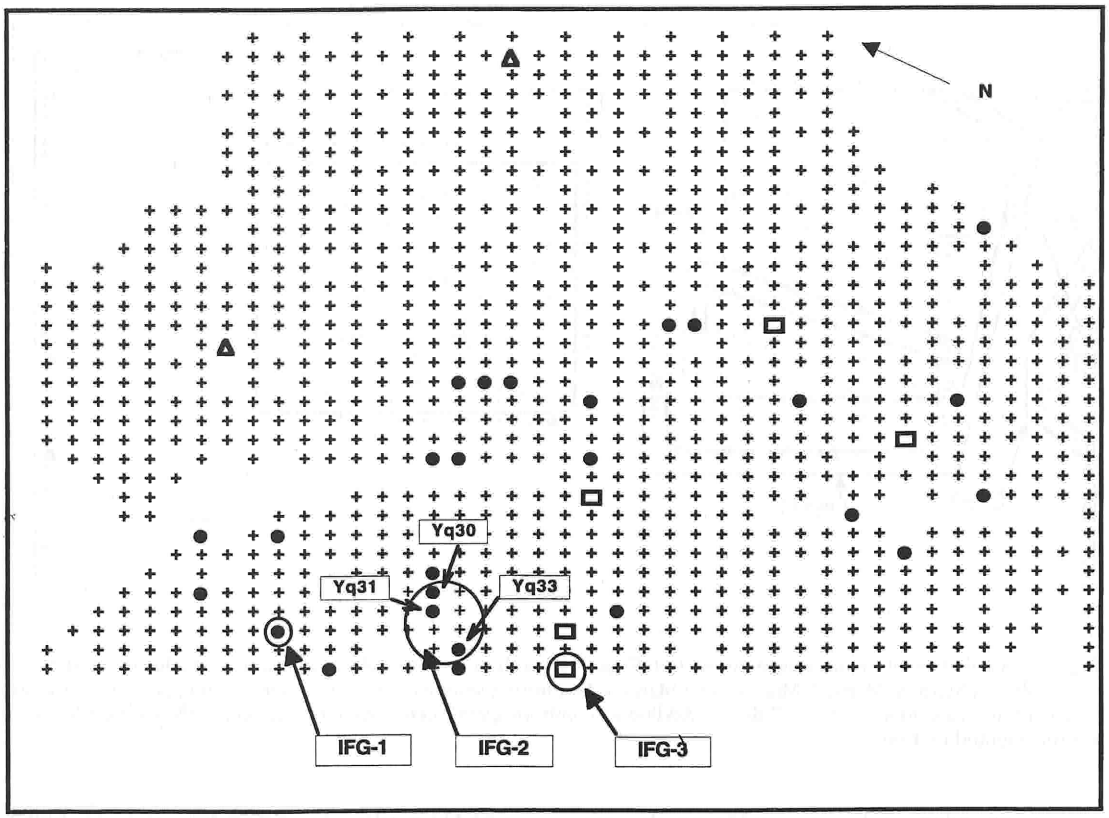

Fig. 1. Distribution of a portion of the monitoring stations in the western section of the Eddy Arboretum of the Institute of Forest Genetics near Placerville, CA, demonstrating the locations of *Reticulitermes* colonies IFG-1, IFG-2, and IFG-3. Cuticular hydrocarbon phenotype occupying each monitoring station: A, circle; B, square; C, triangle.

sulted in marked termites never showing up in another station (Fig. 1; Table 1). The next two attempts netted similar results. In a different phenotype A monitoring station (Yq31), marked individuals traveled to only two additional stations (Yq30 and Yr33), resulting in a maximum foraging distance of 6.3 m between Yq30 and Yr33 and a minimum total foraging distance of 12.8 m among all three monitoring stations of this colony (IFG-2). In a phenotype B station (IFG-3), marked termites never moved from their original monitoring station, even though another phenotype B station was only 4 m away. Thus, at IFG we characterized three colonies; two of these colonies (IFG-1 and IFG-3) occupied a single monitoring station, and the other (IFG-2) occupied three monitoring stations (Fig. 1; Table 1).

Studies at the Novato site, St. Francis Church, also initially resulted in very restricted movement of marked termites for two colonies. In May 1995, dyed termites were placed in St18 and recovered in St18 and St25 (Fig. 2; Table 1). The mark-release-recapture study was continued, but the blue termites occurred only in St18 and St25, monitoring stations only 6.6 m apart. In July 1995, we marked workers in St57 with Sudan Red 7B so that they would not be confused with any of the other phenotype A′ monitoring stations. Here, too, movement was limited. Red termites reappeared only in St57 the first 2 wk (Table 1). However, after a second marking of termites in St57, red-stained workers showed up in St87, 11.7 m away on the opposite side of the building (Fig. 2). We never recovered red termites at any other monitoring station and concluded that this colony was limited to these two monitoring stations.

In March 1996 we initiated another series of mark-release-recapture studies. Blue-stained workers were released in St63. At the 2-wk recapture, blue termites were collected in St18, St25, St35, St40, St60, St63, and St78 (Fig. 2). To determine the origin of the blue workers in St35, St60, and St78 (St18 and St25 continued to have blue workers from the mark-release-recapture studies in 1995), we next stained workers in St18 with Sudan Red 7B. Red termites showed up in St18, St25, and St60 only. From this we concluded that the blue workers that showed up in St60 in April originated from St18 or St25. In May, additional red termites were returned to St18; 2 wk later red workers were collected in St12, as well as in St18 and St25. It was apparent from this latest mark-release-recapture study that the original colony of St18 and St25 (Marin-1) was expanding their territory in the spring of 1996 to include St60 (which was subsequently aban-

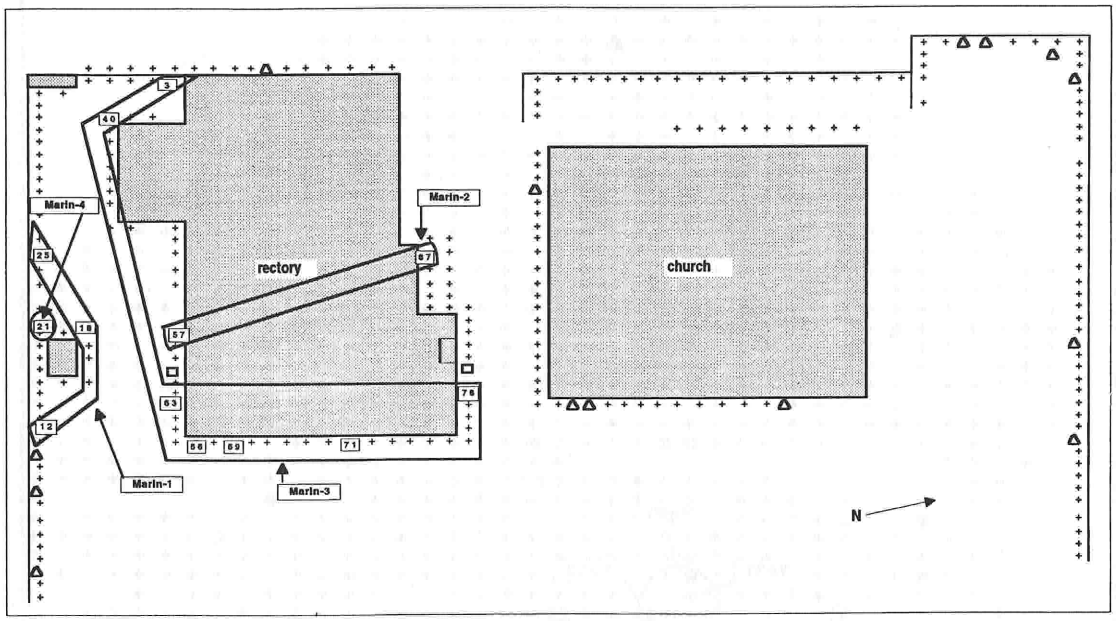

Fig. 2. Distribution of monitoring stations at St. Francis Church in Novato, CA, demonstrating the locations of *Reticulitermes* colonies Marin-1, Marin-2, Marin-3, and Marin-4. Monitoring stations used to estimate foraging population size and foraging distances are numbered (see Table 1). Additional monitoring stations occupied by cuticular hydrocarbon phenotype D are represented by triangles.

doned by this colony and never used by another colony) and to "invade" St12 by displacing the phenotype D colony that was residing in that station. Also, in May, blue termites, but no red termites, appeared in St66, St69, and St71. These workers obviously originated from the stained individuals that originated from St63. Agonistic behavior studies corroborated that St35, St40, St63, St66, St69, St71, and St78 were all used by the same phenotype A′ colony (Haverty et al. 1999b).

One additional colony was characterized at the Novato site. Dyed termites placed in St21, a monitoring station occupied by phenotype D foragers, never traveled to another monitoring station (Fig. 2; Table 1). Thus, at this site we were able to characterize four colonies. Marin-1 had the largest estimated foraging population and initially occupied two monitoring stations. It expanded its foraging range to two other monitoring stations, then abandoned one, with a resulting minimum total foraging distance of 26.4 m. Marin-2 occupied only two monitoring stations 11.7 m apart, but traversed the width of the structure. Marin-3 occupied the most monitoring stations and had the largest minimum total foraging distance. Marin-4 occupied only one monitoring station (Fig. 2; Table 1).

At the Larkspur site, we characterized two additional colonies. Marin-5 occupied only one monitoring station, but Marin-6 occupied two monitoring stations only 1.8 m apart (Fig. 3; Table 1).

At one of our Marin County sites, St. Francis Church, we observed an instance where one species displaced another within a monitoring station. Monitoring station St12 was originally occupied by phenotype D termites (Fig. 2). In June 1996, phenotype A′ termites (which originated from stations St18 and St25) appeared in St12. This discovery was made by mark-release-recapture experiments and was corroborated by analysis of the cuticular hydrocarbons and agonistic behavior studies (Haverty and Nelson 1997, Haverty et al. 1999b). A similar displacement occurred at IFG. This displacement was concurrently discovered by examination of a dramatic shift in body weights, morphological measurements of soldiers in voucher specimens, abnormalities in results of agonistic behavior bioassays, and finally confirmed by an additional characterization of the cuticular hydrocarbons of the workers (Haverty and Nelson 1997, Haverty et al. 1999b).

These two discoveries of displacement of one colony by another within an occupied monitoring station were purely serendipitous. The displacements were unequivocally verified by characterization of the cuticular hydrocarbons, even though other observations suggested a change. Additional displacements within monitoring stations will likely be discovered with additional scrutiny of worker weights, occupancy trends, agonistic behavior, and cuticular hydrocarbon analyses. Displacement of colonies with the same cuticular hydrocarbon phenotype will be the most difficult to determine; in these instances the agonistic behavior of workers will be the best means of detecting these shifts in occupancy.

In summary, we have learned that the area or territory used by a colony is often not very large for the *Reticulitermes* that we studied near Placerville and in

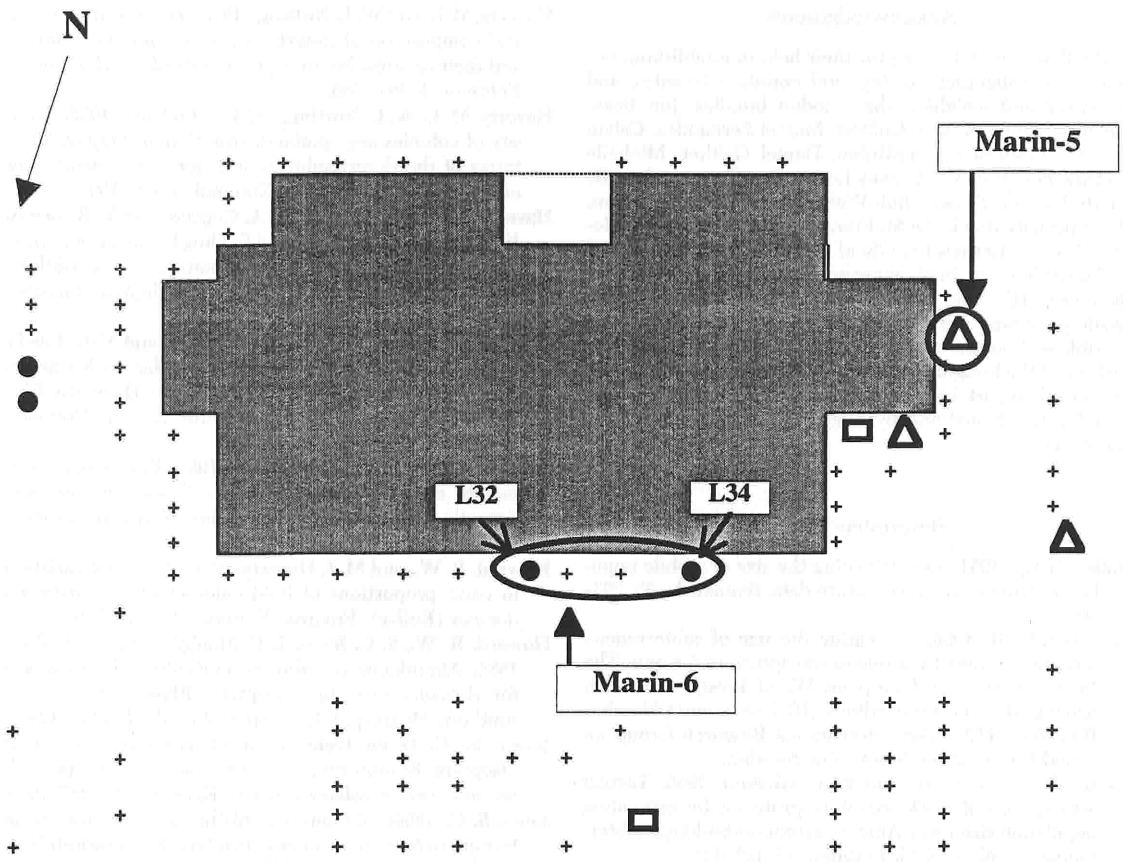

Fig. 3. Distribution of monitoring stations at the Lesneski residence in Larkspur, CA, demonstrating the locations of *Reticulitermes* colonies Marin-5 and Marin-6. Cuticular hydrocarbon phenotype occupying each monitoring station: A, circle; A′, square; D, triangle.

Marin County. The foraging areas of different colonies can overlap or be within the territory of another colony. Foraging territories are not static; they can change because of abandonment of a foraging site or displacement of one colony from a foraging site by another colony.

We never found more than one hydrocarbon phenotype in a monitoring station at the same time. Therefore, we suspect that they are not able to partition the resources (i.e., wooden bundle) within a monitoring station, between or among colonies at least of different phenotypes. Because of their agonistic relationships with other phenotypes, and even conspecifics (Haverty et al. 1999b), we feel that it is appropriate to consider the occupied monitoring station as part of their defended foraging territory rather than a foraging area as suggested by Thorne (1998).

The concept of foraging range seems to be a more appropriate descriptor of where the termites are working than the arbitrary foraging territory or area (Thorne 1998). Simply surrounding the foraging locations or monitoring stations occupied or used by a colony subtends a great deal of real estate that the termites are not using or defending. We have expanded on the idea of foraging range by calculating the total minimum distance that foragers might travel within the galleries occupied and defended by their colony. Of course, we know that the galleries are not straight lines barely under the soil surface. Rather, these galleries are a vast network of interconnected runways and tunnels within the soil interspersed among food sources. Of the colonies that we studied, this distance varied from 0 to 291.6 m.

We were able to use mark-release-recapture studies to determine the foraging territory and maximum foraging distance of colonies without any difficulty. We also were able to determine the number of colonies of each cuticular hydrocarbon phenotype at each site without a hitch. Accurately estimating the foraging population of *Reticulitermes* colonies remains an obstacle. We would welcome additional research to investigate the ecological and mathematical assumptions of indices used in mark-release-recapture studies for *Reticulitermes* and the consequences of not meeting these assumptions.

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