Mark–Release–Recapture Estimates of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) Colony Foraging Populations from Georgia, U.S.A.

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ABSTRACT Three subterranean termite species [eastern subterranean termite, *Reticulitermes flavipes* (Kollar); *R. virginicus* (Banks); and *R. hageni* (Banks)] were included in 67 mark–release–recapture experiments conducted with 57 different colonies in Georgia over 3 yr (1992, 1993, and 1995). Data were collected in 1992–1993 under a triple-mark-release protocol and analyzed using 2 mathematical models—the Lincoln index and a weighted mean model. During 1995, data were collected using a single release of marked termites followed by 3 collections and analyzed using the Lincoln index. In addition, 71 different termite infested logs were returned to the laboratory where termites were extracted and counted. Termite foraging population estimates ranged from 106 to 1,453,021 for the weighted mean model and 127 to 384,617 for the Lincoln index in 1992–1993. The 1995 Lincoln index estimates ranged from 1,463 to 3,547,152 termites per colony The numbers of termites extracted from infested logs ranged from 1,033 to 344,457 termites per log Both mathematical models applied to the 1992–1993 data provided similar population estimates. The 1995 Lincoln index data provided population estimates which were higher than the 1992–1993 data, median 98,202 and 28,473 termites per colony, respectively. Results of these mark–release–recapture experiments, when examined by capture cycle, suggest that the biology of subterranean termites may violate some of the assumptions of these mathematical models for estimating population size.

KEY WORDS Isoptera, *Reticulitermes*, population estimate, Lincoln index, weighted mean model, mark–release–recapture

STUDIES OF THE population dynamics of subterranean termites from the genus *Reticulitermes* in the field are complicated by the small size, cryptic nature, and eusocial behavior of these insects. Measuring changes in the size of termite populations over time could give indications of treatment efficacy for strategies aimed at controlling this serious economic pest (Su 1994). In addition, documenting termite colony population fluctuations and correlating these with environmental conditions could allow researchers to develop models for predicting the potential for structural damage by termites. These data also could be important in determining the ecological role these insects play in the larger scheme of soil faunal interactions.

Understanding subterranean termite population dynamics would be facilitated by credible estimates of how many termites are in a colony. Numerous studies have estimated subterranean termite field populations using a variety of techniques including habitat sampling (Haverty et al. 1975), radioactive tracers (Spragg and Paton 1980), and exhaustive trapping (French and Robinson 1981). Mark–release–recapture techniques have been used because they directly estimate population size and, being nondestructive, permit long-term study of the same termite populations. Mark–release–recapture techniques have generated estimates of *Reticulitermes* spp. foraging populations ranging from 300,000 to 5 million termites per colony (Esenther 1980, Grace et al. 1989, Grace 1990, Su et al. 1993, Su 1994). However, the number of colonies estimated using these techniques has been limited to 6 or less colonies per study and the biology, and movement of termites to and between monitoring stations has not been critically evaluated relative to the model assumptions.

We conducted 67 mark–release–recapture experiments on 57 separate colonies of 3 species of *Reticulitermes* in Georgia over 3 yr. The following were our 3 objectives in this study: (1) to generate estimates of *Reticulitermes* foraging populations using mark–release–recapture techniques, (2) to compare the relative merits of using the Lincoln index and the weighted mean model in estimating termite populations, and (3) to evaluate termite movement during mark–release–recapture experiments relative to the model assumptions. This article describes the results of these mark–release–recapture studies. In addition, we examined the

Table 1. Sequence of triple mark–release–recapture events by week from 1992–1993 studies of *Reticulitermes* field colonies in Georgia

Week 1, 1st collection	Week 2, 2nd collection	Week 3, 3rd collection	Week 4, 4th collection	Week 5, 5th collection
Dye	Dye 1st release	Dye 2nd release 1st recapture	3rd release 2nd recapture	3rd recapture

data with regard to their valid use in the study of termite biology.

Materials and Methods

Establishment of Field Sites. Areas of termite activity were located using the bait-stake method with wooden survey stakes (1.5 by 3.5 by 30 cm) purchased from a local lumber yard (Thompson 1985). Stakes were placed ≈27 cm into soil in inconspicuous locations (i.e., along fence rows, hedges, base of trees) in residential areas or on 1-m centers in grids of various sizes in forested habitats. Stakes were examined each month for signs of termite activity. When termites were found feeding on a stake, they were dislodged by gently tapping the stake over an (44 by 29 cm) aluminum baking pan. The stake was replaced with a termite monitor, the dislodged termites deposited inside the newly established monitor, and a thin layer of soil (1–3 cm) was placed over each monitor.

Termite monitors consisted of a PVC pipe receptacle, an undisturbed feeding site, and a removable food and aggregation substrate. Termite monitor receptacles (16 cm long) were made from PVC pipe (10 cm diameter). A block of white pine (4 by 8 by 3 cm) was buried below the PVC pipe receptacle to serve as an undisturbed feeding site. Two termite feeding and aggregation substrates (sandwiches) were placed on top of the undisturbed feeding site inside the monitor. Termite sandwiches were composed of 10 pieces of weathered white pine wood (4 cm by 12 cm by 2 mm each) and separated by wooden dowels (2 mm diameter). This arrangement was held together by 18-cm length of plastic cable ties (GB Electric, Milwaukee, WI). Wood was weathered by placing uncut lumber on the roof of the laboratory for at least 7 mo before use in termite sandwiches. Termite monitors were capped using a 10-cm-diameter plastic knock-out plug.

Population Estimates. When several active monitors were established in the same area, termites from one monitor were removed, marked with spray paint, and immediately released. One week later, termites from all monitors in the area were recaptured and examined for the presence of painted termites. Those monitors containing painted termites were considered as visited by the same colony of termites (Forschler 1994). Once colony monitor use was determined, foraging populations were estimated using the fat soluble dye Nile Blue A and 1 of 2 protocols. In none of our studies did the recovery of dyed termites dispute the topical mark (spray paint) delineation of termite monitor usage.

A triple mark–release–recapture protocol was used to estimate termite foraging populations for the 1992–1993 experiments (Su et al. 1993). Termites were captured, marked, released, and recaptured over a period of 5 consecutive weeks (Table 1). Captured termites were marked by feeding them paper stained with a fat soluble dye. No more than 2 g of termites were placed in a petri dish 100 by 15 mm with a 9-cm-diameter No. 1 Whatman filter paper stained with a 0.05% (wt:vol) solution of Nile Blue A in distilled water. These termites were maintained in complete darkness in an environmental chamber at 24°C for 1 wk. Termites that became visibly marked by the blue dye were then counted and released into the termite monitor from which they were collected initially.

Termites collected the 1st wk, taken to the laboratory, marked (dyed), and released the 2nd wk constituted the 1st release of marked termites (Table 1). Termites collected in the 2nd wk immediately before the 1st release were returned to the laboratory, marked as described previously, and released 1 wk later as the 2nd release. Marked termites captured in the 3rd collection just before the 2nd release were the 1st marked–recaptured termites. Unmarked termites from this collection were returned to the laboratory, marked as described above, and released the following week as the 3rd release. Termites collected from monitors at the time of the 3rd release were the 4th collection; marked termites within this group were the 2nd marked–recaptured. Marked termites collected in the 5th wk constituted the 3rd marked–recaptured group.

In 1995, a single release protocol was employed. All termites collected from monitors known to be visited by a single group (colony) were marked using the fat-soluble dye Nile Blue A as described previously. Marked termites were returned 1 wk later to the monitor from which they were collected. Termites were then recovered from all monitors, for that colony, at monthly intervals and the number of marked and unmarked termites recorded separately for each recapture cycle.

Termite numbers were determined by separating castes and weighing 5 groups of 10 workers to obtain an average weight per termite and dividing by the total weight of termites collected. Marked termites and castes with low numbers of individuals (soldiers and prealates) were counted individually. Numbers of marked and unmarked termites captured and the number of marked termites released at each cycle were used in a weighted mean model for estimating termite foraging populations and associated standard errors for the 1992–1993 data (Begon 1979). If either no termites or no marked termites were recovered, we used zero values for that cycle in the weighted mean model because the model does not address the probability of capture. It only considers that the probability of recapture is the same for all marked animals released. For comparison, population estimates generated by the Lincoln index were computed using the 1st marked–release–recapture cycle where marked termites were recovered from that colony (Lincoln 1930).

The numbers of marked termites released and the numbers of marked and unmarked termites recovered during the 1995 trials were analyzed using the Lincoln index for each collection cycle. Therefore, we obtained 3 separate Lincoln index population estimates for most colonies examined. These individual estimates were averaged to obtain another population estimate for each colony (mean Lincoln index). In addition, the numbers of marked and unmarked termites collected following the single release were summed across monthly collections and analyzed using the Lincoln index to provide yet another population estimate for that colony (summed Lincoln index). If no marked termites were recovered during a particular recapture cycle, no Lincoln index estimate was attempted for that cycle. If marked termites were not recovered after the 1st recapture, neither a summed nor mean Lincoln index was calculated. If marked termites were recovered on the 1st and 2nd recapture cycles but not the 3rd, only the 1st and 2nd recapture data were included in the summed Lincoln index estimate. However, if marked termites were not recovered during the 2nd cycle but were found during the 3rd recapture, the number captured during the 2nd cycle was added to the calculated summed Lincoln index for that colony.

In 1992–1993, a group of 35 colonies were characterized in 3 soil provinces including the Blue Ridge soils (Union County), Piedmont soils (Gwinnett, Lamar, and Spalding counties), and Coastal Plain soils (Sumter County) in Georgia. In 1995, 28 colonies were characterized in the above Soil Provinces with the addition of the Atlantic Coastal Flatwoods soils (McIntosh and Chatham counties). Four colonies characterized in 1992 were characterized again in 1993 using the triple mark–release protocol. These colonies are numbers 3 and 4; 5 and 6; 7 and 8; and 9 and 10 in Table 2. One colony was characterized in the spring and again in the fall of 1993 (colony numbers 1 and 2, Table 2). Five of the colonies characterized in 1993 also were characterized in 1995. They include from Table 2, colonies 1, 16, 24, and 38, which are the same colony, respectively, as colonies 2, 3, 8, and 9 in Table 3. The other colonies characterized in 1993 were not characterized in 1995 because they had been involved in baiting or chemical control studies during 1994. Species were identified, when possible, by alates obtained from the various colonies (Weesner 1965).

Collection of Termites From Logs. Termite-infested logs were collected at the University of Georgia Westbrook Farm in Spalding County. Logs were cut into 0.5- to 0.75-m sections using a chain saw and transported to the laboratory. Log sections were placed in sheet metal trays (38 by 53 by 11 cm) and allowed to air dry under ambient conditions. Moistened cardboard rolls (14 by 40 cm) were placed inside PVC pipe sleeves (2 cm diameter) at the base of logs in the trays. Termites were collected by removing the cardboard from the PVC pipe sleeves and gently tapping termites from the cardboard over an aluminum baking pan (44 by 29 cm). Collected termites were separated by caste and weighed. The number of termites collected from each set of logs was calculated as previously described for the mark–release–recapture studies.

Results and Discussion

The combined 1992–1993 data provided an overall mean ± SEM termite foraging population of 89,246 ± 228,714 (median, 36,370; range, 106–1,453,021) using the weighted mean model and 61,829 ± 90,209 (median, 28,473; range, 127–377,700) for the Lincoln index (Table 2). If the 2 population estimates that provided the highest and lowest estimates (numbers 35 and 38) are excluded, the mean population estimates are 54,796 ± 45,962 (range, 970–195,069) and 54,959 ± 75,259 (range, 1,111–384,615) for the weighted mean and Lincoln index, respectively. The mean from the 1995 experiments for the 1st recapture period Lincoln index estimates was 462,640 ± 575,752 (median, 98,202; range, 1,463–3,547,152) (Table 3).

The mean number of termites recovered from infested logs was 36,825 ± 60,663 (median, 9,889; range, 1,033–344,457) (Table 4). Because one-third of the logs provided <5,000 termites and <10% of the mark–release–recapture estimates were in this range we removed those logs from the mean number of termites collected per log to obtain a mean number of termites collected per log of 55,585 ± 68,572 (median, 24,618; range, 5,072–344,457; n = 46) (Table 4).

Su et. al. (1993) conducted mark–release–recapture experiments on 6 *Reticulitermes* colonies in Florida. They determined use of individual monitors (by the same colony) as they conducted the population estimate. This was accomplished by releasing dyed termites into 1 monitor on the 1st release cycle and adding monitors on each successive cycle as marked termite appeared in nearby monitors. Their data provided population estimates ranging from 170,832 to 5,009,612 using the weighted mean model (Su et al. 1993). Because

Table 2. Comparison of population estimates using Lincoln index and weighted mean model techiques from field data collected in Georgia, 1992–1993, including species, number of monitors per colony, soil province, and date experiment was conducted

No.[a]	Spp.	No. monitors[b]	Soil	Date[c]	Population estimates	
					L.I.	W.M.M.
1	*R.f.*	3	P	July 1993	39,456 ± 6,987	98,449 ± 8,668
2	*R.f.*	7	P	Nov. 1993	17,048 ± 1,519	29,299 ± 2,267
3	*R.f.*	3	P	Aug. 1992	384,615 ± 1,920,762,869	104,963 ± 24,119
4	*R.f.*	3	P	May 1993	41,803 ± 5,014	52,826 ± 5,231
5	*R.f.*	3	P	May 1992	1,111 ± 222	106,550 ± 9,418
6	*R.f.*	4	P	May 1993	11,278 ± 1,315	27,667 ± 1,066
7	*R.f.*	2	P	Aug. 1992	122,989 ± 22,361	113,786 ± 9,230
8	*R.f.*	3	P	May 1993	9,499 ± 2,360	18,117 ± 880
9	*R.v.*	2	P	Aug. 1992	51,131 ± 17,837	156,997 ± 21,991
10	*R.v.*	2	P	July 1993	18,893 ± 4,153	20,109 ± 3,278
11	*R.f.*	1	P	Oct. 1993	11,739 ± 8,194	23,278 ± 7,040
12	*R.f.*	1	P	Oct. 1993	23,066 ± 1,212	26,912 ± 1,170
13	*R.f.*	4	P	May 1993	103,177 ± 15,606	81,437 ± 7,009
14	*R.f.*	1	CP	Nov. 1993	18,701 ± 4,764	26,237 ± 3,712
15	*R.f.*	2	P	May 1993	59,456 ± 5,618	87,939 ± 4,494
16	*R.f.*	2	P	Nov. 1993	9,660 ± 5,530	5,131 ± 1,628
17	*R.f.*	3	P	May 1993	27,211 ± 1,543	31,242 ± 1,200
18	*R.f.*	1	P	Nov. 1993	2,244 ± 1,563	9,287 ± 4,644
19	*R.h.*	1	P	Nov. 1993	28,473 ± 13,199	59,937 ± 12,064
20	*R.h.*	1	P	Nov. 1993	47,689 ± 11,714	35,781 ± 7,638
21	*R.h.*	1	P	May 1993	4,417 ± 1,771	970 ± 73
22	*R.f.*	2	P	May 1993	18,040 ± 762	19,662 ± 668
23	*R.f.*	1	P	May 1993	47,861 ± 9,136	195,069 ± 37,576
24	*R.f.*	1	BR	Sept. 1993	191,892 ± 77,807	121,263 ± 31,380
25	*R.?*	3	CP	Oct. 1993	207,581 ± 20,695,840,000	108,806 ± 143,937
26	*R.f.*	2	CP	Oct. 1993	19,344 ± 19,304	13,339 ± 3,198
27	*R.f.*	2	P	May 1993	84,367 ± 6,009	48,098 ± 1,790
28	*R.v.*	2	P	Aug. 1993	36,200 ± 1,357	42,998 ± 1,157
29	*R.f.*	1	P	Sept. 1993	43,806 ± 19,524	45,296 ± 7,313
30	*R.h.*	2	P	Sept. 1993	14,418 ± 1,983	37,006 ± 4,164
31	*R.f.*	1	P	Sept. 1993	4,876 ± 2,160	3,119 ± 1,043
32	*R.v.*	2	P	Sept. 1993	153,945 ± 29,027	92,299 ± 4,864
33	*R.h.*	1	P	Sept. 1993	17,237 ± 3,075	24,322 ± 2,278
34	*R.f.*	1	BR	Oct. 1993	30,258 ± 4,004	36,370 ± 3,567
35	*R.h.*	1	P	Sept. 1993	127 ± 539	106 ± 53
36	*R.f.*	1	P	Nov. 1993	9,100 ± 5,100	17,038 ± 11,665
37	*R.f.*	1	CP	Oct. 1993	81,585 ± 19,678	75,110 ± 18,251
38	*R.f.*	1	BR	Oct. 1993	377,700 ± 26,700,190,000	1,453,021 ± 389,283
39	*R.f.*	1	CP	Nov. 1993	39,327 ± 6,287	30,762 ± 4,227
			Combined median		28,473	36,370
			Combined mean ± SE		61,829 ± 90,209	89,246 ± 228,714

Species of termite: *R.f.*, *Reticulitermes flavipes*, *R.v.*, *R. virginicus*, *R.h.*, *R. hageni*; *R.?*, undescribed or unknown species. Soil province where colony was located: BR, Blue Ridge, CP, Coastal Plains; P, Piedmont. L.I., Lincoln index; W.M.M., weighted mean model.

[a] Colony number designation.

[b] Number of termite monitors known to be used by that colony of termites.

[c] Month that mark–release–recapture was conducted for that colony.

they included the entire data set we were able to calculate Lincoln index estimates, from their 1st mark–release–recapture cycle. The Lincoln index estimates for the Florida colonies ranged from 188,693 to 3,624,094 termites per colony.

Grace et. al (1989) and Grace (1990) estimated 4 Canadian *Reticulitermes* populations using a mark–release–recapture methodology. They conducted 1 release of marked termites followed by 4–5 recapture cycles then used a Lincoln index model to obtain estimates for each recapture cycle and reported only the mean of those individual estimates. Their termite population estimates based on the Lincoln index means ranged from 722,679 to 3,187,538 termites per colony.

Our 1995 data were within the range of populations reported by Su et. al. (1993), Grace et. al (1989), and Grace (1990) although we report a higher percentage of population estimates <100,000 termites per colony (50% versus 0). However, our 1992–1993 estimates are within the range reported by Howard et. al (1982) (51,505–363,512) who used an exhaustive trapping technique on 6 *Reticulitermes* colonies in Mississippi.

These population estimation studies may indicate geographic differences in termite population sizes. The *Reticulitermes* colonies in Canada, and perhaps in southern Florida, may be considered exotic or introduced species that may not be under the same competitive pressures as colonies in

Table 3. Summary of Lincoln index estimates by colony and recapture cycle for termite colonies from 1995 mark–release–recapture studies in Georgia, including species, number of monitors per colony, and soil province

No[a]	Spp.	No. M[b]	Soil	Lincoln index estimates				
				1st	2nd	3rd	Mean	Summed
1	*R.f.*	3	AF	74,121	127,672	124,094	108,629	95,811
2	*R.f.*	10	P	114,748	—	494,436	304,592	504,311
3	*R.f.*	4	P	38,850	43,890	96,353	59,691	54,672
4	*R.f.*	6	AF	191,660	587,970	—	389,815	295,996
5	*R.f.*	3	AF	110,056	103,017	—	106,537	107,255
6	*R.h.*	2	P	132,842	235,094	152,074	173,337	138,858
7	*R.h.*	2	BR	209,996	182,600	—	196,298	195,986
8	*R.f.*	4	BR	383,531	—	—	—	—
9	*R.f.*	5	BR	625,468	3,580,686	—	2,116,577	908,398
10	*R.h.*	1	P	172,315	79,239	495,891	249,815	168,388
11	*R.f.*	1	P	26,975	—	—	—	—
12	*R.f.*	1	P	309,739	—	132,095	221,322	325,034
13	*R.h.*	1	P	3,547,152	23,845	29,384	1,200,127	43,987
14	*R.h.*	1	CP	2,234	1,482	766	1,497	1,388
15	*R.f.*	1	CP	14,565	23,890	29,171	22,541	22,427
16	*R.f.*	1	CP	29,162	61,386	57,200	49,249	41,405
17	*R.?*	1	CP	4,620	—	—	—	—
18	*R.f.*	1	CP	66,778	—	—	—	—
19	*R.f.*	1	BR	1,176,320	—	—	—	—
20	*R.f.*	1	P	34,532	41,571	45,524	40,542	36,838
21	*R.?*	1	P	399,762	—	—	—	—
22	*R.f.*	1	P	2,885	—	3,654	3,629	4,007
23	*R.f.*	1	AF	1,463	18,144	32,566	17,391	10,834
24	*R.f.*	1	AF	70,376	27,027	—	48,701	37,076
25	*R.f.*	1	AF	86,347	—	—	—	—
26	*R.f.*	1	AF	3,509,396	1,744,567	—	2,626,981	1,997,126
27	*R.f.*	1	AF	761,807	—	—	—	—
28	*R.f.*	1	AF	1,216,233	—	—	—	—
Combined median				98,202	70,313	74,122	108,629	95,811
Combined mean				462,640	430,130	130,246	417,732	262,621
± SE				575,752	577,854	115,925	493,736	286,080

Species of termite: *R.f.*, *Reticulitermes flavipes*, *R.h.*, *R. hageni*, *R.?*, Undescribed or unknown species. Soil province where colony was located: AF, Atlantic Coast Flatwoods; BR, Blue Ridge; CP, Coastal Plains; P, Piedmont. Lincoln index population estimates by recapture cycle 1st = 1st recapture cycle 1 mo after release of marked termites; 2nd = 2nd recapture cycle 2 mo after release of marked termites; 3rd = 3rd recapture cycle 3 mo after release of marked termites; Mean, mean of previous single Lincoln index population estimates; Summed, population estimate obtained by summing recapture data from all cycles where marked termites were recovered and estimating population using Lincoln index. Marked termites were released in June for all colonies with the exception of colonies 6 through 19 where the 1st release was conducted in July.

[a] Colony number designation

[b] The number of termite monitors known to be used by that colony of termites.

Table 4. Record of termites collected from logs found at University of Georgia Westbrook Farm

Log no.	Termite no.	Log no.	Termite no.	Log no.	Termite no.	Log no.	Termite no.
1	110,740	21	9,889	41	1,766	61	31,716
2	2,074	22	7,854	42	3,655	62	158,827
3	205,990	23	26,076	43	1,283	63	2,083
4	60,105	24	20,797	44	1,906	64	7,246
5	48,705	25	1,366	45	3,418	65	1,637
6	32,257	26	1,381	46	128,011	66	114,948
7	152,834	27	2,885	47	1,879	67	21,177
8	5,072	28	114,523	48	21,707	68	1,312
9	151,589	29	72,762	49	27,493	69	1,611
10	7,955	30	1,783	50	3,467	70	1,024
11	64,006	31	344,457	51	1,033	71	4,837
12	5,767	32	2,627	52	36,122		
13	6,119	33	1,996	53	4,195		
14	12,579	34	3,819	54	10,171		
15	138,713	35	6,972	55	5,265		
16	16,437	36	21,328	56	7,082		
17	5,997	37	15,808	57	3,219		
18	24,618	38	57,382	58	31,633		
19	1,426	39	10,733	59	29,790		
20	130,255	40	16,774	60	20,646		

Georgia and Mississippi. Another explanation for the disparity in the population estimates conducted by Su et al. (1993), Grace et al. (1989), and Grace (1990) compared with our experiments could be the result of differences in technique combined with variability in termite behavior and the limited number of colonies estimated in the aforementioned studies.

The higher estimates of mean population size we obtained in 1995 could be viewed as verification of the hypothesis presented by Forschler and Henderson (1995) that saturated soil conditions are a limiting factor on termite population growth. Between 1993 and 1995 there were no periods of prolonged saturated soil conditions comparable to those found during the winter of 1992–1993. However, dye loss over the 3-mo test period, during the 1995 experiments, also could have been a factor in those higher population estimates (Thorne et al. 1996).

The question of dye loss is difficult to test under field conditions. However, there were indications

Table 5. Numbers of termites marked, released, and recaptured by colony and monitor from 1995 Lincoln index population estimates

Colony no.[a]	Monitor[b]	Mark–release–recapture cycle						
		R	N1	M1	N2	M2	N3	M3
1	1	3,876	1,354	73	1,129	31	75	6
	2	0	42	0	46	4	345	7
	Total	3,876	1,396	73	1,175	35	420	13
2	1	36	351	3	162	0	745	2
	2	0	38	0	317	0	355	0
	3	445	54	0	94	0	28	0
	4	0	0	0	0	0	0	0
	5	0	28	0	0	0	126	1
	6	0	0	0	87	0	172	1
	7	0	59	0	259	0	701	2
	8	124	39	0	423	0	415	0
	9	0	0	0	655	0	727	0
	10	0	0	0	0	0	0	0
	Total	605	567	3	1,997	0	3,269	4
3	1	777	0	0	299	10	183	5
	2	0	244	0	148	0	54	0
	3	0	106	7	123	0	391	0
	Total	777	350	7	570	10	628	5
4	1	0	0	0	270	0	9	0
	2	0	0	0	0	0	256	0
	3	227	0	0	0	0	213	0
	4	0	0	0	3,079	8	317	0
	5	234	1,557	14	0	0	148	0
	6	1,242	2,382	21	881	4	5	0
	Total	1,703	3,939	35	4,230	12	948	0
5	1	454	1,928	12	1,344	3	327	0
	2	231	0	0	472	7	0	0
	3	0	0	0	327	4	288	0
	Total	685	1,928	12	2,143	14	615	0
6	1	3,177	1,784	43	68	0	244	7
	2	748	619	28	54	2	415	10
	Total	3,925	2,403	71	122	2	659	17
7	1	797	169	17	295	10	0	0
	2	2,872	804	0	755	9	921	0
	Total	3,669	973	17	950	19	921	0
8	1	0	542	0	30	0	0	0
	2	421	91	0	32	0	170	0
	3	0	822	0	342	0	64	0
	4	0	367	2	230	0	15	0
	Total	421	1,822	2	634	0	249	0
9	1	2,258	1,155	10	1,041	0	0	0
	2	0	0	0	0	0	0	0
	3	667	446	3	57	0	0	0
	4	2,118	408	4	63	0	0	0
	5	0	708	4	265	2	0	0
	Total	5,043	2,717	21	1,426	2	0	0
10	1	2,651	1,105	17	361	12	566	3
11	1	857	661	21	361	0	108	0
12	1	1,399	1,107	5	1,016	0	665	7
13	1	1,512	2,346	1	1,657	105	2,339	112
14	1	525	217	89	51	15	36	11
15	1	1,205	278	23	1,051	52	253	10
16	1	1,658	2,181	124	2,321	58	143	4
17	1	90	462	9	1,220	0	24	0
18	1	702	761	8	1,144	0	0	0
19	1	2,560	2,757	6	3,556	0	414	0
20	1	1,190	3,046	106	767	20	428	11
21	1	562	283	4	0	0	0	0
22	1	577	45	9	23	0	579	5
23	1	935	230	147	1,769	78	836	22
24	1	1,389	152	3	195	10	0	0
25	1	1,440	1,619	27	0	0	0	0
26	1	3,394	1,034	1	3,085	6	0	0
27	1	1,145	1,996	3	781	0	254	0
28	1	3,609	1,685	5	258	0	588	0

Mark–release–recapture cycle: R, number of termites released; N1, number of termites in 1st recapture; M1, number of marked termites recovered in N1 recapture; N2, number of termites in 2nd recapture; M2, number of marked termites recovered in N2 recapture, N3, number of termites in 3rd recapture; M3, number of marked termites recovered in N3

[a] Colony number designation corresponding to numbers in Table 3.

[b] Number of monitors associated with each colony

that dye loss may have been a factor using the longer time frame between captures in our 1995 experiments. The percentage of colonies from the 1992–1993 experiments where termites were recovered on the last capture cycle (4 wk after 1st release) but no marked termites were captured was 6% compared with 41% from the 1995 experiments (3 mo after 1st release). Examining the 1995 first Lincoln index estimates for only those colonies where marked termites were recovered on the last capture cycle, we found a median population estimate of 38,850 (n = 13) termites per colony. In contrast, a median value of 209,996 (n = 9) termites per colony was obtained using the 1st Lincoln index estimates for those colonies where termites were collected on the last capture cycle without finding marked termites. However, 30.5% of the termites captured on the final capture cycle from colony number 14 were marked, indicating a degree of unpredicatability in dye loss which may be colony specific (Table 5).

Because our 1992–1993 studies were conducted with a protocol that required weekly disturbance of each termite monitor, we examined the data to determine if a "monitor shy" effect could have resulted in fewer recaptures. We combined the number of termites captured from the first 2 capture periods and the last 2 recapture periods to obtain a mean number of termites captured per colony for comparison. The 1992–1993 data provided a mean number of termites captured per colony on the first 2 capture periods of 2,812 ± 2,435 (median, 2,212) (Table 6). The second 2 capture periods provided a mean of 1,491 ± 1,741 (median, 1,062) termites captured per colony (Table 6). This would indicate that termites were less likely to visit monitors following weekly disturbance. However, the 1995 data, which were obtained using a monthly disturbance factor, provided an equal disparity. The first 2 captures averaged 3,077 ± 1,983 (median, 2,836) termites captured per colony and the last two 1,708 ± 1,460 (median, 1,221) termites captured per colony (Table 5). Therefore, it is questionable whether disturbance was a contributing factor, although it could have been important with certain colonies.

Table 6. Summary of termite captures and releases from each mark–release–recapture cycle, by colony, during termite field population estimation studies conducted during 1992–1993 in Georgia

No.[a]	Cycle	Period		
		1st	2nd	3rd
1	R	1,097	5,481	1,052
	N	1,115	1,015	667
	M	31	60	39
2.	R	1,745	375	887
	N	1,104	415	763
	M	113	21	34
3.	R	924	1,595	1,484
	N	1,665	82	115
	M	4	3	13
4	R	960	914	2,890
	N	2,963	490	378
	M	68	28	7
5.	R	49	1,596	168
	N	544	4,992	3,335
	M	24	70	35
6.	R	693	2,724	1,009
	N	1,123	2,779	1,293
	M	69	300	184
7.	R	5,088	1,536	665
	N	701	924	1,094
	M	29	73	51
8	R	79	39	1,026
	N	39	1,249	750
	M	0	16	38
9	R	1,350	1,148	261
	N	303	1,328	1,685
	M	8	18	26
10	R	634	2,570	579
	N	596	0	108
	M	20	0	18
11	R	301	420	74
	N	78	0	352
	M	2	0	10
12.	R	4,588	1,902	1,209
	N	1,458	1,608	1,087
	M	290	328	138
13	R	1,678	1,989	1,855
	N	2,644	263	1,058
	M	43	28	65
14	R	493	1,220	624
	N	670	400	154
	M	15	18	18
15.	R	3,716	7,070	1,593
	N	1,680	1,732	745
	M	105	158	120
16.	R	161	110	162
	N	180	93	18
	M	3	4	4
17	R	2,183	1,556	3,121
	N	3,565	2,559	729
	M	286	228	165
18	R	67	324	67
	N	67	113	16
	M	2	1	2
19.	R	3,833	1,742	75
	N	104	190	29
	M	14	12	0
20	R	1,648	449	440
	N	463	46	0
	M	16	7	0
21	R	155	126	170
	N	171	505	23
	M	6	164	6
22.	R	5,278	1,273	957
	N	1,357	1,395	199
	M	397	377	94
23.	R	1,728	791	0
	N	0	494	1,770
	M	0	26	2
24.	R	2,599	395	320
	N	443	225	72
	M	6	5	5
25.	R	1,243	1,138	128
	N	167	0	4
	M	1	0	0
26.	R	78	33	243
	N	248	452	610
	M	1	7	12
27.	R	5,481	4,937	1,973
	N	2,940	1,572	224
	M	191	449	83
28.	R	5,024	4,284	3,355
	N	4,417	1,562	2,020
	M	613	299	471
29.	R	298	731	726
	N	735	698	498
	M	5	6	28
30	R	1,602	450	291
	N	423	604	484
	M	47	5	28
31	R	92	151	256
	N	265	79	11
	M	5	2	3
32.	R	692	7,384	6,206
	N	6,229	1,184	2,512
	M	28	157	176
33.	R	2,424	177	135
	N	192	165	719
	M	27	23	65
34.	R	2,173	4,350	676
	N	738	348	0
	M	53	52	0
35.	R	106	789	0
	N	6	0	0
	M	5	0	0
36.	R	525	937	51
	N	52	28	0
	M	3	0	0
37.	R	571	2,791	2,412
	N	2,429	12	0
	M	17	1	0
38.	R	200	4,287	3,503
	N	3,777	4,960	31
	M	2	9	4
39.	R	1,133	3,723	1,143
	N	1,319	41	0
	M	38	15	0

Mark–release–recapture cycle: R, number marked–released, N, number captured; M, number marked recaptured. Mark-recapture period: 1st, 1st release–recapture period; 2nd, 2nd release–recapture period; 3rd, 3rd release–recapture period.

[a] Colony number corresponding to colony designation in Table 2.

Our 1992–1993 data provided no discernable trends in mean population estimates between colonies visiting 1, 2, 3, or >4 monitors (Table 7). This indicates that the number of monitors used in a

Table 7. Summary of mean population estimates by number of monitors/colony and time of year that data were collected from the 1992–1993 termite mark–release–recapture studies

No. Monitors[a]	n^b	Population estimate	
		L.I. ± SE (range)	W.M.M. ± SE (range)
1	18	54,450 ± 92,027 (127–377,700)	121,326 ± 335,790 (106–1,453,021)
2	11	53,495 ± 48,251 (9,660–153,945)	57,942 ± 48,419 (5,131–156,997)
3	7	101,611 ± 143,109 (1,111–384,615)	74,421 ± 39,212 (18,117–108,806)
≥4	3	43,834 ± 51,473 (11,278–103,177)	46,134 ± 30,583 (27,667–81,437)

L.I., Lincoln index estimate; W.M.M., weighted mean method estimate.

[a] Number of monitors used by colonies for the mean population estimates in that row.

[b] Number of colonies used for the mean population estimates in that row.

Table 8. Summary of mean population estimates by time of year that data were collected from the 1992–1993 termite mark–release–recapture studies

Month[a]	n^b	Population estimates	
		L.I. ± SE (range)	W.M.M. ± SE (range)
4–6	10	40,711 ± 33,442 (4,417–103,177)	56,303 ± 56,054 (970–195,069)
7–9	14	77,192 ± 106,858 (127–384,615)	69,090 ± 49,868 (106–156,997)
10–12	15	61,567 ± 101,050 (2,244–377,700)	130,020 ± 367,006 (5,131–1,453,021)

L.I., Lincoln index population estimate; W.M.M., weighted mean method population estimate.

[a] Month that mark–release–recapture was conducted for mean population estimates in that row.

[b] Number of colonies used for the mean population estimates in that row

mark–release–recapture experiment is not a limiting factor. However, the 1995 data showed 60% (n = 20) of the colonies visiting 1 monitor yielded estimates of <100,000 termites per colony compared with 22% (n = 9) of the colonies visiting 2 or more monitors. Despite this, there was, on average, 2 times more termites collected per monitor per collection cycle between those 1995 colonies visiting only 1 monitor 1,105 ± 954 (mean ± SE, n = 69) when compared with those visiting >1 monitor, 578 ± 751 (mean ± SE, n = 100). The resulting higher population estimates for the colonies visiting >1 monitor in 1995, however, can be explained by the lower mean percent ± SE recapture rates for those colonies 1.5% ± 1.3 versus 7.2% ± 13.3 for the colonies visiting only 1 monitor. Therefore, the number of termite monitors used in a mark–release–recapture protocol does not appear to be a limiting factor.

The data also provided no indication of trends involving species or soil provinces. Although using the Lincoln index estimates from the 1992–1993 experiments indicated that *Reticulitermes hageni* (Banks) had smaller colonies (median, 15,827 termites per colony) in comparison to the eastern subterranean termite, *R. flavipes* (Kollar) (median, 28,785), that trend was reversed with the 1995 data (median, 172,315 and 86,347, respectively) (Tables 2 and 3). Similarily, the Coastal Plain estimates in 1992–1993 provided a median of 39,327 termites per colony compared with 23,066 termites per colony from the Piedmont soils. However, the 1995 showed that colonies from the Coastal Plain soils provided a median population estimate of 14,564 termites per colony compared with the Piedmont colonies with a median of 77,255 (Tables 2 and 3).

The 1992–1993 population estimates when examined for a seasonality effect, using either mathematical model, showed only slightly lower mean population estimates for colonies examined from April through June compared with the July through September or October through December estimates (Table 8). This trend could indicate reduced termite populations in the spring following alate flights and a slight rise during the summer with production and maturation of replacement workers. However, we feel that data from several years would be necessary to verify this trend.

Comparison of the 2 mathematical models with the 1992–1993 data indicate that the weighted mean model using the triple mark–release–recapture technique reduced the estimate of the standard error compared with the Lincoln index model and a single mark–release–recapture technique. Fifty-four percent of our weighted mean estimates provided standard errors over 10% of the population estimate compared with 82% of the Lincoln index estimates. Therefore, the weighted mean model could be viewed as an improvement in statistical precision. However, the low standard errors could be associated with the low percentage recapture rates and represent a mathematical aberration because it combines data from multiple mark–recapture periods rather than true standard error values (Thorne et al. 1996). Because these standard error values provide no valid mathematical information relative to the accuracy of these estimates they were not included with the 1995 data tables.

When comparing the estimates obtained using the 2 procedures for the same colony from the 1992–1993 data, 57% of the foraging population estimates were within 10,000 termites of one another (Table 2). This percentage was 58% when comparing the 1995 first Lincoln index estimates with the summed Lincoln estimates (Table 3). Considering that mark–release–recapture estimates are, at best, rough estimates of termite colony foraging populations, it is reasonable to place them in categories of small, medium, large, and mega–colonies. If our termite foraging population estimates are placed within population categories by increments of <100,000 termites = small colony, 100,001–500,000 = medium colony, 500,001–1 million = large colony, and >1 million a mega–

colony, then 85% of the 1992–1993 data provide estimates within the same category when both the Lincoln index and weighted mean model estimates are compared (Table 2). Using the 1995 data and placing the various population estimates into these same categories finds 89% of the data providing the same category when the 1st Lincoln estimate is compared with the summed Lincoln, the mean Lincoln, or the 2nd or 3rd Lincoln estimate (Table 3).

Despite increasing use of mark–release–recapture techniques to estimate subterranean termite foraging population sizes, a basic question remains. How accurate are these estimates at yielding the true number of termites within a given colony? Given the constraints imposed on termite field research because of the cryptic lifestyle and ephemeral nature of a subterranean termite colony's network of foraging tunnels, this question may never be answered with a high degree of certainty. If we assume that the numbers of termites recovered from infested logs are representative of 73% (range, 22–96%) of the entire population of a termite colony as reported by Howard et al. (1982), our population estimates from the mark–release–recapture studies are remarkably similar to real population values. However, the number of termites we collected from a each log certainly represent only a fraction of the entire population of the termite colony that was using that log at the time it was collected. It is, therefore, impossible to correlate the number of termites collected from logs with the "real" population of a colony without knowledge of the other sites also occupied by that particular colony.

It also is questionable whether termite biology fits the mark–release–recapture model assumptions of equal mixing of marked and unmarked individuals, mark persistence, or mark–mortality effects making these estimates only best-guess estimates (Thorne et al. 1996). The numbers of termites collected from each of our mark–release–recapture cycles by colony for the 1992–1993 experiments and by monitor and colony for the 1995 experiments was included to illustrate the variability and allow for independent assessment of our conclusions. These data indicate that a high degree of variability is to be expected with mark–release–recapture techniques when applied to *Reticulitermes* species (Tables 5 and 6).

It is assumed that the size of a termite population varies depending on numerous factors, including age of the colony, seasonal activity, availability and number of quality food resources, competition, predation pressure, and environmental stresses. These same factors, however, also are likely to affect termite visitation to monitors used in mark–release–recapture research. The impacts of these factors for any specific group of termites are not easily quantified.

The record of termite recovery, by colony from those groups known to visit >1 monitor, from the 1995 experiments indicates an unequal mixing of marked and unmarked termites or at least a nonrandom movement pattern. Nearly one-third (29%, n = 17) of the monitors from multiple-monitor colonies provided no recovery of marked termites from the monitor into which they were released (Table 5). In addition, only slightly over half (56%, n = 16) of the monitors where no marked termites were released provided marked termites during 1 of the 3 recapture cycles. There also were 3 colonies in 1995 where marked termites were recaptured on the 1st and 3rd recapture periods but not on the 2nd. Furthermore, 59% of the colonies studied under the multiple mark–release–recapture protocol (the 1992–1993 experiments) did not conform to the multiple mark–release–recapture model, which implies one should find an increasing proportion of marked individuals recaptured at each successive recapture cycle (Table 6) (Thorne et al. 1996).

The unknown factors affecting termite visitation to monitors were manifested in the variability of our data. For 10 of the 39 (26%) experiments conducted in 1992–1993, we failed to collect termites on at least 1 of the mark–release–recapture cycles (Table 6). The 1995 experiments showed that 6 of the 29 (21%) colonies examined provided no termites on at least 1 of the collection periods (Table 5). In contrast, other colonies consistently visited monitors throughout the experiments (Tables 5 and 6). However, the model assumptions do not address the probability of capture. Therefore, researchers are left with deciding how to handle zero capture values. It could be argued that zeros should be ignored because it is known that termites are (were) there. Yet, the zeros represent information relative to the movement, activity, or catchability of termites that only highlights the question of the validity of mark–release–recapture techniques with termites. Because the model does not address capture probabilities we maintained the zeros in our data.

The unpredictable nature of termite visitation to monitors also is illustrated by the numbers of termites collected by colony and mark–release–recapture cycle (Tables 5 and 6). The worst-case scenario is shown by colony number 35 where termites failed to return after the first 2 captures (Table 6). As a result, the population estimate was ≈100 foraging termites for that colony. However, there were 789 termites collected on the 2nd capture cycle, which were released back into the colony. The fact that termites did not revisit this monitor during the remainder of the mark–release–recapture experiment resulted in the low population estimate. Despite our efforts to present each monitor as an equivalent feeding site throughout all of our experiments, the factors that resulted in the lack of termite recaptures in this case certainly affected each of the other colonies tested to various degrees.

We could exclude those groups that failed to appear in monitors during the course of a mark–release–recapture cycle, failed to provide increasing proportions of marked individuals captured per cycle, or indicated a degree of nonrandom mixing. Although one could identify those colonies that do not consistently visit monitors, we cannot quantify the factors influencing termite catches for those colonies that consistently visited termite monitors or how the movement of individuals within those colonies might have affected the resulting population estimates. We believe that researchers are obliged to include each mark–release–recapture termite population estimate in their data set. Removing data from consideration based on lack-of-fit to mathematical models risks pursuing statistical significance at the cost of biological significance. As a result, by recording mark–release–recapture data only from those colonies that conform to mathematical model assumptions, researchers compromise their view of termite biology.

Based on the variability of our data set, we suggest that it is not appropriate to use these techniques to ascribe attributes to a single colony under the assumption that these estimates are true population values. This point is illustrated by colony estimates numbers 1 and 2 from Table 2, which are of the same group of termites taken during the same calendar year. The lower population estimate for this colony in the fall is in contrast to the trend in the combined data, which indicates smaller springtime population estimates (Table 4). Another example, from the 1995, data would be colony estimate number 13 where the population was estimated at >3 million based on the 1st recapture and <30,000 for the next 2 recapture cycles (Table 3). This example is contrary to the full mixing of marked and unmarked individuals model assumption and to the dye loss question. The variability in these data points out the individual nature of each termite colony and their reaction to participation in termite monitor visitation. This individuality is affected by all of the aforementioned factors whose combined effects manifest themselves in variable termite monitor visitation.

In conclusion, the use of the mark–release–recapture population estimates to measure efficacy of termite control strategies against a single colony must be used with extreme caution because the validity of such estimates cannot be verified. Given the uncertain accuracy, the time and effort involved, and the overall similarity between estimates using the 2 models tested we prefer the Lincoln index as the method of choice for termite population estimation using a mark–release–recapture methodology. We also feel that using these estimates to place colonies in categories of small, medium, large, and mega-sizes allows for cautious interpretation given the variability in the data and uncertainty of compliance with the model assumptions. These studies exemplify the need for more information concerning the biology of subterranean termites in the field and how aspects of the natural history correlates with the assumptions of any mark–release–recapture technique before widespread use of these techniques can be warranted.

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