

Seasonal Variation in Caste Proportions of Field Colonies of *Reticulitermes flavipes* (Kollar)^{1,2}

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ABSTRACT

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When seasonal variation of caste proportions was quantified in "nests" of the subterranean termite *Reticulitermes flavipes* (Kollar), workers comprised the most abundant caste, with a 2-year average of 84.0% of the individuals. Larvae comprised 8.7%, nymphs 5.0%, adult soldiers 2.1%, and presoldiers and neotenic reproductives 0.1% each. Alates and eggs were found infrequently. Caste proportions changed significantly with season, apparently varying according to the reproductive cycle. Larvae are most abundant in the summer and least abundant in the winter. Soldiers were most abundant immediately preceding alate flights, and least abundant immediately thereafter. Nymphs showed two peaks of abundance (early fall and early summer). Workers were most abundant during the spring and summer months.

Knowledge of the mechanisms involved in termite caste determination has progressed greatly in recent years (Wilson 1971, Lüscher 1977), but understanding of the ecological importance of the various caste forms has progressed much more slowly (Brian 1978, Oster and Wilson 1978). Quantitative information about seasonal variations in caste proportions within a colony is necessary for such understanding. Previous studies have been restricted to the family Termitidae or Kalotermitidae (Banerjee 1966, Bodot 1969, Sands 1965, Sen-Sarma and Mishra 1969, 1972). Subterranean termites (Rhinotermitidae), besides being of immense economic importance, occupy distinctly different niches from the termitids and kalotermitids. Important differences in their caste ecology can therefore be expected.

The caste structure of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), has been described by Banks and Snyder (1920) and by Esenther (1969). Their studies were based on small sample sizes, and they did not adequately quantify caste proportions. We have initiated research to investigate the demography of mature colonies⁵ of *R. flavipes* in southern Mississippi. Our earlier report (Howard and Haverty 1980) regarding the abundance and sex ratio of neotenic reproductives noted the marked association of soldiers with such reproductives. Here we report on the seasonal variations in relative abundance of larvae, workers, nymphs, presoldiers, soldiers, and neotenic reproductives.

Materials and Methods

One hundred colonies of *R. flavipes* were located and numbered in Harrison, Jackson, and Stone Counties in southern Mississippi in February and March 1976. Each colony was in a fallen pine log or stump and probably contained more than 50,000 termites. Every colony was at least 50 m from the nearest numbered colony. At ca. 0.5-m intervals around the periphery of each source colony, we placed six to eight sampling baits consisting of

pine bolts (0.5 by 0.1 m diameter) which had been weathered for 6 months without ground contact (Fig. 1). In August 1976, 20 of the 100-source colonies were randomly selected, and three sampling baits were randomly taken from each. The removed baits were replaced with three newly weathered bolts. Beginning in October 1976 and continuing every other month thereafter until June 1978, 15 of the 100 source colonies were randomly sampled and treated as described above. Most colonies were not sampled more frequently than once every 6 months. Eleven colonies were never sampled, and 15 colonies were sampled twice within a 6-month period.

The infested baits were individually placed in labeled plastic bags and returned to the laboratory, and all termites were removed by carefully splitting the wood along the growth ring. The volume of termites recovered from each bait was measured with a graduated cylinder. After these termites were thoroughly mixed, a 5-ml subsample was taken from each bait and counted by caste. Live biomass estimates for each caste were obtained at each sampling period by weighing at least three replicates of at least 50 individuals of each caste (except for neotenic reproductives, where 10 were weighed). With these data, we estimated total number of termites and caste proportions (by number and biomass) of each bait sampled. The reliability of this estimate was verified by counting all termites in 10 baits from the October 1976 sample.

Six of the 20 colonies sampled by baits in August 1976 were also sampled by cutting three randomly selected 0.1-m-thick cross sections from the log itself. These samples were treated the same as bait samples. The individuals collected in the three log sections were pooled, and caste proportions were calculated from these totals. The similarity of caste proportions between bait and log samples was tested with a paired *t* test.

Different colonies were sampled at different times over the 2 years of sampling. We used a *t* test to see if the proportions of all castes were the same for both sampling years (1976 to 1977 and 1977 to 1978). No significant differences were found for any caste between the two sampling years. The data for each bimonthly sampling interval (August, October, December, February, April, and June), of the first and second sampling

¹ Isoptera: Rhinotermitidae.

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⁵ Colonies in the reproductive stage of their life cycle (Oster and Wilson 1978).

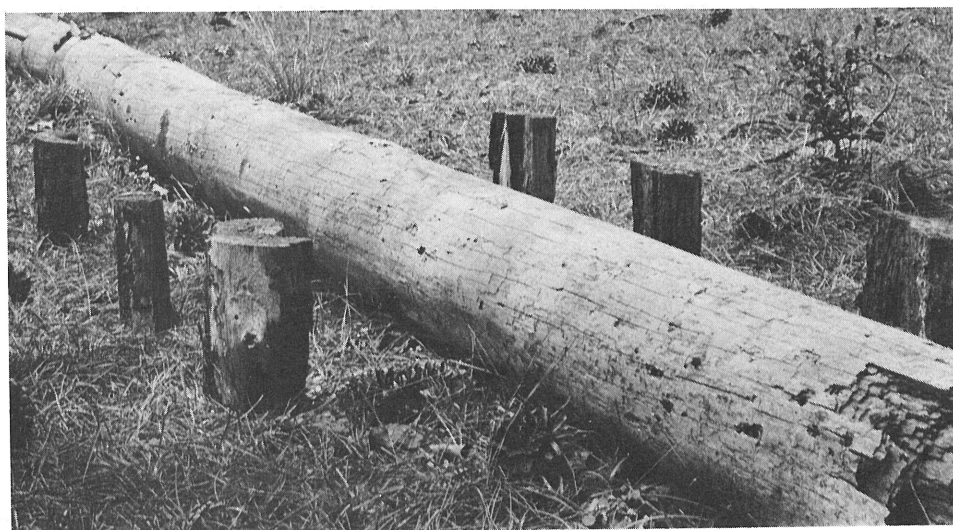


FIG. 1.—A fallen log containing a large colony of *R. flavipes*. Weathered pine bolts adjacent to colonized log were used as sampling baits.

year, were therefore considered together. Means for the proportions of each caste for each sampling interval were calculated from the proportions in the three 5-ml subsamples of each sampled colony. Differences in proportions of each caste between sampling periods were tested by analysis of variance. Before analysis, proportional caste data were transformed to arc sine of the square root of the percent. Significantly different means were separated by Tukey's test ($\alpha = 0.05$).

Caste forms were characterized according to the terminology of Miller (1969). Workers (pseudergates) are undifferentiated individuals of at least the third stage. Nymphs are individuals of at least the third stage possessing external wing pads. Larvae are undifferentiated individuals of less than the third stage.

Results and Discussion

Central to the success of any quantitative study of a termite population is the selection of a suitable sampling method. Our method takes advantage of the tendency of *R. flavipes* to form diffuse, multicompartmental nests, distributed between the soil and a substantial mass of wood. Many termites were found in the baits at every sampling date ($5,339 \pm 212$ [mean $\pm$ SD] termites per bait, $n = 489$), and no significant differences were found between log and bait caste proportions for any caste (Table 1).

All castes except presoldiers, neotenic reproductives, and alates were found at every sampling interval (Table 2). Workers comprised between 79.7 and 89.6% of the termites with 80.7 to 94.2% of the biomass. Nymphs varied from 3.0 to 8.4% of the termites, with 2.6 to 13.0% of the biomass, whereas soldier percentages varied from 1.2 to 2.9% of the population, with a biomass from 2.0 to 4.4%. Larvae were always present in large numbers (6.1 to 10.8%), but because they are small, they never accounted for more than 2.0% of the biomass. Presoldiers, neotenic reproductives, and alates never exceeded 0.4% of the population.

Eggs were recovered twice from sampling baits (August 1976 and June 1978). We estimated that ca. 10 ml of eggs was in one sample bait of the 1976 sample and ca. 2 ml of eggs was in a second bait from the same colony. Similar numbers were in the 1978 sample. Alates were only found twice (June 1978) in the baits. We suspect that this was a result of our sample timing. *R. flavipes* has two flight periods in southern Mississippi: mid-March to early April (the major flight), and mid-September to early October (a minor flight). Both flights probably occurred shortly before we sampled.

The proportions of all castes changed significantly throughout the 2-year study. Worker proportions were greatest from February to June, reflecting a decrease in larval and nymphal proportions. Larvae were most abundant during summer months, suggesting a peak in egg production concurrent with or shortly after release (flight) of alates. But larvae were collected at every sampling period, so egg production may be continuous throughout the year, or winter larvae may be the results of eggs laid earlier in the fall.

Soldier proportions also seemed to be linked with alate production. Their proportions were highest in February and lowest in April (immediately after the main alate flight). Termite soldiers have been reported to

Table 1.—Comparison of the mean proportions of five castes of *R. flavipes* found in sampling bolts associated with six sampled colonies in fallen logs^a

Caste	Bolt	Log	Difference			
			$\bar{d}$	S_d^b	t	Power ^c
Workers	72.5	87.2	12.0	8.90	1.35	0.93
Nymphs	3.6	2.4	1.2	1.01	1.18	0.80
Soldiers	1.2	1.9	0.7	0.53	1.32	0.87
Presoldiers	0.43	0.17	0.26	0.20	1.31	0.85
Larvae	19.8	8.3	11.5	9.19	1.25	0.83

^a Comparison of sample means; paired observation (Steele and Torrie 1960).

^b Sample standard deviation of $\bar{d}$.

^c Power is the probability of detecting a difference of the size of $\bar{d}$ with a sample size of six and $\alpha = 0.05$.

Table 2.—Average composition of *R. flavipes* (Kollar) colonies in southern Mississippi sampled bimonthly over a 2-year period from August 1976 to June 1978^a

Caste	August 1976, 1977	October 1976, 1977	December 1976, 1977	February 1977, 1978	April 1977, 1978	June 1977, 1978	Mean
Total no.							
Worker	82.0a	79.7a	82.0ab	86.9bc	89.6c	84.0ab	84.0
Nymph	4.9ab	8.4c	5.7b	3.2a	3.0ab	5.1b	5.0
Soldier	1.8ab	2.3bc	2.9c	2.9c	1.2a	1.3a	2.1
Presoldier	0.3c	0.1b	0.0a	0.0a	0.1b	0.3c	0.1
Total soldier	2.0b	2.3bc	2.9c	2.9c	1.3a	1.6ab	2.2
Larva	10.8b	9.5b	9.2ab	6.9ab	6.1a	9.2ab	8.7
SR ^b	0.4	0.1	0.0	0.0	0.0	0.1	0.1
Biomass							
Worker	86.4b	80.7a	84.4ab	90.3c	94.2d	84.9b	86.9
Nymph	8.2bc	13.0d	9.3c	5.5ab	2.6a	10.7cd	8.1
Soldier	3.0bc	4.0cd	4.4d	3.5cd	2.0a	2.1ab	3.1
Presoldier	0.4b	0.1a	0.0a	0.0a	0.1a	0.4b	0.2
Total soldier	3.4bc	4.1cd	4.4d	3.5bcd	2.1a	3.1ab	3.4
Larva	1.2a	2.0b	1.6ab	0.8a	1.1a	1.6a	1.4
SR	0.9	0.2	0.0	0.0	0.1	0.2	0.2

^a Each value represents mean percentage of total numbers or biomass of termites sampled. Means for each 2-month interval result from three subsamples of 15 sampled colonies (20 for August 1976). Different colonies were sampled in two consecutive years. Significant differences between means, in the same row, were tested by analysis of variance. Means followed by the same letter are not significantly different at the $\alpha = 0.05$ level by Tukey's test.

^b SR, Supplementary reproductive.

"accompany" alates to the periphery of the gallery system, or even out into the open, when the alates begin their flight. The soldiers are thus exposed to predators (Nutting 1969). Consistent with this interpretation is our observation that presoldiers were not found in December or February but began to appear again in April. Presoldiers occurred in maximum proportions in June and August, apparently replacing soldiers lost at the time of the alate flights. Their presence brought the soldier proportions back to the expected 2% of the individuals in the colony (Howard and Haverty 1980, Haverty and Howard, 1981).

We expected maximum nymph proportions in the February samples. Instead they occurred in the October samples (Fig. 2). We believe that this happened for two reasons. October nymphs would be mostly early to mid-instars still functioning at least in part as "workers." As such, they would still be found throughout the nest system. As they molt into late-instar nymphs however they progressively withdraw from the main portion of the colony in preparation for their metamorphosis into alates (Nutting 1969). Such a withdrawal could explain their lower representation in the February samples.

The observed seasonal caste compositional changes in *R. flavipes* showed only one maxima per year for each caste (Fig. 2). This, taken in conjunction with our field experience of usually only a single yearly alate flight per colony, suggests that mature *R. flavipes* colonies go through only one complete reproductive cycle per year. To make further progress in understanding the caste ecology of this cryptic subterranean species, we will need to develop ways to estimate population sizes and growth rates and to determine foraging strategies.

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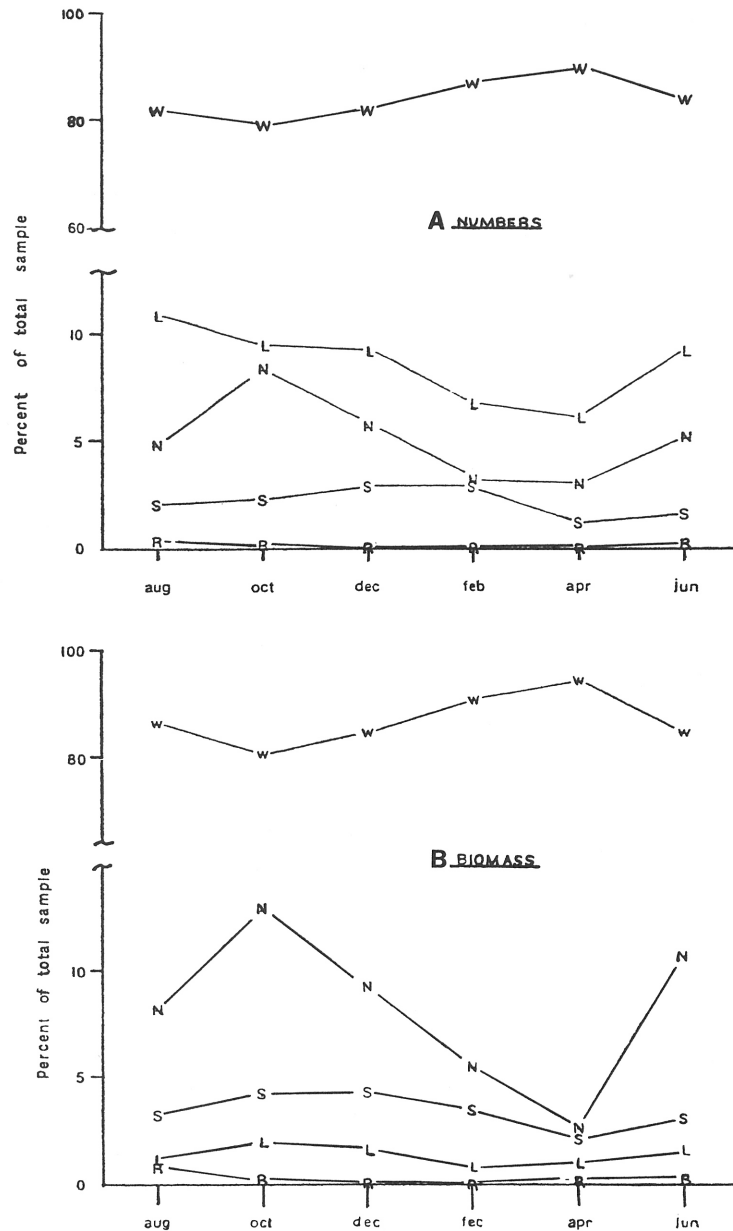


FIG. 2.—Seasonal proportions of various castes of *R. flavipes*. Caste proportions are presented as percentage of total numbers (A) and total biomass (B) samples. W, Workers; L, larvae; N, nymphs; S, soldiers (adult soldiers and presoldiers) R, neotenic reproductives.

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