Reproductives in Mature Colonies of *Reticulitermes flavipes:* Abundance, Sex-Ratio, and Association with Soldiers[1,2]

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Reproductives in Mature Colonies of *Reticulitermes flavipes*: Abundance, Sex-Ratio, and Association with Soldiers[1,2]

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ABSTRACT

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Soldier and reproductive proportions of *Reticulitermes flavipes* (Kollar) were determined in sampling baits from 89 colonies and 5 logs. Soldiers averaged 2% of the colony and neotenics, when present, accounted for up to 1.28%. The sex-ratio of *R. flavipes* neotenics was ca. 2 females for every male. Soldier proportions were always high in the vicinity of the neotenics.

Demography of mature colonies of *Reticulitermes flavipes* (Kollar), the most economically important termite species in the United States, has been studied only twice. Banks and Snyder (1920), after observing 21 logs or stumps for 2 yr near Falls Church, VA, reported that 13 of these colonies contained mature primary reproductives (reproductives of "the first form"). The remaining 8 contained many mature neotenic reproductives (reproductives of "the second form"). They also reported soldier proportions of 8.4 and 10.8% from 2 collections of less than 1,000 individuals. Esenther (1969) studied *R. flavipes* in Wisconsin. From samples taken from miscellaneous wood debris, timbers, dead trees, and wooden structures such as fences, he reported that an unspecified number of colonies contained at least 100 grossly physogastric brachypterous neotenics. He did not report soldier proportions.

Recently we began study of the demography of mature colonies of *R. flavipes* in southern Mississippi. Here, we report our findings on the abundance and sex-ratio of neotenics in mature[5] *R. flavipes* colonies, and the association of soldiers with such repoductives.

Methods and Materials

One hundred colonies of *R. flavipes* were located and numbered in Harrison, Jackson, and Stone Co., MS, in early spring 1976. Fallen pine logs or stumps were selected that were heavily infested by termites. We estimated that at least 50,000 termites were contained in each colony. Every numbered colony was at least 50 m from the nearest numbered termite-infested log. Six to 8 sampling baits consisting of pine bolts, 0.5 X 0.1 m diam, which had been weathered for 6 mo without ground contact, were placed at ca. 0.5-m intervals around the periphery of each source colony. In Aug. 1976, 20 of the 100 source colonies were randomly selected and 3 sampling baits randomly taken from each. The removed baits were replaced with 3 newly weathered bolts. Beginning in Oct. 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 mo. Eleven colonies were never sampled and 15 colonies were sampled twice within at 6-mo period. The 45 infested baits were individually placed in plastic bags, taken back to the laboratory, and all termites removed. 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. These data yielded an estimate of the temites and caste proportions in each bait. A total of 12 bimonthly collections was made.

Besides the 89 colonies sampled by baits, 5 additional *R. flavipes* colonies were sampled completely. Three were collected in late summer 1977 in Harrison and Jackson Co. The termites were extracted from the logs as completely as possible, but total numbers were not measured. Each colony had many neotenics, which were collected and counted by sex. Two additional colonies of *R. flavipes* were located in Harrison Co., during late spring 1978 in fallen pine logs ca. 20 m long and 0.3 m diam. Nearly all termites appeared to be within a 6-m length of each log, so only these sections were taken to the laboratory. Each log portion was carefully dissected (to extract as many of the termites as possible) and the termites from each colony were measured volumetrically and thoroughly mixed. Three 5-ml subsamples were taken from each colony and counted. From these data, we estimated the number of termites in each colony. All extracted termites were then examined, and the soldiers and neotenics (by sex) counted and recorded.

We used paired *t*-tests to compare proportions of soldiers present in sampling baits with and without reproductives. Abundance of soldiers and neotenics in complete colonies was restricted to summary statistics.

Results

Reproductives were found at least once in sampling baits from 26 of the 89 colonies and in all 5 of the logs sampled. Only 3 of the 26 colonies contained primary reproductives. All other reproductives found were neotenic. The female reproductives were markedly physogastric. Sample baits averaged 142.1 ($S_{\bar{x}}=40.2$) neotenic reproductives, with a ♀ : ♂ sex ratio of 1.88 ($S_{\bar{x}}=0.32$). The 5 log samples averaged 792.4 ($S_{\bar{x}}=392.7$) neotenics with a ♀ : ♂ sex ratio of 2.33 ($S_{\bar{x}}=0.94$). Clearly, neotenics, when present, occur in fairly large numbers and the sex ratio is heavily skewed in favor of the females. Neotenics accounted for 0.98 and 1.28% of the termites in the 2 logs sampled in 1978 and ca. 0.74% of the termites in the sampling baits in which they were found.

We expected relatively constant soldier proportions within the 3 randomly chosen sampling baits from each colony, and such was the case unless a bait contained reproductives (Table 1). When reproductives were present, 1 of the 3 baits sampled from the same colony usually contained all of the reproductives. This bait also contained a significantly higher proportion of soldiers than either of the other 2 baits. The proportion of soldiers associated with primary reproductives did not differ significantly from the proportion associated with neotenic reproductives (*t*-test for groups of unequal sizes). Also, the proportions of soldiers in the nonreproductive-containing baits are essentially the same for colonies with both types of reproductives. The 1st of the whole logs sampled in 1978 yielded ca. 140,000 termites, of which soldiers constituted 1.86% (2614 soldiers). The 2nd whole log yielded ca. 161,400 termites, of which soldiers constituted 2.35% (3795 soldiers). So, the overall proportions of soldiers in these 2 "complete" colonies were close to the 1.98% proportion of soldiers in all sampling baits without reproductives.

Discussion

Lower termites, unlike other social insects, are thought to have equal proportions of males and females in their nonreproductive castes (Wilson 1971). Neotenic reproductives are derived from these nonreproductive forms, so one would expect that they too would have a 1:1 sex ratio. Such is not the case for *R. flavipes.* At least 2 hypotheses can explain this. Perhaps the nonreproductive castes do not actually exist in equal proportions of males and females. No external sex differences are known for the Rhinotermitidae, and few workers have had the patience to conduct dissections for sex determination (Weesner 1969). Another possible explanation is that some physiological or behavioral process may induce more females than males of *R. flavipes* to transform into functional reproductives. The stimuli that trigger such transformations are unknown.

The processes leading to the unusually large numbers of neotenics in *R. flavipes* colonies are also poorly understood. Higher termites frequently have colonies as large as or larger than *R. flavipes,* yet normally have only primary reproductives (Wilson 1971). Higher termites often construct large, sturdy, well-defined nests with a special "royal chamber" that is strongly defended. *R. flavipes,* however, have a poorly defined nest without a special "royal chamber." Under such circumstances, *R. flavipes* reproductives are subject to greater chances of predation. It would, therefore, be adaptive for the colony to have multiple reproductives. Also, rhinotermitids are well known for their propensity to undergo colony fragmentation or division (Wilson 1971). Again, the production of many neotenic reproductives in each divided colony would allow for rapid colony growth and increased chances of survival.

Experimental work quantifying the natural proportions of soldiers in termite colonies has been

Table 1.—Soldier proportions in sampling baits collected from field colonies with and without reproductives in the baits[a].

Source	No. of samples	Percent soldiers ($\bar{x}\pm$95% CI)
Colonies with primaries in baits		
Sampled baits with primaries	3	3.18±0.68
Sampled baits without primaries	6	2.26±0.68
Colonies with neotenics in baits		
Sampled baits with neotenics	25	3.76±1.02
Sampled baits without neotenics	49	1.76±0.71
Baits without reproductives		
All colonies	532	1.98±0.18

[a]Only a single reproductive type was ever found for any given numbered colony during the 2-yr sampling period.

quite limited (Haverty 1977). In general, however, the proportions are relatively constant for any given species. Haverty and Howard 1980 showed that the percentage of *R. flavipes* soldiers differentiating in laboratory experimental groups of undifferentiated larvae and workers averaged 1.75% but varied from 0.38 to 2% depending on the time of year the termites were collected. These laboratory data agree with what we report here from field colonies. Soldiers, on the average, account for ca. 2% of the individuals in mature colonies of *R. flavipes,* and vary throughout the year from 1.2 to 2.9% (unpublished data). Banks and Snyder's (1920) report of 8.4 and 10.8% soldiers for colonies of *R. flavipes* seems somewhat high. None of the colonies we have examined have soldier proportions of this magnitude. Banks and Snyder, because they were reporting on small groups associated with reproductives, may have been reporting without being aware of it, what we observed in this study—soldiers are present in abnormally large proportions when associated with reproductives. Local concentrations of soldiers have been reported to be associated with reproductives and alates at the periphery of a colony (Stuart 1969) or with foraging parties and groups engaged in mound repair (Watson and McMahan 1978). What causes local concentrations of soldiers within termite colonies remains to be elucidated.

Footnotes

[1]Isoptera: Rhinotermitidae.

[2]Received for publication Nov. 27, 1979.

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[5]Colonies in the reproductive stage of their life cycle.

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