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SOLDIER PRODUCTION AND MAINTENANCE OF SOLDIER PROPORTIONS IN LABORATORY EXPERIMENTAL GROUPS OF *COPTOTERMES FORMOSANUS* SHIRAKI

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SUMMARY

Experimental groups of 100 percent pseudergates of *Coptotermes formosanus* Shiraki were set up in the laboratory and allowed to differentiate for either 4, 8 or 12 weeks. The average percentage of pseudergates differentiating into presoldiers and soldiers at these time intervals was 3.8, 14.2, and 21.9 percent, respectively. Differentiation to the soldier caste was affected both by initial group size and colony origin. Groups initially composed of 100 pseudergates produced a significantly smaller proportion of soldiers than did groups of 300, 500, or 1000. Recently collected field colonies produced soldiers at significantly higher rates than one which had been maintained in the laboratory for 8 years. The number of soldiers produced was highly correlated with the total number of all individuals at 4, 8, and 12 weeks, which indicates a precise physiological mechanism for regulating soldier proportions.

Experimental groups were also set up with " normal " (24 percent), " below normal ", and " above normal " initial proportions of soldiers with pseudergates. When soldiers were present in " below normal " proportions they inhibited the presoldier production, so that presoldier development gradually declined as the initial soldier-pseudergate ratio approached the norm. This species can tolerate and will maintain an exceptionally high proportion of soldiers (ca. 38 percent) which is far above the assumed " normal " proportion. Many, but not all, of the excess soldiers were probably eliminated by cannibalism. Groups severely overloaded with soldiers succumbed to microbial contamination after the excess soldiers starved to death.

From these results I conclude that colonies of *C. formosanus* do maintain numerically constant proportions of soldiers within broad limits. Thus, colonies might be controlled by chemically inducing the production of superfluous soldiers. Successful control would require the proportion of soldiers be so great that the pseudergates could not

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effectively reduce the numbers of soldiers by cannibalizing the excess individuals before their death by starvation resulted in microbial contamination of the entire colony.

RESUME

Production des soldats et maintien des proportions de soldats dans des groupes expérimentaux de Coptotermes formosanus **Shiraki**

Des groupes expérimentaux, entièrement constitués de pseudergates de *Coptotermes formosanus* Shiraki, se sont différenciés librement au laboratoire pendant 4, 8 ou 12 semaines. Les pourcentages moyens de pseudergates qui se sont différenciés en soldats ou en soldats blancs ont été de 3,8 pour cent au bout de 4 semaines, 14,2 pour cent au bout de 8 semaines et 21,9 pour cent au bout de 12 semaines. La différenciation en soldat a été influencée par la taille initiale du groupe et le lieu d'origine de la colonie. Des groupes composés initialement de 100 pseudergates ont produit significativement une proportion plus faible de soldats que des groupes de 300, 500 ou 1000. Des colonies qui venaient d'être récoltées dans la nature ont fourni des taux significativement plus élevés de soldats qu'une colonie qui était gardée au laboratoire depuis 8 ans. Le nombre de soldats obtenu était en corrélation hautement positive avec le nombre total d'individus au bout de 4, 8 et 12 semaines. Ceci indique qu'il existe un mécanisme physiologique précis dans la régulation des proportions de soldats dans les colonies.

Nous avons aussi constitué des groupes expérimentaux qui comprenaient des proportions « normales » (24 %), « en dessous de la normale » et « au dessus de la normale » de soldats par rapport aux pseudergates. Lorsque la proportion de soldats était « en dessous de la normale », il y a eu inhibition de la production de présoldats de sorte que le développement en présoldats a progressivement diminué à mesure que la proportion de soldats par rapport aux pseudergates approchait de la « normale ». *Coptotermes formosanus* Shiraki peut tolérer et maintenir une proportion remarquablement élevée de soldats (environ 38 %), ce qui est bien au dessus de la proportion considérée comme « normale ». Un grand nombre (mais pas tous) des soldats en surnombre ont été probablement éliminés par cannibalisme. Des groupes suchargés en soldats ont succombé à la contamination microbienne après que les soldats en surnombre fussent morts de faim.

Je conclus de ces résultats que les colonies de *Coptotermes formosanus* gardent des soldats en proportion constante.

INTRODUCTION

Numerous authors have suggested that for a given termite species there is an approximately constant proportion among castes and that in colonies of comparable size and age, there are behavioral and physiological mechanisms for maintaining these ratios (GRASSÉ, 1939 ; MILLER, 1942 ; EMERSON, 1956 ; LUSCHER, 1961 ; HEWITT et coll., 1969 ; SPRINGHETTI, 1969, 1972*a*, 1972*b* ; BOUILLON, 1970 ; HOWSE, 1970 ; NUTTING, 1970 ; MOORE, 1969). CASTLE (1934) and LIGHT (1942-1943, 1944) were among the first to postulate that the development of castes in termites was under the control of "ectohormones". LUSCHER (1961) suggested that the production of soldiers might be suppressed by a pheromone produced by existing members of this caste. This pheromone (or pheromones) is distributed throughout the colony by trophallaxis. Differentiation is inhibited through the neurosecretory system whenever the titer of this pheromone is sufficiently high. Soldiers are produced when the proportion of this caste (and hence the titer of inhibiting pheromone) falls below the normal level (WEESNER, 1960), while extra individuals are eliminated by cannibalism when their numbers (or pheromone titers) become too great (MORGAN, 1959 ; LUSCHER, 1961 ; MCMAHAN, 1966 ; NAGIN, 1972 ; STUART, 1972 ; and YIN and GILLOTT, 1975).

Literature reports on the caste proportions of *Coptotermes formosanus* Shiraki are few and vary widely. NAKAJIMA et coll. (1964) found that entire colonies of *C. formosanus* contained ca. 5.0 percent soldiers while SMYTHE and MAULDIN (1972) and MAULDIN and RICH (1975) reported ca. 10.0 and 5.0 percent, respectively, for apparently stabilized laboratory test groups of this species. KING and SPINK (1974, 1975) reported young laboratory and field colonies of *C. formosanus* to contain ca. 10.0 percent soldiers. FUJII (1975) reported foraging groups of two colonies of *C. formosanus* to have mean soldier percentages of 5.0 and 4.7. A few literature records are available for soldier proportions in other *Coptotermes* species : *Coptotermes heimi* (Wasmann) at 33 percent (SEN-SARMA, 1974); *Coptotermes lacteus* (Froggatt) at 1.8-2.9 percent (GAY and GREAVES, 1940); and *Coptotermes vastator* Light at 9.1 percent (PANGGA, 1936).

With this much variation in the literature, it is necessary to obtain experimental evidence for the establishment and maintenance of " normal " soldier proportions for experimental groups in the laboratory. Doing so is a necessary first step for evaluating the effects of chemicals, such as juvenile hormone analogues, which cause pseudergates to differentiate into numerous superfluous soldiers (HRDY, 1973 ; WANYONYI and LUSCHER, 1973 ; WANYONYI, 1974 ; SPRINGHETTI, 1974 ; FRENCH, 1974 ; CHU et coll., 1974 ; HRDY, 1972 ; LENZ, 1976*a* and 1976*b* ; and HRDY and KRECEK, 1972).

Therefore, the two objectives of this study were to determine the effects of group size and colony origin on the proportion of soldiers produced as a result of differentiation in experimental groups of externally undifferentiated pseudergates (or large larvae) and to determine the ability of experimental groups installed with " normal " or " abnormal " proportions of soldiers to maintain or establish "normal" ratios over limited time intervals.

METHODS AND MATERIALS

1. Effect of group size and colony origin on production and proportion of soldiers

Externally undifferentiated pseudergates of at least the third instar were used from three colonies of *C. formosanus*. Colonies 1 and 2 were collected in cypress *(Taxodium* *distichum* [L.] Rich.) snags near Lake Charles, Louisiana, approximately 6 weeks before this phase of the test was initiated. Colony 3 had been maintained as a laboratory colony at Gulfport, Mississippi, for nearly 8 years and was collected from the same general vicinity as colonies 1 and 2. Colonies 1 and 2 contained an estimated 25 percent soldiers initially, whereas colony 3 was estimated to have at least 35 percent. All three colonies had nymphs and presoldiers present but in very low numbers (probably less than 1 percent). All estimates are visual; no counts were made.

By necessity the experimental units were set up in containers of different sizes. The group sizes were 100, 300, 500, and 1 000 pseudergates each. Screwtop glass jars 5.0 cm in diameter × 3.5 cm in height were used for the 100 individual groups; 6.0 × 9.5 cm for 300 and 500 per group; and 7.5 × 11.0 cm for 1 000 per group. Fifty g (35 ml) of sterile, washed sand, moistened with 7 ml of deionized water was used as a substrate for the 5.0 × 3.5 cm container; 150 g sand with 21 ml of water for the 6.0 × 9.5 cm container; and 300 g sand with 42 ml of water for the 7.5 × 11.0 cm container. For each 100 termites per container, a 2.0 × 2.0 × 1.5 cm block of ovendried slash pine, *Pinus elliottii* Engelm. var. *elliottii*, was used as food. All wood blocks were from the same tree. The containers were placed in an incubator at 28° C for up to 12 weeks. Every four weeks (at 4, 8, and 12 weeks) one-third of the containers were disassembled. The termites in each disassembled unit were counted and identified by caste, and then excluded from the test. Each treatment combination (group size × colony × time period) was replicated two times.

2. Effect of "abnormal" proportions of soldiers on the production, and elimination, and the maintenance of a normal proportion

Externally undifferentiated pseudergates of at least the third instar and adult soldiers in various proportions were used from five colonies of *C. formosanus*. Colonies 1, 2, and 3 are the same as those used in the previous experiment. At the time this portion of the experiment commenced colonies 1 and 2 had been maintained at Gulfport as laboratory colonies for only 6 months, colony 3 for 8 years, and colony 4 for 6 years. Colony 5 was collected near Lake Charles, Louisiana, from short pine logs placed around the buried portion of a cypress snag which contained a natural colony. Colony 5 had a flight of alates before and during the removal of pseudergates and soldiers for this experiment. All colonies contained only a few presoldiers and nymphs and a soldier proportion roughly estimated to be 25 percent. Colony 3 contained some young larvae, but none were visible in any of the other colonies.

All experimental units contained 300 termites. Containers were set up, incubated and disassembled as in section 1. The "normal" percentage of soldiers was assumed to be 24 percent (see Table I p. 74). "Abnormal" group composition was initiated at 0, 5, 12, 48, and 72 percent soldiers which are, 0, 0.25, 0.5, 2.0, and 3.0 times the "normal" soldier percentage. Each treatment combination (group composition × colony × time period) was replicated two times.

The data for both the group size and the abnormal proportion sections of the experiment were subjected to analysis of variance utilizing a randomized complete-block design. Colony origin was used as a block effect to separate any errors due to differences in colonies from experimental error. There were four response variables: percent survival, percent presoldiers, soldiers, and total soldiers (presoldiers and soldiers). The percentage of pseudergates is 100 minus the percentage of presoldiers and soldiers. These proportions were transformed to arc sine of the square root of the percentage before analysis. Means of treatments with significant differences were separated at the $\alpha = 0.05$ level by Student-Newman-Keuls' test. Any significant differences for percent total soldiers are exactly the same for percent pseudergates. The data were also analyzed by linear regression to evaluate the constancy of the total soldier proportion.

For the linear regression analysis, the total number of individuals in the group was the independent variable, and number of soldiers and presoldiers was the dependent variable.

RESULTS AND DISCUSSION

1. Effect of group size and colony origin on production and proportion of soldiers and group survival

Group size

The percentage of soldiers and group survival after 4, 8, and 12 weeks is given in Tab. I. After 4 weeks there were no significant differences among group sizes in proportions of presoldiers, soldiers, or both. However, soldier differentiation had begun with an average of 3.5 percent of the termites differentiated to presoldiers and 0.2 percent had already differentiated to the adult soldier caste. After 8 weeks there were no significant differences among group sizes for percentage of presoldiers. The percentage of soldiers and total soldier population (presoldiers and soldiers) for groups of 100 was significantly lower than the three other group sizes. The percentage of individuals differentiating to the soldier caste had also increased to an average of 4.8 percent presoldiers and 9.4 percent soldiers. After 12 weeks there were also statistically significant differences in the percentage of soldiers and the total soldier population. The percentage of these categories was again less in groups of 100 than in the three larger groups. There were no such differences in presoldiers. After 12 weeks the proportion of individuals differentiating to the soldier caste had begun to slow down, to an average of 2.9 percent presoldiers and 19.0 percent soldiers. The percentage of presoldiers at 12 weeks was slightly over half of the percentage at 8 weeks, suggesting that the presence of adult soldiers had an inhibitory effect on further presoldier development.

This lower proportion of soldiers in smaller groups agrees with the observations of McMahan (1966) for *Cryptotermes brevis* (Walker) that smaller colonies of termites have a lower percentage of soldiers but contradicts Luscher's (1961) findings of *Kalotermes flavicollis* Fabr., that small field colonies have a high proportion of soldiers. My results support an explanation offered by McMahan.

" The ratio of soldier to nonsoldier, for example, is believed to be regulated by the amount of soldier-inhibiting pheromone produced by the soldiers present and distributed via food exchange to colony members. Theoretically, as the colony increases in number of individuals, the average amount of pheromone reaching members becomes too small to be effectively inhibiting, and other soldiers develop... The larger the colony, then, the greater the chances that, for a given time interval, some individuals will receive little pheromone or none at all. It follows that small termite colonies should have a lower soldier-to-nonsoldier ratio (fewer soldiers per unit of population) than large colonies. "

Table I. — Percentage of presoldiers (PS), soldiers (SO), and total soldiers (PS+SO), and percent group survival after 4, 8, and 12 weeks of differentiation by groups of *Coptotermes formosanus* initially composed of 100 percent pseudergates but differing in initial group size and colony origin.

Tableau I. — Pourcentage de soldats blancs (PS), de soldats (SO) et de tous les soldats (PS + SO), et pourcentage de survie après 4, 8 et 12 semaines de différenciation dans des groupes de *Coptotermes formosanus* qui étaient initialement composés uniquement de pseudergates. Les groupes différaient quant au nombre des individus et quant au lieu d'origine de la colonie.

Treatment	4 weeks a				8 weeks a				12 weeks a			
	PS	SO	PS +SO	Surv.	PS	SO	PS +SO	Surv.	PS	SO	PS +SO	Surv.
Initial group size b												
100	3.0	0.2	3.1	96.3	3.5	6.1a	9.6a	95.7	2.5	13.3a	15.8a	91.8
300	3.6	0.1	3.6	95.8	6.4	11.0b	17.4b	83.7	3.1	21.3b	24.4b	82.0
500	4.0	0.4	4.4	93.6	4.7	10.4b	15.1b	86.0	3.7	19.9b	23.7b	78.4
1 000	3.5	0.3	3.8	92.8	4.5	10.0b	14.6b	84.3	2.1	21.5b	23.6b	82.9
Colony origin b												
1	4.8a	0.2a	5.0a	91.8	6.8a	10.5a	17.3a	79.1	1.8	22.2a	24.0a	85.2
2c	4.9a	0.5b	5.4a	97.0	4.4b	11.3a	15.7a	96.6	—	—	—	—
3	0.9b	0.0c	0.9b	95.1	3.0b	6.4b	9.4b	86.6	4.0	15.8b	19.8b	82.3
Grand Mean	3.5	0.2	3.8	94.6	4.8	9.4	14.2	87.4	2.9	19.0	21.9	83.8

a Means in a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level as determined by Student-Newman-Keuls' test. Means in columns without letters do not differ significantly.

b Means for each initial group size are the average of all colonies. Likewise, means for each colony are the average of all group sizes.

c At 12 weeks only four of eight experimental units contained live termites, therefore, this colony was left out of the analysis of variance for this time period.

But the results reported here do agree with LUSCHER's observation on *K. flavicollis* that the proportion of soldiers stabilizes once the colony exceeds 250 individuals.

In this study there were no significant differences in survival with respect to initial group size; however, LAFAGE (1976) found that initial group size could have a significant effect on group survival for the drywood termite, *Marginitermes hubbardi* (Banks).

Colony origin

Differences in the production rate of soldiers between colonies became apparent at 4 weeks (Tab. I). Colonies 1 and 2 were producing a significantly higher proportion of presoldiers at this time than was colony 3. The former also contained individuals which had already molted to the soldier caste. Colony 3 contained no soldiers at the end of 4 weeks. By the time 8 weeks had passed, the difference in production of presoldiers had become insignificant between colonies 2 and 3. However, colonies 1 and 2 had a significantly higher total soldier population than colony 3. After 12 weeks, four of eight experimental units of colony 2 had dried out and all the termites had died. As a result this colony was dropped from the experiment for this time period only. At this time there was a significant difference in the percentage of total soldiers between colonies 1 and 3. The percentages of presoldiers, however, were not significantly different between colonies.

The differences in the percent of total soldier population between colonies is not evidence against a species-specific soldier proportion. The differences are probably due to different rates in the production of soldiers by the three colonies. If the test had been allowed to proceed for an additional 4 weeks the differences between colonies 1 and 3 might very well have been insignificant.

There were no significant differences in survival with respect to colony origin at 4 and 12 weeks. Colony 2 had a significantly higher survival rate than did the other two colonies at the end of 8 weeks. The high mortality in colony 2 at 12 weeks was obviously due to experimental conditions and not colony vitality. Four of the eight experimental units dried out and all the termites died. Throughout the experiment there were no significant correlations between percent survival and percent of the total soldier population.

Correlation of the number of soldiers to total number of termites

The total soldier population (soldiers and presoldiers) was highly correlated ($\alpha = 0.01$) with the total number of individuals in a group. This correlation improved after each successive time period (fig. 1-3). If colony 3, which has a lower soldier production rate, is left out of the regression the correlation coefficient for the data for week 4 is even more improved. Leaving colony 3 out of the regression at 8 weeks had no significant effect on the correlation coefficient.

The average proportion of pseudergates differentiating to soldiers in this experiment was higher than any previously recorded. Entire colonies and foraging groups of *C. formosanus* have been reported to contain between 4.7 and 10 percent soldiers (FUJII, 1975; KING and SPINK, 1974, 1975; and NAKAJIMA et coll. 1964). Working with laboratory groups of 100 pseudergates, SMYTHE and MAULDIN (1972) observed that about 10 percent of the survivors had differentiated to soldiers after 8 weeks. Because the production of presoldiers had slowed by this time, they concluded that the 10 percent proportion they observed was the "normal" proportion.

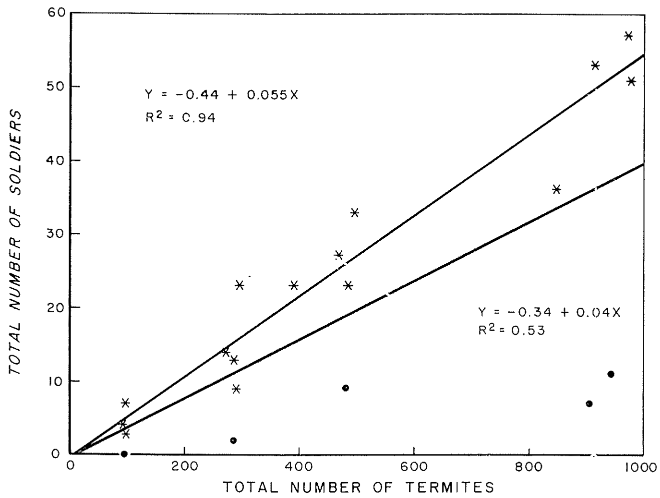

Fig. 1. — Relationship between the number of soldiers (soldiers and presoldiers) and total number of termites for all experimental groups after 4 weeks of differentiating by pseudergates. Data from all colonies (* and ●) result in the lower regression line, whereas data from colonies 1 and 2 only (*) result in the upper regression line.

Fig. 1. — Relation entre le nombre de soldats (soldats et soldats blancs) et le nombre total de Termites dans tous les groupes expérimentaux après 4 semaines de différenciation des pseudergates. La droite de régression du bas a été construite à partir des données obtenues sur toutes les colonies (* et ●), alors que la droite de régression du haut a été construite à partir des données obtenues sur les colonies 1 et 2 (*).

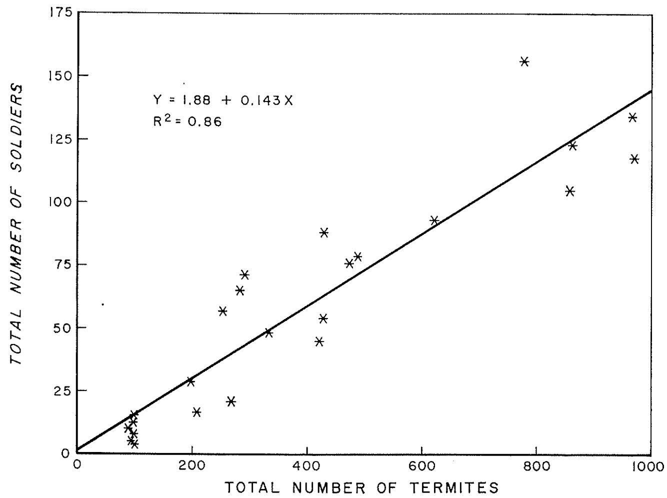

Fig. 2. — Relationship between the number of soldiers (soldiers and presoldiers) and total number of termites for all experimental groups after 8 weeks of differentiating by pseudergates.

Fig. 2. — Relation entre le nombre de soldats (soldats et soldats blancs) et le nombre total de Termites dans tous les groupes expérimentaux après 8 semaines de différenciation des pseudergates.

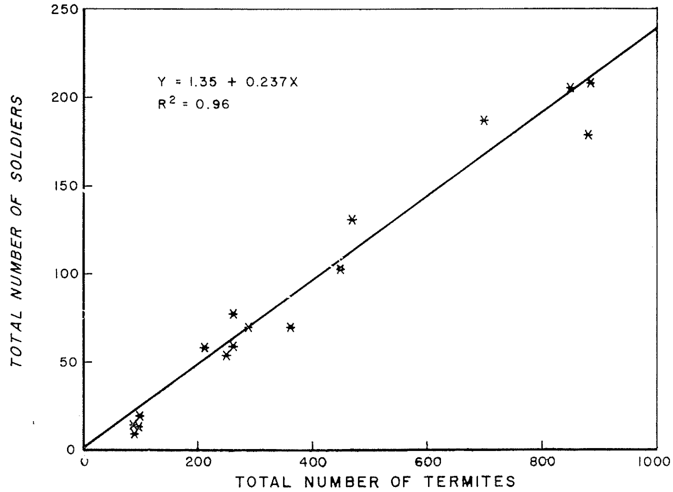

Fig. 3. — Relationship between the number of soldiers (soldiers and presoldiers) and total number of termites for experimental groups of colonies 1 and 3 after 12 weeks of differentiating by pseudergates.

Fig. 3. — Relation entre le nombre de soldats (soldats et soldats blancs) et le nombre total de Termites dans les groupes expérimentaux issus des colonies 1 et 3 après 12 semaines de différenciation des pseudergates.

In this study I have essentially duplicated a portion of the experiment by SMYTHE and MAULDIN (1972) and have obtained similar results ; that is, after 8 weeks about 10 percent of the surviving 100 pseudergates have also differentiated into soldiers. Yet, the ratio of soldiers to presoldiers was much lower in this study than in that of SMYTHE and MAULDIN. It would appear that the termites I used, under these experimental conditions, had not yet reached an equilibrium of soldiers to nonsoldiers after 8 weeks of differentiation. As a result I doubt if either SMYTHE and MAULDIN (1972) or I could state unequivocally that the particular experimental condition of 100 pseudergates per group and 8 weeks would allow the termites to reach their " normal " proportions. In fact, groups of 300, 500, or 1000 pseudergates may not have yet reached an equilibrium proportion after 12 weeks, since almost all experimental units still had over 2 percent presoldiers at this time (Tab. I). In comparison, LENZ (1976*a*) found that groups of 1000 *Coptotermes amanii* (Sjöstedt) did reach equilibrium at 12 weeks and maintain a worker-to-soldier ratio of 4 : 1 for another 6 months. He feels that for *C. amani* 12 weeks is the minimum time required to reach equilibrum proportion (LENZ, personal communication).

2. Effect of "abnormal" proportions of soldiers on the production, elimination, and maintenance of this caste's proportions

Apparently, the presence of soldiers in the groups at the onset inhibited the production of presoldiers after 4 weeks (Tab. II). Presoldier production

Table II. — Percentage of presoldiers (PS), soldiers (SO), and total soldiers (PS+SO), and percent group survival after 4, 8 and 12 weeks in groups of 300 termites differing in initial percentages of soldiers and pseudergates (PG), and colony origin.

Tableau II. — Pourcentage de soldats blancs (PS), de soldats (SO) et de tous les soldats (PS + SO), et pourcentage de survie après 4, 8 et 12 semaines dans des groupes de 300 Termites qui différaient entre eux quant au pourcentage initial de soldats et de pseudergates et aussi quant à l'origine de la colonie.

Treat-ment	Initial		4 weeks a				8 weeks a				12 weeks a			
	PG	SO	PS	SO	PS +SO	Sur b	PS	SO	PS +SO	Sur b	PS	SO	PS +SO	Sur b
1	100.0	0.0	3.9a	0.3a	4.2a	92.0a	6.4a	9.9a	16.3a	92.0a	1.7	20.2a	21.9a	92.5a
2	94.0	6.0	1.7b	5.3b	7.0b	93.7a	4.5b	12.8a	17.3a	87.5a	1.6	17.6a	19.2a	91.1a
3	88.0	12.0	0.6c	10.6c	11.2c	92.7a	3.7b	14.3a	18.0a	90.3a	1.3	20.3a	21.6a	89.2a
4	76.0	24.0	0.0d	19.8d	19.8d	89.4a	2.6b	23.5b	26.1ab	88.3a	0.9	24.9b	25.8b	85.1a
5	52.0	48.0	0.0d	37.6e	37.6e	76.5b	1.0cc	40.2cc	41.2bc	71.bc	0.6	37.3c	37.9c	68.5b
6d	28.0	72.0	0.0	36.7	36.7	12.1	0.0	38.8	38.8	5.2	0.0	38.5	38.5	4.7
Colony e														
1	73.0	27.0	0.9	16.6b	17.5bc	91.0c	4.0a	20.ab	24.1	89.3	1.1a	23.9a	25.0a	86.4
2	73.0	27.0	1.2	16.6b	17.8bc	92.6c	4.6a	21.4ab	25.0	92.0	0.4a	30.2b	30.6b	89.1
3	73.0	27.0	0.9	12.4a	13.3a	87.0b	3.3a	17.2ab	20.5	86.1	0.7a	21.4a	22.1a	84.1
4	73.0	27.0	1.4	10.4a	11.8a	83.6a	4.9ac	16.4ac	21.3c	77.8c	1.4ab	21.5a	22.9a	83.0
5	73.0	27.0	1.7	17.4b	19.1c	90.1bc	1.8b	23.2b	25.0	84.1	2.4b	23.5a	25.9a	83.8
Grand Mean			1.2	14.7	15.9	88.9	3.6	19.9	23.5	85.9	1.2	24.1	25.3	85.3

a Means within a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level as determined by Student-Newman-Keuls' test. Means in columns without letters do not differ significantly.

b Mean percent survival is based on all observations for each group size.

c One group had 100 percent mortality. Means are based on nine observations. Therefore, at eight weeks the overall mean percentage is slightly different than the means of soldier percentages and survival as a function of both treatment and colony origin.

d Treatment 6 was not included in the analysis of variance because so many data points were missing due to high mortality. There were no survivors in 7 groups at 4 weeks, 8 groups at 8 weeks, and 9 groups at 12 weeks.

e Treatment 6 is not included in the average for each colony.

was inhibited even in groups with "below normal" proportions of soldiers. The rate of production of this caste in the "below normal" groups was significantly different from that of the "normal" (treatment 4) and one of the "above normal" groups (treatment 5), neither of which produced presoldiers after 4 weeks. Treatment 6 was dropped from the analysis of variance due to its extremely heavy mortality, but none of the three surviving groups produced any presoldiers at this time. Within groups with "below normal" proportions of soldiers the percentages of presoldiers differentiating after 4 weeks were significantly different from each other. There was a gradual decline in presoldier development as the percentage of soldiers at the onset approached the norm. The total soldier population percentage for each treatment was significantly different from all others after 4 weeks. This is obviously a reflection of the proportions established in the initial mix.

Fewer differences are apparent in presoldier production after 8 weeks. Production of this caste had resumed in the "normal" group, apparently in response to the depressed soldier percentage in this treatment at 4 weeks (Tab. II). The proportion of presoldiers in treatment 1 was significantly higher than in any other treatment after 8 weeks. Conversely, the proportion of this caste was significantly lower in treatment 5 than all other treatments at this time. There was no significant difference among treatments 2-4, although there was still a trend in these three treatments toward increased production of presoldiers when fewer soldiers were present in a group's initial population. There were also fewer significant differences in the total soldier population after 8 weeks than there were after 4. By the end of 8 weeks the "below normal" groups were approaching a "normal" mix of soldiers. Although the soldier population of treatment 5 was significantly higher than in treatments 1-3 but not in treatment 4, the percentage of all soldiers was not significantly different between treatments 1-4.

At the end of 12 weeks of study presoldier production dropped considerably. By that time there were no significant differences among the treatments in the percentage of presoldiers. The total soldier population, however, differed significantly at 12 weeks among the treatments which commenced with "below normal", "normal", and "above normal" proportions of soldiers. It appears true of these 12-week data, as it was true in section 1, that soldier differentiation may still have been continuing, especially for treatments 1, 2, and 3, because a substantial proportion of presoldiers was still present.

Overloading the experimental units with higher than normal proportions of soldiers affected the groups' survival considerably. This result was evident at 4, 8, and 12 weeks. For groups initiated with 48 percent soldiers (treatment 5) survival was significantly lower than in all the other treatments analyzed. Groups initiated with 72 percent soldiers (treatment 6) had extremely high mortality, even higher than the 48 percent group.

Most of the high mortality in the group initially stocked with 48 percent soldiers was due to deaths of excess soldiers. Examination of these experimental units during the course of the test revealed pseudergates occasionally carrying abdomens through the tunnels. When the experimental units were disassembled some soldiers' mandibles were visible in the sand, but no soldiers' bodies were found. Among others, two explanations are likely. These excess soldiers may have been killed and eaten by the pseudergates. Cannibalism in termites has been reported by numerous authors including LUSCHER (1961), STUART (1972), and NAGIN (1972). However, LENZ (personal communication) has observed that workers do not necessarily consume dead soldiers. Instead they cover or bury excess soldiers with excreta and other material after killing them. Under these conditions the bodies of the soldiers disintegrate very quickly leaving only the mandibles.

Groups initially stocked with 72 percent soldiers were apparently unable to feed the soldiers or consume the excess soldiers and, as a result, many of the soldiers apparently died and decomposed within the sand matrix. This event led to microbial contamination of the entire population within the jar and 100 percent mortality in 24 of the 30 experimental units. Similarly the pseudergates in treatment 6 (Tab. II) were undoubtedly under a great deal of stress from the excess burden of feeding so many soldiers which probably weakened their resistance to microbial attack. The six experimental units in this treatment which survived (all from colony 4) behaved much as those with on initial proportion of 48 percent soldiers. That is, they were apparently able to consume excess soldiers and prevent microbial contamination of the population. These surving experimental units in treatment 6 developed soldier proportions similar to those of groups installed with 48 percent soldiers.

There does not appear to be an overshoot in the production of soldiers in groups with " below normal " soldier proportions (fig. 4) as has been reported for supplementary reproductive in other species (HEWITT et coll., 1969 ; NAGIN, 1972). In fact, groups commencing with 12 and 24 percent soldiers suffered a slight drop in the soldier percentage at 4 weeks which later rebounded upward toward the final percentage. The percentage of soldiers in groups with 48 and 72 percent soldiers at the onset dropped drastically to 37.6 and 36.7 percent within 4 weeks. It is surprising that this high percentage was essentially maintained even after 8 and 12 weeks (fig. 4). Given ample food, then, this species is able to tolerate a very high proportion of soldiers for at least 12 weeks, a proportion much higher than was found when termites were allowed to differentiate from a " below normal " proportion up to their own optimum.

There is evidence from both sections of this study to infer that even 12 weeks is an insufficient amount of time for the soldier population to equilibrate. In moderate sized, experimental groups in the laboratory, the

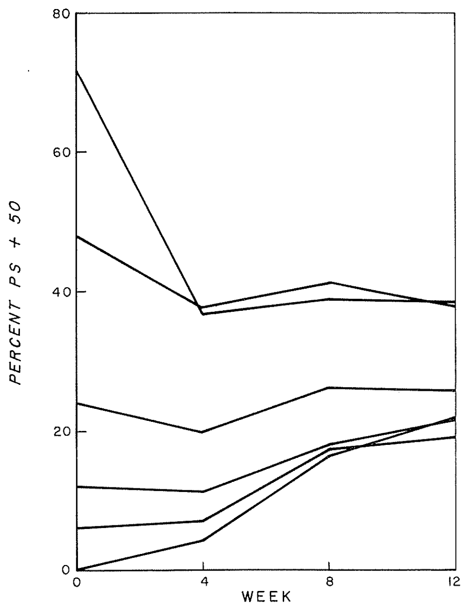

Fig. 4. — Mean percentage of soldiers in groups of termites initially and 4, 8, and 12 weeks after being mixed in different initial proportions.

Fig. 4. — Pourcentages moyens de soldats dans des groupes de Termites au début des expériences, puis 4, 8 et 12 semaines après avoir été mélangés dans différentes proportions.

optimal soldier proportion for this species is probably slightly above 25 percent. This is indicated by the high percentage of presoldiers in all group sizes and colonies after 12 weeks in section 1 and the general upward trend toward 25 percent of the soldier percentage in groups with an initial mix of 2, 6, and 12 percent soldiers in section 2.

At 4 weeks there were significant differences among colonies in both total soldier population and group survival. These differences became less apparent or less than significant at 8 and 12 weeks. One curious observation has come out of this section and the preceding one. Survival or vigor and total soldier population of older, laboratory-maintained colonies are consistently lower, though not always statistically different, than colonies which have recently been collected in the field. McMahan and Watson (1975) have observed that individuals of *Nasutitermes exitiosus* (Hill) from laboratory colonies are smaller in size than those collected from the field. Is it possible that the general physiological condition of the colonies has contributed to these differences in survival and soldier production and maintenance ?

A haunting question emerges from this study for which I have no concrete answer, only speculation. Why is it that orphaned groups of pseudergates of *C. formosanus* produce and maintain a much higher percentage of soldiers than do entire colonies of this species ? The results in section 2 indicate that the presence of soldiers in a group of pseudergates will inhibit or reduce the production of new soldiers. There were no reproductives in the laboratory groups to stimulate the production of soldiers as has been suggested for *K. flavicollis* by SPRINGHETTI (1973) and for *Hodotermes mossambicus* (Hagen) by HEWITT et coll. (1969). I think the most plausible hypothesis is this one. Colonies can simply tolerate a high proportion of the population which are not food producers (soldiers, larvae, nymphs, and reproductives) ; and other non reproductive castes (larvae and nymphs) in a colony exert an inhibitory effect on the production of soldiers. From the experiences of the entomologists at the Forestry Sciences Laboratory it is apparent that the pseudergates of *C. formosanus* do not differentiate into supplementary reproductives and seldom into nymphs in laboratory experimental groups. It is possible that the only developmental pathway available to pseudergates is toward the adult soldier caste. Thus all of the non-food producers tolerated by the experimental groups of this study were limited to soldiers. The results of this study then support the hypothesis that within a colony there exists a balanced proportion of the food producers (pseudergates or " workers ") and the " parasitic " castes (larvae, nymphs, soldiers, and reproductives) (BUCHLI, 1956).

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