# Fluctuation of Survival, Growth and Differentiation in Biweekly Samples of *Reticulitermes flavipes* Workers

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## 1. Introduction

Worker termites maintain the homeostatic regulation and self stability of a colony (A. E. EMERSON, 1956, 1962); therefore, it is generally assumed that the worker component of a colony remains in a relatively stable state. Indeed, if workers are isolated from a colony and maintained at uniform conditions, they tend to have reproducible survival and behavior. However, considerable fluctuation in behavior and vigor of *Reticulitermes* workers has been noted in natural colonies (G. R. ESENTHER, 1969) and even in laboratory groups (G. BECKER, 1973). Moreover, the caste-instar frequencies in a colony are in a continuous state of flux because of reproduction, growth, differentiation, and mortality cycles (G. R. ESENTHER, 1969). Nevertheless, to my knowledge, no one has tested the "worker stability hypothesis".

The purpose of this study was to measure the magnitude of fluctuation in the physiological condition of workers relative to cyclic changes in the caste composition of a *Reticulitermes* colony. The results are presented in terms of survival, growth and differentiation.

## 2. Materials and Methods

### 2.1 Termites

A *Reticulitermes flavipes* (Kollar) colony was collected at Janesville, Wisconsin (USA), July 23, 1971, and maintained in a 20-gallon metal trash can at ambient room temperature (20 - 25° C).

### 2.2 Experimenta1 procedure

Beginning March 27, 1974, a sample of 800 workers (fourth instar and older undifferentiated forms, including pseudergates) was isolated from the colony at each biweekly interval for 64 weeks. Each sample was subdivided into eight groups of 100 workers. The groups were paired so that the average weights of each set (paired groups) were approximately equal. Additional workers at each biweekly extraction were removed and stored at - 20° C for use as a dietary supplement. Notes on the caste forms in the colony at each isolation were recorded.

Worker groups from two of the four biweekly sets were placed separately on about 3 $cm^3$ water-moistened aspenwood sawdust (*Populus grandidentata* Michx.; Wiley-milled with 1 mm screen, washed overnight with hot tap-water, and oven-dried at 105° C) in a cylindrical polystyrene container (5.0 cm diameter, 3.5 cm height), and incubated at 25° C for eight weeks. The sawdust diet of one set was supplemented by the addition of five frozen workers thrice weekly (Monday, Wednesday, and Friday). Termites differentiating to soldier or apterous neotenic reproductive forms were removed from each group at weekly inspections to alleviate their suppressive effect on the growth and differentiation of the remaining termites. The termites as workers or pre-neotenic forms were counted and weighed before resetting them on fresh sawdust to continue the incubation. This procedure was repeated with the other two sets of workers using powdered cellulose (Avicel, FMC Corporation, Markus Hook, Pennsylvania) rather than sawdust as the basic diet.

## 3. Results

### 3.1 Initial condition of samples

The average initial weight of workers in the 33 biweekly samples fluctuated between 2.06 and 3.02 mg per worker (Table 1) as a result of changes in caste-instar frequencies and growth in the source colony. Samples 1 - 3 showed a progressive increase in worker size with small workers becoming rare. Two weeks later (sample 4) the previously largest sized workers were noticeably less abundant and several neotenic reproductives were seen. Stunting of all workers was very noticeable in the 6th sample, apparently because of the stress on workers from a peak period of reproduction and egg hatching. New early instar workers, however, did not become abundant until the 11th sample. The average weight of the workers remained relatively stable in the next four samples (12- 15) while nymphs were abundant in the colony.

Table 1. Average survival and growth of workers[a)] in biweekly samples after 8-weeks incubations on four diets.

| Bi-weekly sample no. | Initial weight (mg/worker) | Percent survival as workers on diet[b)] | | | | Percent growth of workers on diet[c)] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | C | S | C + sup | S + sup | C | S | C + sup | S + sup |
| 1 | 2.77 | 80 | 75 | 91 | 73 | 6 | 1 | 32 | 36 |
| 2 | 2.87 | 86 | 75 | 92 | 86 | −7 | −1 | 14 | 26 |
| 3 | 3.02 | 15 | 72 | 77 | 88 | −40 | −4 | 13 | 17 |
| 4 | 2.73 | 0 | 75 | 65 | 82 | −100 | −3 | 3 | 18 |
| 5 | 2.82 | 0 | 62 | 75 | 86 | −100 | −2 | 5 | 22 |
| 6 | 2.47 | 57 | 58 | 53 | 75 | −7 | 2 | 17 | 37 |
| 7 | 2.75 | 80 | 74 | 90 | 91 | −2 | 1 | 24 | 23 |
| 8 | 2.76 | 82 | 76 | 90 | 90 | −5 | 0 | 37 | 33 |
| 9 | 2.72 | 78 | 72 | 92 | 91 | 0 | 3 | 37 | 35 |
| 10 | 2.58 | 69 | 73 | 79 | 75 | 12 | 10 | 38 | 41 |
| 11 | 2.06 | 87 | 78 | 93 | 94 | 7 | 8 | 62 | 63 |
| 12 | 2.30 | 85 | 79 | 91 | 94 | 5 | 5 | 49 | 50 |
| 13 | 2.42 | 87 | 80 | 95 | 91 | −5 | 0 | 44 | 41 |
| 14 | 2.43 | 86 | 81 | 91 | 95 | −3 | 1 | 35 | 37 |
| 15 | 2.48 | 87 | 81 | 76 | 82 | 9 | 10 | 39 | 38 |
| 16 | 2.24 | 79 | 84 | 91 | 89 | −1 | 11 | 43 | 45 |
| 17 | 2.47 | 67 | 77 | 69 | 88 | −24 | −8 | 16 | 31 |
| 18 | 2.55 | 44 | 65 | 62 | 80 | −30 | −29 | −23 | 0 |
| 19 | 2.66 | 49 | 62 | 56 | 70 | −33 | −37 | −20 | 24 |
| 20 | 2.57 | 0 | 3 | 1 | 25 | −100 | −8 | −24 | −20 |
| 21 | 2.68 | 0 | 23 | 15 | 71 | −100 | −26 | −20 | −6 |
| 22 | 2.70 | 0 | 0 | 0 | 0 | −100 | −100 | −100 | −100 |
| 23 | 2.70 | 74 | 77 | 14 | 86 | −23 | −22 | −29 | 3 |
| 24 | 2.70 | 26 | 60 | 34 | 87 | −23 | −22 | −14 | 1 |
| 25 | 2.58 | 71 | 79 | 81 | 84 | −8 | −2 | −1 | 21 |
| 26 | 2.66 | 92 | 87 | 87 | 90 | −12 | −8 | 3 | 10 |
| 27 | 2.45 | 82 | 79 | 86 | 79 | 2 | 0 | 16 | 28 |
| 28 | 2.78 | 71 | 72 | 89 | 88 | −10 | −8 | 14 | 17 |
| 29 | 2.72 | 84 | 81 | 89 | 87 | −9 | −6 | 21 | 24 |
| 30 | 2.76 | 72 | 77 | 85 | 85 | −17 | −8 | 17 | 22 |
| 31 | 2.66 | 83 | 72 | 81 | 81 | −12 | −5 | 21 | 30 |
| 32 | 2.52 | 84 | 72 | 85 | 83 | −7 | 0 | 23 | 33 |
| 33 | 2.39 | 80 | 70 | 84 | 79 | −6 | −6 | 31 | 40 |

a) Differentiated forms deleted at weekly inspections are not included in calculations.

b) Cellulose powder (C); sawdust (S); frozen worker supplement (sup).

c) Calculated by: 100 (average final weight per surviving termite ÷ average initial weight per worker) − 100 percent.

Stunting of workers again occurred in the 16th sample, apparently because the biweekly extraction of workers, coupled with growth of nymphs, became a significant stress factor. Thereafter, a prolonged period occurred in which a low frequency of nymphs and new young workers was associated with a low frequency of larger sized workers. New young instar workers became noticeably more abundant in the

27th sample while larger sizes of workers remained rare. Small to large worker sizes occurred in the next few samples and the small young workers became especially abundant again in the final two samples. Therefore, the biweekly fluctuation of worker sample weights reflected the effects of two cycles of reproduction, growth, development, and mortality interacting with the stress on the colony of biweekly extraction of workers.

### 3.2 Survival after incubation

The summary of survival data (Table 1) shows two types of physiological condition in the biweekly worker samples. During the two periods of developmental-reproductive stress (approximately in the 3 - 6 and 18 - 24 samples) survival tended to drop below 70 percent and once reached complete mortality on all diets. Between the stress periods survival generally remained above 70 percent and that on the two supplement diets tended to be 5 - 10 percent higher than on the two basic cellulosic diets. Although the survival was similar on the two basic diets, the cellulose powder diet seemed slightly inferior because complete mortality of worker samples on these diets occurred with five samples and one sample, respectively.

The biweekly samples with low survival or complete mortality were associated with microbial contamination. Termites died and were not cannibalized. These corpses became centers of microbial growth which contributed to an acceleration of termite mortality. Incomplete ingestion of the frozen worker dietary supplement also contributed to such contamination. This contamination effect was not appreciably alleviated by the weekly transfer of termites to fresh diets because weakened and diseased termites were included in the transfer.

### 3.3 Growth after incubation

The growth data (Table 1) reflect the same information on worker condition as mentioned for survival data, but they give more insight into the relationship of condition and diets. The two basic cellulosic diets resulted, at best, in only slight growth of surviving workers during the period when survival tended above 70 percent (maximum 12 percent on the powder and 10 percent on the sawdust); therefore, these diets were at best marginal. Diets were markedly improved by the addition of the frozen worker supplement, with the growth clearly progressing to and declining from the maximum growth in a sample (62 percent on cellulose and 63 percent on sawdust). Only the growth data with the supplemented diets illustrated the full amplitude of worker condition that paralleled the fluctuations in the source colony.

Table 2. Total differentiation in biweekly worker samples during 8 weeks on four diets.

| Bi-weekly sample no. | Number of terminal forms[a] on dietary | | | | | | | | | | | | Sample totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cellulose | | | Sawdust | | | Cell. + sup. | | | Sawdust + sup. | | | |
| | S | F | M | S | F | M | S | F | M | S | F | M | |
| 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 1 | 5 | 0 | 12 |
| 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 |
| 3 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 2 | 2 | 0 | 2 | 3 | 14 |
| 4 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 7 | 1 | 1 | 3 | 1 | 17 |
| 5 | 1 | 1 | 0 | 1 | 4 | 3 | 0 | 8 | 1 | 0 | 4 | 6 | 29 |
| 6 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 5 | 1 | 10 |
| 7 | 0 | 4 | 7 | 0 | 0 | 1 | 0 | 5 | 3 | 0 | 3 | 0 | 23 |
| 8 | 0 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 8 | 2 | 2 | 5 | 25 |
| 9 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 3 | 4 | 2 | 0 | 4 | 15 |
| 10 | 1 | 5 | 1 | 0 | 0 | 2 | 2 | 4 | 5 | 1 | 6 | 7 | 34 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 1 | 2 | 9 |
| 12 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 5 | 5 | 0 | 1 | 5 | 21 |
| 13 | 0 | 1 | 0 | 0 | 2 | 2 | 1 | 2 | 7 | 1 | 3 | 6 | 25 |
| 14 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 4 | 0 | 2 | 2 | 12 |
| 15 | 0 | 1 | 6 | 0 | 0 | 6 | 0 | 3 | 22 | 1 | 2 | 15 | 56 |
| 16 | 1 | 0 | 2 | 0 | 1 | 3 | 1 | 0 | 4 | 0 | 0 | 10 | 22 |
| 17 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 12 | 0 | 0 | 8 | 24 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 5 |
| 19 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 8 |
| 20 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 |
| 25 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 1 | 2 | 12 |
| 26 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 12 |
| 27 | 0 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 4 | 0 | 1 | 3 | 13 |
| 28 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 6 |
| 29 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 4 | 11 |
| 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 |
| 31 | 0 | 2 | 1 | 1 | 3 | 2 | 3 | 3 | 4 | 0 | 6 | 2 | 27 |
| 32 | 0 | 3 | 1 | 0 | 2 | 5 | 0 | 3 | 1 | 0 | 4 | 2 | 21 |
| 33 | 0 | 6 | 5 | 0 | 0 | 6 | 0 | 10 | 5 | 0 | 8 | 10 | 50 |
| Diet total . . | 3 | 33 | 43 | 3 | 23 | 42 | 11 | 73 | 111 | 12 | 67 | 106 | 527 |

a) Differentiating to soldiers (S) and female (F) or male (M) apterous neotenic reproductives.

### 3.4 Differentiation during incubation

Differentiation to soldiers or apterous neotenic reproductives occurred in rill except three of the 33 biweekly samples during the eight-week incubation period. (Table 2). Usually the differentiation began after the fourth week of incubation. The earliest development to terminal forms

was noted at a second (male neotenic), third (female neotenic), or fourth (soldier) weekly inspection. The largest sized workers appeared approximately equal in size to the individuals which had progressed to pre-terminal or terminal form, indicating that the terminal forms were developing from the largest sized workers. The terminal forms were weighed to the nearest milligram at the time of their weekly removal from a sample group and, with rare exception, each weighed 5 mg. More pre-terminal forms were observed than were accounted for by the removal of terminal forms; thus, the likelihood was that cannibalism of both pre-terminal and terminal forms was occurring. Occasionally, partly eaten, but live individuals were seen during weekly inspections.

The total differentiation was similar for the two basic diets (79 on cellulose and 68 on sawdust and also for the two supplemented diets respectively, 195 and 185). The total differentiation in individual biweekly worker samples was 0 - 17 on basic diets and 0 - 43 on supplemented diets. The terminal forms on basic diets appeared to develop primarily from workers already large-sized at the time of removal from the source colony, whereas many of the terminal forms on the supplemented diets apparently originated from individuals which grew to large size on the diet.

Because of cannibalism and removal of terminal forms, the growth data (Table 1) often greatly underestimated the actual growth. For example, if the 25 terminal forms in the 15th sample on the supplemented cellulose diet (Table 2) were included in the calculations of percentage growth and percentage survival, the growth estimate is 64 percent rather than 39 percent and the survival estimate is 99.5 rather than 87 percent.

## 4. Discussion

The ultimate purpose of this study was to isolate three elements, i. e., survival, growth, and differentiation, so that the physiological condition of the worker samples could be assessed more completely. Weekly removal of terminal forms was the key to isolation of the elements because it alleviated their repressive effects on growth and differentiation of the remaining workers. The results confirm the effectiveness of the technique. If the terminal forms had not been removed, the variable differentiation in individual worker groups of the samples would have confounded any comparative analysis of the biweekly samples.

This study, to my knowledge, is the first time that termites themselves have been used deliberately as a dietary supplement. Relative to the results with basic cellulosic diets, the supplement was exceptionally

beneficial to growth and differentiation of workers. Unfortunately, the technique may not be applicable to all species of termites; for instance, I have not been successful in using it with *Coptotermes formosanus* Shiraki. However, J. K. MAULDIN and N. M. RICH (1975) demonstrated benefits to termites with synthetic supplements to a cellulose diet. Their best result was a 37 percent decrease in group weight after one year on a diet, but they allowed differentiation and reproduction to occur and encountered problems with microbial contamination. Undoubtedly, both of these factors masked the true benefits of the diets. Nevertheless, my results provide a benchmark for the benefits that may be achieved with improved diets. On my results, one can only speculate on the extent to which methodology (G. R. ESENTHER, 1976), contamination problems, and usage of marginal diets have masked significant differences between treatment variables in previous work (G. BECKER, 1969) with termites.

Decayed wood diets especially deserve a more intensive investigation because they improve development of reproductive termite forms (G. BECKER, 1965; M. LENTZ and G. BECKER, 1975).

The results disprove the "worker stability hypothesis". Except during periods of developmental-reproductive stress, the survival data with all diets and the growth data with basic cellulosic diets, seem to favor the hypothesis; the physiological condition of the workers appeared to remain relatively stable for prolonged periods in the colony. However, the growth data with supplemented diets coupled with the differentiation data for all diets reveals a remarkable fluctuation of worker condition. This matches the cyclic caste-instar changes in the colony which may affect worker condition even in a large, well-established natural colony (G. R. ESENTHER, 1969).

The results do not weaken the concept (A. E. EMERSON, 1956, 1962) of homeostatic stability of a termite colony. Indeed, they demonstrate an exceptional flexibility of the homeostatic system to compensate for major disruptions in a colony. This is particularly noticeable in the recovery of the colony after the extremely low vitality of the 20 - 22 biweekly worker samples.

The results demonstrate that measurement of growth is essential to assess the final condition of termites in an experiment. Survival data also are essential. Fortunately, both growth and survival are reflected in a single record when the final condition of the termites is expressed as percentage of the initial group weight (G. R. ESENTHER, 1976). This percentage is easy to obtain because it requires only initial and final group weight.

Nevertheless, as mentioned previously, the effects of differentiation also must be considered in a final analysis worker condition. If these effects are not isolated, an analysis becomes confounded by speculations as to the relative impact of differentiation in the individual groups. This confounding can be alleviated by the removal of terminal forms or by limiting an incubation period to four weeks, because differentiation usually began after four weeks of incubation. Only after survival, growth, and differentiation potentials are measured can termite investigations proceed to the measurement of the precise impact that different termite forms have on the homeostatic system of a colony.

The biweekly removal of worker samples had a disruptive effect on the colony, and this may be similar to the effect of insecticidal baits wherein foraging workers eat the lethal bait (G. R. ESENTHER and R. H. BEAL, 1974, 1976). Both worker removal and bait treatment result in a depletion of the worker component. The colony was able to recover from the impact of the worker removals, but the response of the termite homeostatic system to bait effects has not been established.

## 5. Summary

Survival, growth, and differentiation in 33 biweekly samples of *R. flavipes* workers were measured relative to two cellulosic diets, with or without frozen termites as a dietary supplement. Weekly removal of terminal forms during an eight-week incubation permitted fuller expression of the growth and differentiation capacity of the workers. The results show a remarkable magnitude of fluctuation in these physiological capabilities. The fluctuation matched the caste-instar changes which were occurring in the source colony. The significance of the results relative to the homeostatic system of termites is discussed.

## Zusammenfassung

### Schwankungen von Überlebensrate, Wachstum und Differenzierung bei zweiwöchentlich enlnommenen Proben von *Reticulitermes flavipes* Arbeitern

Überlebensrate, Wachstum und Differenzierung von 33 Proben von *R. flavipes* Arbeitern, die in zweiwöchentlichem Abstand aus der Kolonie entnommen waren, wurden vergleichend auf 2 Cellulose-Diäten - mit und ohne Zusatz von gefrorenen Termiten als Zusatznahrung - bestimmt. Wöchentliches Entfernen der Endstadien während einer 8wöchigen Versuchsdauer gestattete eine vollständigere Erfassung der Wachstums- und Differenzierungsfähigkeit der Arbeiter. Die Ergebnisse zeigen eine bemerkenswert große Schwankung dieser physiologischen Fähigkeiten. Die Schwankungen entsprachen den Änderungen in der Kastenzusammensetzung in der Ausgangs-Kolonie. Die Bedeutung der Ergebnisse für das homöostatische System der Termiten wird erörtert.

## Résumé

### Fluctuations de la survie, de la croissance et de la différenciation d'échantillons d'un prélèvement bihebdomadaire d'ouvriers de *Reticulitermes flavipes*

La survie, la croissance et la différenciation de 33 échantillons d'un prélèvement bihebdomadaire d'ouvriers de *R. flavipes* ont été déterminées en fonction de deux rations cellulosiques avec ou sans termites congelés comme supplément alimentaire. Le prélèvement hebdomadaire de formes terminales pendant une incubation de huit semaines a permis une expression plus complète de la capacité de croissance et de différenciation des ouvriers. Les résultats montrent une remarquable fluctuation dans ces capacités physiologiques. Les fluctuations coincident avec les changements de caste qui avaient lieu dans la colonie d'origine. On discute enfin de la signification des résultatas en fonction du système homeostatique des termites.



## Resumen

### Fluctuaciones en la supervivencia, el crecimiento y la diferenciación en muestras bisemanales de obreros de *Reticulitermes flavipes*

Se procedió a determinar la supervivencia, el crecimiento y la diferenciación en 33 muestras de obreros de *R. flavipes*, recogidas de la colonia bisemanalmente y nutridas, a fines de comparación, con dos dietas de celulosa: una con, la otra sin termitos congelados en calidad de alimento suplementario. Una recogida semanal de las formas terminales durante un período de incubación de ocho semanas permitió observar un cuadro más completo de la capacidad de crecimiento y diferenciación de los obreros. Los resultados demuestran una notable magnitud de fluctuación de estas aptitudes fisiológicas. Las fluctuaciones correspondieron a los cambios en la composición de castas en la colonia de origen. Se procede a discutir el significado de los resultados para el sistema homeostático de los termitos.


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