Effects of Starvation on Survival and Maintenance of Soldier Proportion in Laboratory Groups of the Formosan Subterranean Termite, *Coptotermes formosanus* (Isoptera: Rhinotermitidae)

NAN-YAO SU[1] AND JEFFERY P. LA FAGE

Department of Entomology, Louisiana Agricultural Experiment Station,
Louisiana State University Agricultural Center,
Baton Rouge, Louisiana 70803

Ann. Entomol. Soc. Am. 79: 312–316 (1986)

ABSTRACT Laboratory groups of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, had ca. 2% soldier proportions under starvation conditions and ca. 11% when food was provided, regardless of initial soldier proportions. In the absence of food, soldiers were starved or cannibalized before workers were sacrificed. Data suggest that soldiers may represent an emergency food ration for colony survival under starvation conditions.

THE SOLDIER/WORKER RATIO of termites is thought to be a species-specific characteristic of the mature colony (Haverty 1977, 1979, Oster and Wilson 1978). A summary of solder/worker ratios for 112 species (Haverty 1977) revealed mean soldier proportions that varied from 0% (*Anoplotermes* spp., *Skatitermes* spp., and *Speculitermes* spp.) to 41.8% (*Tenuirostritermes tenuirostris* [Desneux]). Considerable intraspecific variation was evident with some species exhibiting dramatic variation (e.g., the Formosan subterranean termite, *Coptotermes formosanus* Shiraki [5–60% soldiers]).

Caste regulation in the lower termites is considered most often in light of inhibitory pheromones (Castle 1934, Light 1943, 1944, Lüscher 1961). Miller (1969), however, recognized three possible levels of developmental control: environmental (acting on the entire colony); social (among individuals by pheromones); and individual (by the effects of hormones). Although some information has accumulated on the effects of hormones on development (Yin and Gillott 1975, Lüscher 1976), little is known about environmental effects (Oster and Wilson 1978).

Termite-caste proportions vary with season and colony age (Miller 1942, Grassé and Noirot 1957, Nakajima et al. 1964, Haverty and Howard 1981). Buchli (1958) documented the effects of nutrition on caste differentiation in *Reticulitermes lucifugus* Rossi by showing that a nutritionally inadequate food supply suppressed the formation of soldiers and neotenics in laboratory colonies. Smythe and Mauldin (1972) reported that completely defaunated *C. formosanus* produced fewer soldiers than completely faunated or partially defaunated groups. Lenz (1976) found that food quality affected soldier production in groups exposed to juvenile hormone analogs. Collectively, these results suggest that food availability and quality may be important factors for regulating soldier proportions. This study examined the hypothesis that food availability affects the survival and production of soldiers in laboratory groups of *C. formosanus*.

Materials and Methods

A colony of *C. formosanus* was collected in a cypress (*Taxodium distichum* [L.] Rich.) snag near Lake Charles, La., and held at 22–24°C in a 246-liter can for ca. 12 months before testing. Based on criteria established by Su and La Fage (1984a,b), the colony was characterized before testing as vigorous, with a wood-consumption rate for laboratory groups (130 workers and 20 soldiers) of ca. 60 mg/g/day and a mean worker weight of 2.5 mg. The effects of starvation on survival and soldier proportion were tested in the laboratory using termites extracted from the source colony according to the method described by La Fage et al. (1983). Experimental groups with three different caste compositions were observed while starving or feeding.

The first set of treatments (WS) was established with 300 termites per group and a soldier proportion equal to that observed in the source colony (15% soldiers; 255 workers and 45 soldiers, [unpublished data]). In the second treatments (W), soldiers were omitted so that experimental units contained only 255 workers. In the third set (S), only 45 soldiers were present. Because each of the three group types was tested under starvation (WS/S, W/S, and S/S) and feeding (WS/F, W/F, and S/F) conditions, there was a total of six possible

[1] Current address: Ft. Lauderdale Res. and Educ. Ctr., Univ. of Florida, Inst. Food and Agricultural Science, 3205 College Ave., Ft. Lauderdale, FL 33314.

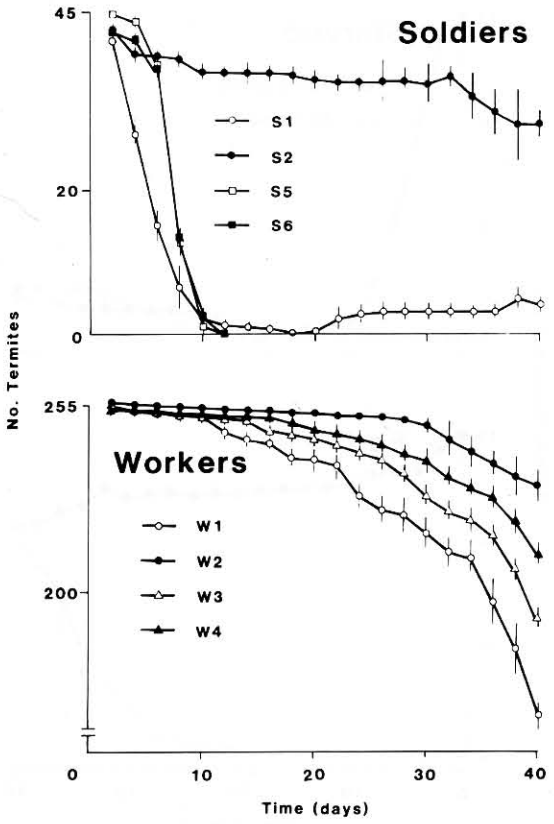

Fig. 1. Numbers of surviving soldiers and workers during the 40-day test period. W1, S1, starved group containing 15% soldiers initially; W2, S2, fed group containing 15% soldiers initially; W3, starved group containing no soldiers initially; W4, fed group containing no soldiers initially; S5, starved group containing no workers; S6, fed group containing no workers.

treatment combinations. Each one was replicated three times to yield 18 experimental units.

Two types of testing chambers were used. The first, in which termites were starved, consisted of a glass petri dish (9.0 cm i.d. by 2.0 cm high) provisioned with two moistened filter-paper disks (Whatman No. 1; 9 cm diam). A stainless-steel screen disk (60 mesh), placed directly on top of the filter paper, prevented termites from feeding on the filter paper but allowed for the maintenance of a high-humidity environment. The second chamber was identical to the first except that it lacked the stainless-steel screen barrier and, thus, allowed termites access to the moistened filter paper. The experiment was conducted in a bioclimatic chamber at 29 ± 1°C in total darkness, except during observations.

The term 'worker' is used here to designate externally undifferentiated larvae of at least the third instar. 'Soldiers' and 'presoldiers' are defined according to Miller (1969).

Observations on survival and soldier proportions among the test groups were made at 2-day intervals for 40 days with records kept on the numbers of live, dead, and cannibalized termites according to caste. When appendages or body parts of partially cannibalized termites were still moving, individuals were classified as cannibalized while alive. Dead and cannibalized individuals were removed at each inspection and counts of remaining live termites were made from photographic transparencies (Kodachrome ISO 64) projected against a screen. The soldier proportion was defined as the number of soldiers and presoldiers divided by the total number of termites present at the inspection. Observations were also made on the numbers of new presoldiers and adult soldiers produced during the 40-day experiment by recording the dif-

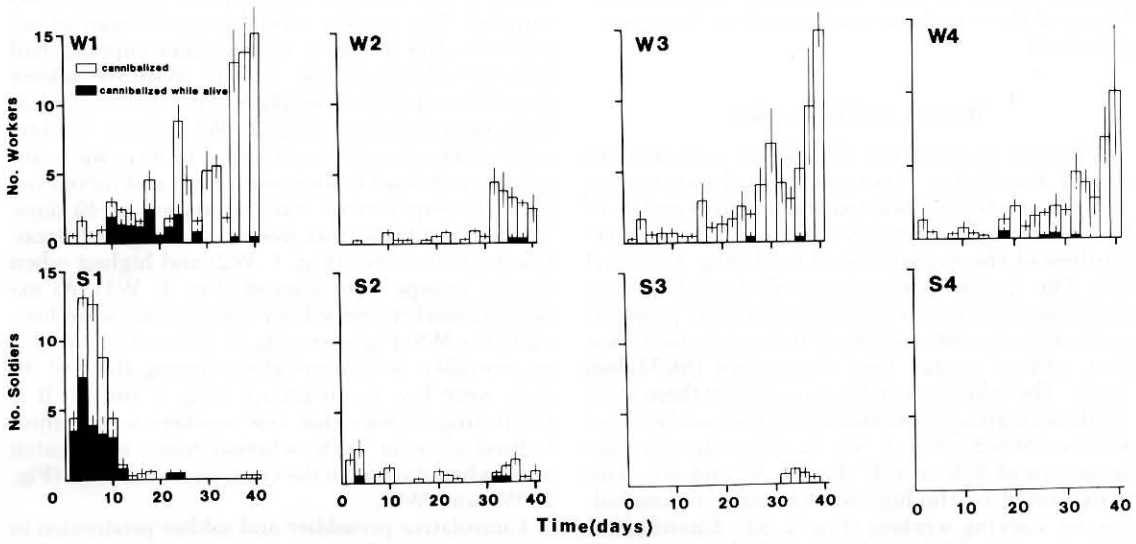

Fig. 2. Numbers of workers and soldiers cannibalized every 2 days. W1, S1, starved group containing 15% soldiers initially; W2, S2, fed group containing 15% soldiers initially; W3, S3, starved group containing no soldiers initially; W4, S4, fed group containing no soldiers initially.

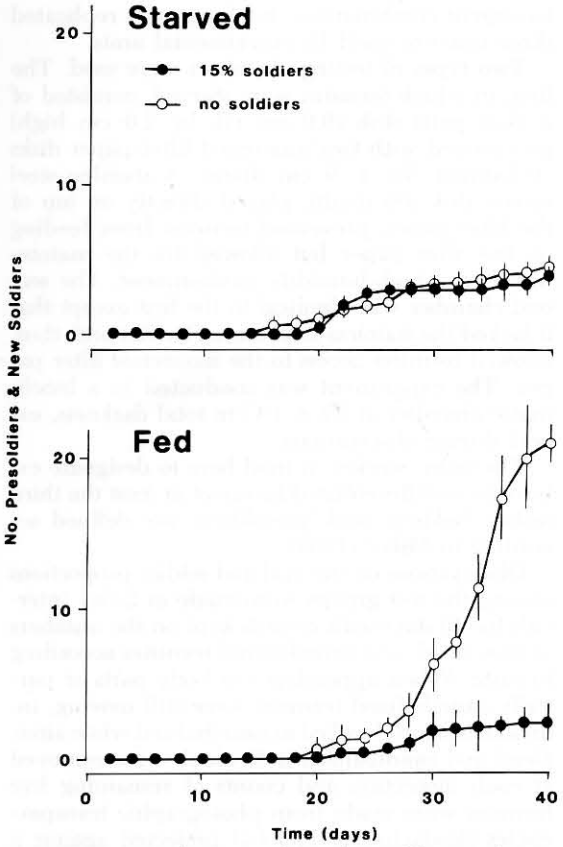

Fig. 3. Cumulative numbers of presoldiers and new soldiers in starved and fed groups. ●, groups containing 15% soldiers initially. ○, groups containing no soldiers initially.

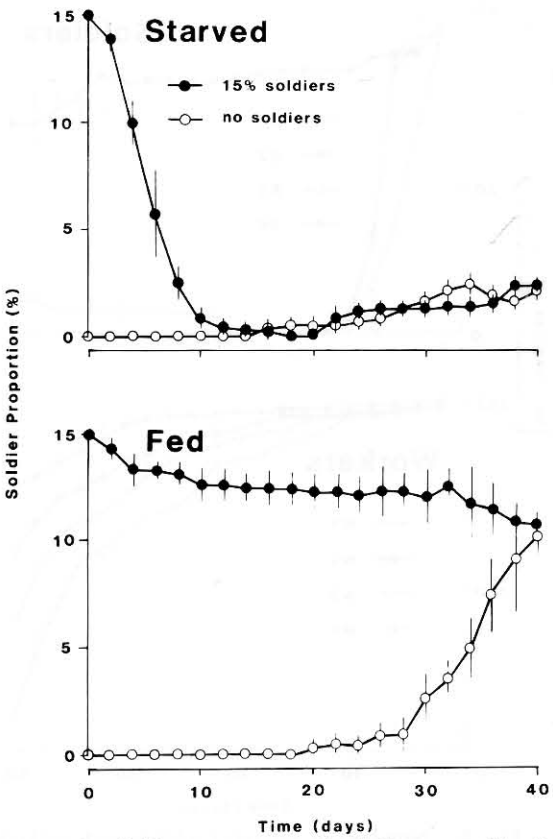

Fig. 4. Soldier proportions (including presoldiers) observed in starved and fed groups of *C. formosanus*. ●, groups containing 15% soldiers initially. ○, groups containing no soldiers initially.

ferences in total numbers of these soldiers (including numbers of cannibalized or dead soldiers) present between two succeeding observations. Means of three replicates and standard errors were presented.

Results and Discussion

Changes in numbers of soldiers and workers during the 40-day experiment are shown in Fig. 1. Treatments with isolated soldiers (S/S and S/F) had nearly total mortality after only 10 days, regardless of the availability of food (Fig. 1, S5 and S6). The similar performance of starved soldiers and those with access to filter-paper food provided in these treatments confirmed the widely held view that soldiers cannot feed themselves (McMahan 1963). The soldier mortality rate during these same 10 days in groups containing starved workers and soldiers (WS/S) (Fig. 1, S1) was even greater than in groups of S/S or S/F (Fig. 1, S5 and S6). This is explained by the high level of soldier cannibalism by starving workers (Fig. 2, S1). Cannibalism was so intense during this period that many soldiers were eaten alive (Fig. 2, S1). Worker mortality among WS/S groups during the same 10 days (Fig. 1, W1) was low, suggesting that starving workers relied on soldiers plus their own metabolic stores in the absence of adequate cellulosic food supplies. The worker mortality rate began to accelerate after 10 days when soldier supplies had become exhausted (Fig. 1, W1). With the soldier population depleted, workers began to cannibalize their own numbers (Fig. 2, W1). Some workers were eaten alive during the next 16 days with cannibalism of dead bodies continuing and increasing until the experiment was terminated at 40 days. Worker mortality was lowest in fed groups containing both castes (Fig. 1, W2) and highest when similar groups were starved (Fig. 1, W1). As expected, worker and soldier cannibalism were lowest in the WS/F groups (Fig. 2, W2 and S2). Worker mortality and cannibalism during the first 10 days were low in all groups (Fig. 1 and 2). It is interesting to note that few workers were cannibalized alive in W/S, whereas more were eaten alive when starved in the company of soldiers (Fig. 2, W1 and W3).

Cumulative presoldier and soldier production in treatments initially containing workers (W and WS) is shown in Fig. 3. The first presoldiers were noted after 16 days in W/S groups and appeared in W/F

and WS/S units at 20 days. The last groups to produce presoldiers were the WS/F, in which they were recorded at 22 days. If the initiation of presoldier production is closely related to the availability of food, one would expect to see the first individuals among the fed treatments. This was not the case. It is possible that other factors, perhaps pheromonal in nature, were important in initiating soldier production. However, the production of additional soldiers is probably regulated by food availability. Soldiers were formed in all treatments and in all units regardless of food availability. The greatest number appeared in W/F treatments as expected (Fig. 3). Likewise, the lowest number was observed in WS/F, where high soldier numbers were maintained throughout the 40-day experiment (Fig. 1, S1) and additional individuals were not needed to maintain a soldier/worker ratio similar to that of the source colony.

Changes in the soldier proportion of fed and starved treatments during the 40-day experiment are shown in Fig. 4. In the fed groups, the soldier proportions in W and WS groups converged at 40 days at ca. 11%. This is less than that in the source colony (15%), but understandable, as the nutritional quality of filter paper with its minimal nitrogen content is lower than the nitrogen content in wood (La Fage 1976). In the starved treatments, convergence was also attained, but at a substantially lower level, ca. 2%.

Haverty (1979) reported that soldier proportions in *C. formosanus* groups initially containing 0–70% soldiers converge at 20–40% after 12 weeks when adequate food is available. He suggests, moreover, that 12 weeks is an insufficient time period for soldier populations to equilibrate and concludes that, in moderate-sized laboratory groups, the average soldier proportion is slightly >25%. In addition, he found that initial group size affected soldier production and smaller groups (100) produced fewer soldiers than larger groups (300, 500, or 1,000). Also, a colony maintained in the laboratory for 8 years produced more soldiers than colonies recently collected. *C. formosanus* probably maintains a range of soldier/worker ratios under normal conditions as reported by Haverty (1979). The results of this study suggest that food availability is one of the factors responsible for the fluctuation of soldier proportions. Other environmental factors such as predation, inter- or intraspecific competition may also alter soldier/worker ratios. Under circumstances where food is in short supply, a colony may alter its caste composition to adjust to environmental stress. In an extreme condition of starvation, as shown in this study, soldiers may serve as the emergency ration for workers.

References Cited

Buchli, H. R. 1958. L'origine des castes et les potentialitiés ontogéniques des termites européens du genre *Reticulitermes* Holmgren. Ann. Sci. Nat. Zool. Biol. Anim. 11: 263–429.

Castle, G. B. 1934. The experimental determination of caste differentiation in termites. Science 80: 314.

Grassé, P. P., and C. Noirot. 1957. La societe de "Calotermes flavicollis" (Insecte: Isoptere), de sa fondation au premier essaimage. C.R. Acad. Sci. 246: 1789–1795.

Haverty, M. I. 1977. The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). Sociobiology 2: 199–216.

1979. Soldier production and maintenance of *Coptotermes formosanus* Shiraki. Insectes Soc. 26: 69–84.

Haverty, M. I., and R. W. Howard. 1981. Production of soldiers and maintenance of soldier proportions by laboratory experimental groups of *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks) (Isoptera: Rhinotermitidae). Insectes Soc. 28: 32–39.

La Fage, J. P. 1976. Nutritional biochemistry, bioenergetics, and nutritive value of the dry-wood termite, *Marginitermes hubbardi* (Banks). Ph.D. dissertation, University of Arizona, Tucson.

La Fage, J. P., N.-Y. Su, M. J. Jones, and G. R. Esenther. 1983. A rapid method for collecting large numbers of subterranean termites from wood. Sociobiology 7: 305–310.

Lenz, M. 1976. The dependence of hormone effects in termite caste determination on external factors, pp. 73–89. *In* M. Lüscher [ed.], Phase and caste determination in insects. Endocrine aspects. Pergamon, New York.

Light, S. F. 1943. The determination of the caste of social insects. Q. Rev. Biol. 18: 46–63.

1944. Experimental studies on ectohormonal control of the development of supplementary reproductives in the termite genus *Zootermopsis* (formerly *Termopsis*). Univ. Calif. Berkeley. Publ. Zool. 43: 413–454.

Lüscher, M. 1961. Social control of polymorphism in termites. pp. 57–67. *In* J. S. Kennedy. [ed.], Insect polymorphism. R. Entomol. Soc. London Symp. No. 1.

1976. Evidence for an endocrine control of caste determination in higher termites, pp. 91–103. *In* M. Lüscher [ed.], Phase and caste determination in insects. Endocrine aspects. Pergamon, New York.

McMahan, E. A. 1963. A study of termite feeding relationship, using radioisotopes. Ann. Entomol. Soc. Am. 56: 74–82.

Miller, E. M. 1942. The problem of castes and caste differentiation in *Prorhinotermes simplex* Hagen. Bull. Univ. Miami 15: 27.

1969. Caste differentiation in the lower termites, pp. 283–310. *In* K. Krishna and F. M. Weesner [eds.], Biology of termites, vol. 1. Academic, New York.

Nakajima, S., K. Shimizu, and Y. Nakajima. 1964. Analytical studies on the vitality of colonies of the Formosan termite, *Coptotermes formosanus* Shiraki: II. Seasonal fluctuations on the external characters of the workers, the ratio of caste number and carbon dioxide in the nest of a colony. Bull. Fac. Agric. Miyazaki Univ. 9: 222–227.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in the social insects. Princeton University, Princeton, N.J.

Smythe, R. V., and J. K. Mauldin. 1972. Soldier differentiation, survival, and wood consumption by normally and abnormally faunated workers of the For-

mosan termite, *Coptotermes formosanus*. Ann. Entomol. Soc. Am. 65: 1001–1004.

Su, N.-Y., and J. P. La Fage. 1984a. Comparison of laboratory methods for estimating wood-consumption rates by *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 77: 125–129.

1984b. Differences in survival and feeding activity among colonies of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Z. Angew. Entomol. 97: 134–139.

Yin, C. M., and C. Gillott. 1975. Endocrine activity during caste differentiation in *Zootermopsis angusticollis* Hagen (Isoptera): a morphometric and autoradiographic study. Can. J. Zool. 53: 1690–1700.

Received for publication 28 August 1984; accepted 21 October 1985.