Laboratory Studies of Colony Establishment and Development in Cryptotermes brevis (Walker) (Isoptera: Kalotermitidae)[1]

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(*Submitted for publication April, 1961*)

INTRODUCTION

Cryptotermes brevis (Walker) is a major pest in Hawaii and other Pacific Islands, the Caribbean islands, South and Central America, Florida and Louisiana in North America, Hong Kong, Madagascar, and South Africa (records from the termite collection of the American Museum of Natural History in the custody of A. E. Emerson). It was probably introduced into all of these areas; its original habitat is unknown. It has been unable to invade the native environment but remains confined to human habitations, infesting a wide variety of wood and cellulose products. *C. brevis* is a drywood species, and the colonies, which consist of only a few hundred individuals each, live entirely within galleries formed as a result of feeding. Infestation is detectable through the discovery of fecal pellets pushed from the galleries (Zimmerman, 1948).

Like other kalotermitid species, *C. brevis* has no true worker caste. The work of the colony is done by the nymphal forms of the soldier and reproductive castes. If the primary reproductive pair is removed from a colony, nymphs of the fourth instar and older are capable of molting and becoming functional reproductives (supplementary reproductives).

In the present study, carried out at the University of Hawaii, colonies were reared in the laboratory in special termitaries, each colony having descended from a single pair of reproductives. Success of colony establishment and rate of colony increase after varying time intervals were studied, and colonies resulting from different combinations of reproductive types were compared. Such investigations of the establishment and development of colonies from their beginnings have not been reported previously for *C. brevis*, although other termite species have been so studied (Buchli, 1950; Castle, 1934; Light and Weesner, 1955a; Pickens, 1934; and Weesner, 1956).

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[1] Portion of a thesis submitted in partial fulfillment of the requirements for the degree Doctor of Philosophy in Entomology, University of Hawaii, Honolulu, Hawaii, 1960. The study was supported in part by National Science Foundation Grant No. G9581 awarded to Dr. L. D. Tuthill. The Diamond Match Company provided some of the materials used in the construction of termitaries, and various other supplies were purchased with two grants-in-aid given by the University of Hawaii Chapter of the Society of the Sigma Xi.

COLONY ESTABLISHMENT BY PRIMARY REPRODUCTIVES

Termitaries. Colonies were reared in wooden termitaries made of birch tongue blades. Each termitary consisted of six unwarped, large blades, 6″ × ¾″ × 1/16″, bolted together to form a solid unit with a ½″ × ¼″ slot cut in the two center blades to form a small central chamber (fig. 1). This laminated type of construction permitted easy access to the termite inhabitants during later examinations. The termitary also appeared to represent a natural environment for *C. brevis* termites.

Each termite pair was deposited in the central chamber of a termitary by means of a camel's hair brush beside the opening which they usually entered immediately. The termitary was then bolted together and placed on a wire rack in a steel cabinet where it was left at room temperature until time for the eventual examination.

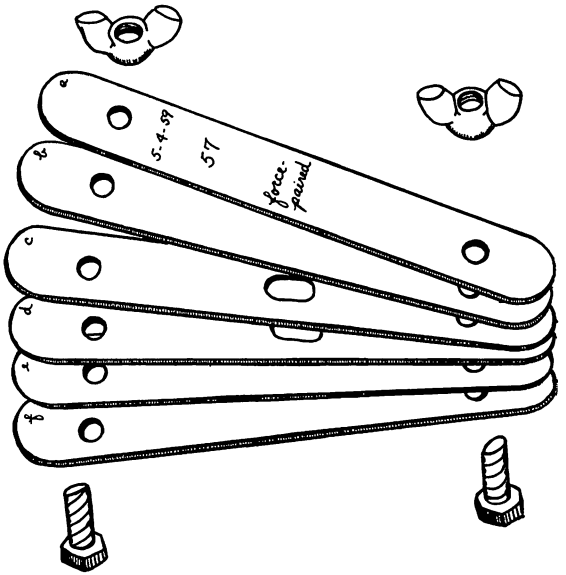

FIG. 1. Dismantled termitary of birch tongue blades.

Experimental Procedure. During the 1959 swarming season from April 29 to June 14, alates were captured and held, usually overnight, in plastic boxes (8″ × 4″ × 5″) until they had lost their wings. These new dealates were used in starting 240 potential colonies in separate termitaries, which were set up on 20 different days, the date and the number on each date being determined by the swarming of alates. A schedule was worked out whereby 20 termitaries were to be opened and examined at each of 12 monthly intervals; *i.e.*, 20 were scheduled to be studied for colony development after one month, 20 after two months,

and so on. In an attempt to control the effect of possible factors affecting termite vigor that might have been associated with a particular swarming day and might have affected success of colony establishment and development, the schedule for opening the termitaries was worked out systematically so that a particular set-up date was represented equally insofar as possible in all the check-up dates.

In half of the cases the dealates were paired by sexing the termites and arbitrarily placing a male with a female in a given termitary, a procedure called "force-pairing." In the remaining half, the dealates were left overnight in plastic boxes containing wooden blocks with many small slots into which pairs entered. This procedure of allowing the reproductives to choose their own mates was called "self-pairing." The results for both groups were essentially the same and they will be combined in the discussion to follow.

In accordance with the experimental schedule 20 termitaries were opened and examined at each of 12 monthly intervals. Because of the termitary construction it was a simple matter to find every egg and every termite present, with little chance of termite injury or loss. The following data were recorded for each termitary: state of vigor of the reproductives; number of eggs present; number of nymphs present; sex, head width, and body length of each nymph. After the occupants of a termitary had been examined, they were preserved in alcohol.

Results. Survival of the colonizing reproductives did not appear to be markedly dependent upon the length of time that had elapsed since the original pairing, except that one- and two-month-old colonies showed higher survival percentages. In 25 cases out of the 240, only one member of a given pair survived to check-up time, in 57 cases both members died, and in one case two females were paired by mistake, leaving a total of 157 pairs for study. Table 1 shows the number of pairs surviving at each of the 12 check-up periods. Survival percentages ranged from 50 to 85.

Colony development data for the 157 colonies according to age of colony are given in Table 2. Eggs were found in termitaries each month during the year, but the greatest numbers occurred during the first three months. It appears that

TABLE 1. Comparisons of survival of primary reproductives from 240 incipient colonies of different ages.

Age of Colony (Months)	1	2	3	4	5	6	7	8	9	10	11	12	Total
Original Pairs	20	20	20	20	20	20	20	20	20	20	20	20	240
Surviving Pairs	16	17	12	14	10	14	11	13	13	13	13	11	157
Survival Percentage	80	85	60	70	50	70	55	65	65	65	65	55	

the first batch of eggs was laid during the first two months of pairing and took another two months, or more, to hatch. Data obtained from other studies in which daily observation of incipient colonies was made (McMahan, 1960) indicate that the time required for *C. brevis* eggs to hatch at room temperature (about 26° C.) is between 75 and 81 days. The number of eggs in the termitaries decreased with hatching until about the ninth month when they began again to increase slightly.

Table 2 also shows the number of nymphs found in each termitary. They are grouped according to head width, an attempt at identifying them to instar. There is no doubt that the first three groupings are instars 1, 2, and 3, but head widths above 0.90 mm. could not be assigned definitely to specific stadia. It seems safe to assume, however, that the smaller heads belong to younger instars.

The data bear out those on egg production in indicating that the first brood was composed of only a few individuals. They hatched from eggs laid within approximately the first two months of colony establishment and developed more or less as a group. By the sixth month almost all of the eggs had hatched and the nymphs had developed to at least the second instar. By the ninth month virtually all nymphs had reached at least the stage of fourth instar; most were undoubtedly older.

Sex was identified for 444 third-instar and older nymphs (it is not easily determined in younger nymphs). The sexes were found to be approximately equal, with 236 males and 208 females, a 1.13 to 1.00 ratio.

In one instance, already mentioned, two self-paired females were found at the time of their checkup (nine months) to have been placed in one termitary. They were alive and active and had produced two eggs. The latter were kept and observed but did not hatch.

No soldiers were found during the experiment.

Colony Establishment by Supplementary Reproductives

Light (1934) and others have reported superiority in egg production on the part of supplementary reproductives. Tests with *C. brevis* appeared to be in line with these findings. In one experiment 10 large *C. brevis* nymphs were confined together in each of 55 termitaries. After two months the termitaries were opened. The 43 termitaries in which a pair of supplementary reproductives had been produced contained 134 eggs, or an average of 3.1 eggs per termitary, with a standard deviation of ± 3.2. This is less than the average of 4.4 ± 1.8 eggs per termitary produced by primary reproductives after two months (see Table 2), but it must be remembered that it takes up to two weeks for nymphs to become supplementaries, a fact which reduced their egg-laying period to only about 6 weeks in the present instance. In another experiment 10 large nymphs were confined together in each of 28 termitaries for a period of four months. In this case 25 pairs of supplementaries were produced and 373 eggs, an average of

TABLE 2. Comparison of progeny in incipient colonies of different ages.

Colonies		Eggs			Nymphal Instars (by Head Width)								
					1st	2nd	3rd	4th +			Total	Aver- age	S.D.
Age (Months)	No.	Total	Aver- age	S.D.	0.4 mm.	0.6 mm.	0.8 mm.	0.9 mm.	1.0 mm.	1.1 mm.			
1	16	29	1.8	±1.3									
2	17	74	4.4	±1.8									
3	12	52	4.3	±2.1	9	6	1				16	1.3	±1.2
4	14	22	1.6	±1.3	6	13	15	2	3	2	41	2.9	±2.1
5	10	10	1.0	±0.9	2	5	12	0	23	1	43	4.3	±1.8
6	14	9	0.6	±0.9	1	3	25	3	35	3	70	5.0	±1.7
7	11	4	0.4	±0.7	1	3	8	27	23	2	64	5.8	±1.3
8	13	5	0.4	±0.5	0	0	1	23	29	5	58	4.5	±1.8
9	13	6	0.5	±0.6	0	1	3	27	33	0	64	4.9	±2.0
10	13	6	0.5	±0.8	0	0	1	11	37	2	51	3.9	±1.8
11	13	9	0.7	±0.8	0	0	1	4	36	0	41	3.2	±1.6
12	11	12	1.1	±1.2	2	1	0	6	25	0	34	3.1	±2.6

14.9 ±6.2 eggs per pair. No young nymphs were found. These figures should be compared with the average of 4.5 ±2.7 offspring (eggs and nymphs) produced by the primaries after four months.

Colony Establishment by Primary Reproductives Paired with Supplementary Reproductives

An experiment was carried out to study the success of colony establishment and development when one member of the original pair was a primary and the other a supplementary reproductive.

During May 1959, 44 termitaries were set up, half containing a male primary and a female supplementary reproductive and the other half containing a male supplementary and a female primary reproductive. The termitaries were opened and their incipient colonies examined one year later, in May 1960. Table 3 presents the data for the experiment and shows the number of eggs and of nymphs (grouped according to head width) present in termitaries representing the two types of pairings. Cases in which the female was a supplementary reproductive appeared to be slightly favored not only from the point of view of adult survival but also in terms of the number of nymphs produced per surviving pair: 3.5 ±1.1 nymphs as compared with 2.9 ±1.2. Termitaries with female primaries, however, contained a few more eggs. These data can also be compared with those of Table 2 in which primary reproductives were paired for a year. Pair survival for primaries (55%) is similar to that for mixed pairs but rate of egg production (12 in 11 colonies) is a little greater. The number of nymphs produced is approximately the same.

Discussion

How representative are these results, obtained under laboratory conditions, for natural incipient colonies of *C. brevis?* In such experiments several factors must be considered for their possible presence and effect on mortality rate of reproductives and on egg production and individual development. These possible factors include injury from handling, delayed entry of reproductives into the termitary, unfavorable temperature and moisture conditions resulting from the small size of the termitary, and inadequacy of new birch tongue blades as a termite diet. One interpretation of the decrease in average number of nymphs in termitaries after the seventh month (Table 2) might be that it represents the cumulative effect of unfavorable conditions of laboratory rearing. On the other hand, the vigor of the surviving individuals, the extent of their wood excavations, and their pellet production all indicate an environment conducive to termite growth and development.

The general finding that colony development during the first year following establishment was at a relatively slow rate is in line with observations by investigators who have studied other termite species (Harvey, 1934; Light, 1934;

Pickens, 1934; Snyder, 1934; Weesner, 1956). Suspension of egg-laying by primary reproductives after an initial period has also been noted. Weesner (p. 296) reports that colonies of *Reticulitermes hesperus* Banks "showed a consistent decline in egg laying by 150 to 175 days after pairing, and egg deposition was not resumed until 75 to 100 days later." In the present experiment with *C. brevis*, the increase in eggs at about the ninth month may indicate the point at which the primaries resumed egg production.

Supplementary reproductives were superior to primaries in egg production. This superiority may have been due to the more favorable environment created by the companionship of the other large nymphs also present in the termitaries containing the supplementaries. (The primaries were alone.) These contrasted circumstances of isolation and lack of it are, of course, the normal ones in nature: primaries, isolated in pairs, begin incipient colonies; supplementaries become functionally mature in the company of other nymphs. The presence of these nymphs may preclude the "need" by supplementaries to suspend egg production after the initial laying period, and may explain the fact that they laid more eggs during a four-month period than did primaries. It may be, however, that suspension of egg production is simply characteristic of the primary female and has nothing to do directly with the absence of nymphs. In those cases in which a primary female was paired with a supplementary male, suspension of egg-laying appeared to occur (Table 3), while in the opposite pairing, either it was not suspended, or the supplementary females resumed laying sooner than did the primary females. This is indicated by the fact that there are five nymphs representing first, second, and third instars in termitaries with female supplementaries and none below fourth instar in those with female primaries. The greater number of eggs found in the case of the latter at the time of opening the termitaries may indicate a recent resumption of egg-laying. These data imply that nonsuspension of egg deposition may be characteristic of supplementary females regardless of the presence or absence of large nymphs.

Snyder (1935) has reported that mating between primary and supplementary reproductives occurs in old established colonies of *Reticulitermes flavipes* Kollar. The present experiments support the view that such matings are not unusual.

The failure of colonies to produce soldiers during their first year has also been found in studies of other termite species (Light and Weesner, 1955b).

SUMMARY

Growth of 157 incipient colonies of *C. brevis*, each established by two primary reproductives, was found to be relatively slow. Egg production appeared to have been suspended about two months after the original pairing and after the first brood had been laid, and not resumed until about the ninth month. Year-old colonies contained on the average three or four nymphs plus one or two eggs. No soldier was produced during the first year. Survival of primary reproductives paired for different intervals up to twelve months varied from 50 to 85 percent.

TABLE 3. Comparison of survival rates and progeny of two combinations of reproductives paired for one year.

Pair Type	Original Pairs	Surviving Pairs		Eggs (Total)	Nymphal Instars (by Head Width)						Total	Average	S.D.
					1st	2nd	3rd	4th +					
		No.	Percentage		0.4 mm.	0.6 mm.	0.8 mm.	0.9 mm.	1.0 mm.	1.1 mm.			
♂Primary ♀Supplementary	22	14	64	5	2	1	2	0	43	1	49	3.5	±1.1
♂Supplementary ♀Primary	22	12	55	8	0	0	0	1	34	0	35	2.9	±1.2
Total	44	26	59	13	2	1	2	1	77	1	84	3.2	

Supplementary reproductives were superior to primaries in egg production at the end of four months, but large nymphs were present with the supplementaries, while the primaries were alone.

Mixed pairs of primary and supplementary reproductives were also successful in producing offspring, colonies with supplementary females showing a slightly greater number of progeny after a year than those with primary females. Colonies begun by such mixed pairs compared favorably with colonies begun by paired primaries in terms of adult survival and total number of eggs and nymphs produced. There is some indication that primary females differ from supplementary females in their tendency to suspend egg production following an initial egg-laying period.

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