

THE PRODUCTION AND REPLACEMENT OF SOLDIERS
IN INCIPIENT COLONIES OF *RETICULITERMES*
HESPERUS BANKS

by

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Most of the studies of caste determination in the Isoptera have been concerned with the production of replacement reproductives. Little information has been obtained regarding the production of individuals of the soldier caste. CASTLE (1934) found that in 45 incipient colonies of *Zootermopsis angusticollis* (Hagen), each produced a soldier within 75 days after the hatching of the first egg and no further soldiers appeared in these colonies during the first year. CASTLE devised an experiment to test: *a.* the ability of the young colony to produce a second soldier if the first one was removed, and *b.* the suppression of soldier production if a soldier-nymph was introduced before the young colony had produced its own soldier.

These experiments demonstrated that more than one of the individuals produced during the first year are capable of becoming soldiers. In 6 of 12 colonies from which the initial soldier was removed, a second soldier was produced. Upon the removal of this second soldier, 4 of 6 colonies produced a third soldier. Two of these 4 colonies produced a fourth soldier upon the removal of the third and 1 of these 2 colonies produced a fifth soldier upon the removal of the fourth. The reciprocal groups, which had received a soldier-nymph, showed a definite suppression of soldier production.

LIGHT (1942-1943) encountered a high initial soldier production in young colonies of *Zootermopsis nevadensis* (Hagen). At that time LIGHT made the generalization that "at least one soldier is present in the first broods of all termites, the development of whose incipient colonies is known". It is now evident that this was an over generalization which cannot be applied to *Reticulitermes*. PICKENS (1932 *a*) does not state the actual number of his colonies of *R. hesperus* Banks which produced a soldier. He does remark that "small colonies, all hatched from one mother, may not produce a soldier for as much as two years." BUCHLI (1950), in his study of *R. lucifugus* (Rossi), obtained an incipient soldier in 20 % of his laboratory colonies.

The present paper is concerned with groups of *R. hesperus* which were

maintained by the late Professor S. F. LIGHT. No attempt was made to follow the exact development of these colonies which were utilized for testing culture methods and were employed as source colonies for later experimental groups. The colonies were examined at various intervals and a general picture of their initial development is available. Of particular interest and significance is the incidence of soldiers in these colonies and a repetition of a portion of CASTLE's experiment for soldier replacement.

DEVELOPMENT OF THE COLONIES

All of the primaries utilized for the culture groups were obtained after normal emergence following the early autumn rains. The alates for series RHI were obtained from Rest Haven, Mendocino County, California. All other alates were obtained from various flights in Berkeley, Alameda County, California. Tandem "pairs" were utilized for setting the groups and many of these were later found to be couples of males or couples of females. The colonies were maintained in various modifications of the "standard" Monterey pine and agar-agar culture method (LIGHT and WEESNER, 1947), utilizing 1 dram, screw-capped vials as containers.

Table 1 presents a summary of the groups to be considered. Of the seven series of cultures, IMV and IN are so small that they will not be discussed in any detail. It should be noted that the period from the appearance of the first egg to the appearance of the first young does not necessarily indicate the time required for egg development, since the records are not continuous enough to permit such a conclusion. In the following accounts of colony development, the days indicated refer to the number of days which have elapsed since the pairs were set in culture. Only the data for initial development are included, except to indicate the later production of soldiers.

Series BRI (64 colonies). No eggs were present at the first observation on the sixth day. At the second observation, 29 days after pairing, 4 colonies each had 1 egg and 1 colony had 2 eggs. At the third observation, 34 days after pairing, a total of 12 eggs was observed in 8 colonies with a maximum of 4 in 1 colony. At 47 days a total of 35 eggs was present in 16 colonies with a maximum of 5 eggs in 1 colony. At 68 days there were 43 eggs in 10 colonies (maximum of 7 eggs) and, in addition, 11 colonies had a combined total of 17 young with a maximum of 4 in 1 colony. At 78 days, 138 eggs were counted in 24 colonies (maximum 11) and a total of 41 young was present in 21 colonies (maximum 5). The maximum combined population, eggs and young, at 78 days was 13. At 116 days no count was made of the young but an increased number of first-instar individuals was noted. At 123 days the colonies were transferred to fresh media. At this time there was a total of 177 young in 28 colonies (maximum 13) and 105 eggs in 25 colonies with a maximum of 11 eggs in 1. The maximum combined population (eggs and young)

TABLE 1.
Summary of the Data for the Incipient Colonies.

CULTURE series.	NUMBER set.	NUMBER considered (1).	NUMBER producing a Soldier.	DAYS AFTER PAIRING TO.		
				First observed egg.	First observed young.	First observed Soldier-Nymph.
BRI	84	64	3	29	68	174
IMM	37	28	12	26	58	113
IM	57	43	4	16	60	115
RHI	29	26	8	48	74	202
BMI	49	31	6	27	69	123
IMV	8	7	1	15	58	126
IN	6	5	0	?	77	—
Total		204	34			

(1) Number set minus initial deaths and couples of males or couples of females.

at 123 days was 17. Three groups from this series subsequently produced a soldier-nymph between 174 and 196 days after pairing.

Series IMM (28 colonies). No eggs were present at the first observation, 15 days after pairing. At 26 days a total of 30 eggs was present in 14 colonies, with a maximum of 3 in 1 colony. At 40 days a total of 61 eggs was present in 21 colonies (maximum 5). At 58 days a total of 73 eggs was present in 21 colonies (maximum 7) and, in addition, a total of 48 young was present in 20 colonies (maximum 5). At 72 days, 84 eggs were counted in 21 colonies (maximum 7). At 89 days, 88 eggs were present in 22 colonies (maximum 8) and 142 young in 25 colonies (maximum 10). At 113 days, a soldier-nymph appeared in each of 7 colonies and 2 more appeared in additional groups at 116 days. Three more soldiers were produced by this series of colonies, 1 at 125 days, 1 at 134 days and the last at 146 days after pairing.

Series IM (43 colonies). One egg was present in a single colony at the first observation, 16 days after pairing. At 27 days a total of 24 eggs was present in 14 colonies (maximum 4). At 39 days a total of 56 eggs was present in 22 colonies (maximum 5). At 60 days, 86 eggs were present in 25 colonies (maximum 6) and, in addition, there was a total of 35 young in 22 colonies (maximum 4). At 74 days, 120 eggs were present in 27 colonies (maximum 8) and 59 young in 27 colonies (maximum 6). At 93 days, a total of 208 eggs was present in 31 colonies (maximum 11)

and 119 young in 29 colonies (maximum 10). The maximum combined population at 93 days, that is, eggs and young, was 18. Two soldier-nymphs appeared at 115 days and 2 additional soldiers at 178 days.

Series RHI (26 colonies). No eggs were observed at the first observation, 28 days after pairing. At 48 days, 4 colonies each had a single egg. At 60 days a total of 10 eggs was present in 6 colonies (maximum 2). At 74 days a total of 7 eggs was present in 6 colonies and, in addition, 9 young were present in 8 colonies. At 94 days, 70 eggs were present in 11 colonies (maximum 8) and a total of 10 young in 9 colonies. At 105 days, 93 eggs were present among 11 colonies (maximum 10) and a total of 12 young in 11 colonies. The maximum combined population of eggs and young in a single colony at 123 days was 15. When the colonies were transferred to fresh culture media at 151 days there were 107 young present in 12 colonies (maximum 8) and 45 eggs in 8 colonies (maximum 8). Eight of the colonies of the RHI series subsequently produced a soldier. Two colonies had soldier-nymphs at 202 days, three more appeared at 215 days, another at 223 days, one at 245 days and the last at 258 days.

Series BMI (31 colonies). One egg appeared in a single colony 27 days after pairing and another in a second colony at 30 days. At 41 days a total of 20 eggs was observed in 7 colonies (maximum 4). At 69 days, 51 eggs were present among 18 colonies (maximum 8) and, in addition, 26 young were present in a total of 13 colonies (maximum 3). At 86 days a total of 97 eggs was present in 21 colonies (maximum 10) and a total of 74 young in 24 colonies (maximum 6). At 100 days a total of 109 eggs was present in 18 colonies (maximum 12) and 106 young in 23 colonies (maximum 8). Soldier-nymphs appeared in each of 3 colonies at 123 days and in 3 additional colonies at 125 days.

SOLDIER REPLACEMENT

Despite the relatively low incident of soldiers in these colonies, as compared with CASTLE's (1934) observations for *Zootermopsis angusticollis*, it seemed desirable to test the ability of the incipient colony of *R. hesperus* to replace the loss of the initial soldier. The soldier-nymph which was produced in each of 13 colonies was removed from its colony of origin and introduced into a similar colony which had not yet produced a soldier. These colonies were selected from among culture series IMM and BMI, where the initial soldier-nymphs appeared 116 to 123 days after pairing. The transfer of soldier-nymphs was made at 121 days after pairing for cultures from the IMM series and at 125 days for cultures from the BMI series. The two groups of colonies, one from which the soldier-nymphs had been removed and the second into which the soldier-nymphs had been introduced, were maintained for one year after the initiation of the experiment. At the time of the transfer each of the colonies contained a

few eggs, a number of first- and second-instar young, from 1 to 6 third-instar young and a pair of primary reproductives.

One of the soldier-nymphs which had been introduced into a new colony did not survive the transfer. The other 12 were apparently accepted by the recipient colonies although some of them were lost between 3 and 12 months after the transfer. No new soldiers appeared in any of the 13 colonies. At the end of one year, there were 11 surviving colonies, 9 of which contained a single soldier and 2 of which lacked a soldier.

Of the 13 colonies from which the soldier-nymph had been removed, one died immediately after resetting. Of the 12 which survived, 6 produced a replacement soldier (table 2). The first replacement soldier-nymph appeared 44 days after the removal of the initial soldier-nymph. Soldier-nymphs were subsequently observed in 2 additional colonies, 1 at 56 days and 1 at 69 days. Seventy three days after the initiation of the experiment, a callow soldier was observed in a fourth colony. At 83 days, two additional colonies contained a replacement soldier. It should be noted that the replacement soldiers all appeared between 160 and 208 days after the pairing of the reproductives, or at the time when some of the colonies (table 1) were producing their first soldier. The 6 colonies which did not produce a replacement soldier survived for the full year of the experiment.

TABLE 2.
Data for Six Colonies Producing a Replacement Soldier.

CULTURE number.	DAYS from Removal of Soldier-Nymph to observation of replacement individual.	TYPES of individuals observed.	DAYS AFTER PAIRING TO.	
			Initial Soldier-Nymph.	Replacement individual.
BMI-48	44	Soldier-Nymph.	123	169
BMI-1	56	Soldier-Nymph.	123	181
IMM-34	69	Soldier-Nymph.	116	190
IMM-4	73	Callow Soldier.	123	194
IMM-28	83	Soldier.	116	204
BMI-43	83	Soldier.	123	208

It is possible that had the experimental groups retained the initial soldier, produced from the first group of young, they might also have produced a second soldier from among the second group of young. If we eliminate those colonies where the initial soldier was derived from the second group of young, as well as those from which the soldier was removed, we have a second control series which produced a soldier at the same time as the initial soldier in the experimental series. Four of the colonies in series IM, 6 in series IMM and 1 in series IMV, or a total of 11 colonies,

produced and retained an initial soldier from the first group of young. None of these produced a second soldier from the subsequent group of young. It seems reasonable, therefore, to conclude that the production of a second soldier in 50 % of the experimental colonies was a direct effect of removing the initial soldier.

DISCUSSION

Although the data available for the initial development of the colonies are general in nature they do exhibit several consistent features: 1. There is a small initial deposition of eggs between 15 and 60 days after pairing which is followed by a secondary flare of egg deposition, usually between 70 and 100 days after pairing. 2. Some colonies produced a soldier very early in colony development and these must be derived from the initial groups of eggs and young. 3. In other colonies a soldier appears much later and is apparently derived from the second group of eggs deposited between 70 and 100 days after pairing. 4. The production of soldiers during the first year varies from one group of colonies to another. 5. The incidence of a soldier among all of the colonies during the first year is relatively low, the average production in 204 colonies being 16 % with a maximum of 42 % in culture series IMM.

The erratic production of soldiers in these colonies suggests that either abnormalities were occurring under the existing laboratory conditions or that the conditions which are prerequisite for soldier production do not occur in all young colonies. A careful consideration of the data available for these groups failed to suggest any consistent variation such as size, rate of development, etc., between colonies which were soldierless as compared with those which did produce a soldier. Certainly the data did not suggest that some were "normal" and others "abnormal" unless the soldier itself is to be taken as an indication of normality. This latter assumption does not seem a safe one without supporting data. Furthermore, a consideration of PICKENS' data (1932 *a*) for the same species, reveals that the soldiers which he obtained appeared much later than did most of those in the present colonies. Indeed, PICKENS concluded that the soldiers produced by his colonies must have been derived from the last eggs which were deposited by the young pair. PICKENS (1932 *a*, 1932 *b*) states that these eggs were laid somewhat after most of the eggs had been deposited, and required a longer period to develop than did the earlier eggs.

In view of the low initial incidence of soldiers, the data obtained on soldier replacement are extremely interesting. Whereas the average production of soldiers in the present cultures was 16 % and the highest initial soldier production was 42 % in any series of cultures, 6 of the experimental group of 12 colonies produced a second soldier when the first one was removed. This incidence of soldier replacement is comparable to that obtained by CASTLE (1934) with the same number of colonies of *Zooter-*

mopsis angusticollis, even though in this species there was a 100 % initial soldier production in the undisturbed colonies. The failure of the groups to produce a soldier when a foreign soldier was introduced is of much less significance here than in Castle's groups, since, again, the initial spontaneous soldier production in *R. hesperus* was much lower than in *Z. angusticollis*. In any case, no second soldier did appear in groups which already possessed a soldier, either normally or by introduction.

The data now at hand indicate that in laboratory colonies of *R. hesperus*, initiated by a pair of primary reproductives and maintained at the same time and under the same conditions, some have a greater tendency to produce soldiers than do others. Furthermore, it is evident, that not all colonies produce a soldier during the first year.

It should be noted that the pattern of egg deposition in the present series of colonies does not agree with that described by PICKENS for the same species. PICKENS (1934) states that "an average of less than ten are produced in the first clutch. The number may be as low as four or six, or as high as fifteen, or in rare cases twenty. The eggs are laid at fairly regular intervals. A period of from one to three days elapses between the deposition of two successive eggs, except for the last two or three, which are laid at increasingly long intervals, of as much as a week or tens days".

The pattern of egg deposition for *R. hesperus* differs strikingly from that which BUCHLI (1950) found in *R. lucifugus*. In the latter species, 10 to 20 eggs are deposited within a month and egg deposition terminates when the first young appears, about 28 days after the deposition of the first egg. In *R. hesperus*, on the other hand, the secondary flare of egg production usually coincides with the hatching of the first eggs.

Summary.

1. Only a small percentage of incipient colonies of *Reticulitermes hesperus* produce a soldier during the first year.
2. In some colonies the soldier is derived from the first eggs and in other colonies the soldier develops from later eggs.
3. Not more than one soldier was present in any one colony during the first year.
4. If the initial soldier, produced from the first group of young was removed, a second or replacement soldier was produced from the second group of young in 50 % of an experimental series of 12 colonies.

Zusammenfassung.

1. Nur in wenigen der jungen Kolonien von *Reticulitermes hesperus* erscheint ein Soldat während des ersten Jahres.

2. In manchen Kolonien entwickeln sich die Soldaten aus den ersten Eiern, während sie sich in anderen Kolonien aus späteren Eiern entwickeln.
3. In jeder Kolonie wurde im Lauf des ersten Jahres nur ein einziger Soldat gefunden.
4. Wenn der aus der ersten Gruppe von Jungen stammende Soldat zerstört wurde, so entwickelte sich aus der zweiten Gruppe von Jungen in 50 % einer Gruppe von 12 Experimentalkolonien, ein zweiter Soldat.

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