STUDIES OF SHOT-HOLE BORER OF TEA IV—LIFE CYCLE OF THE BEETLE.

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In a previous article (Gadd 1941) the life cycle of the shot-hole borer beetle was shown to be made up of the following periods: Pre-oviposition 8.4 days, Incubation 6.9 days, Larval 15.2 days and Pupal 7 days, which together and allowing 2 or 3 days occupation of the old gallery make a total of about 40 days. These observations refer to beetles living at an elevation of 3,500 feet. They were obtained, not by direct measurement of the time stated, but by deduction from data obtained by opening galleries of known ages. Such method had to be used because at that time no means of keeping the insects alive outside their galleries and under conditions allowing direct observation were known. Since then the beetles have been reared under artificial conditions allowing the direct measurement of the various stages of the life history (Gadd 1947). It is therefore of interest to compare the results obtained in that way with those previously published.

Effect of Temperature.—Temperature has a marked effect on the duration of all stages in the life cycle. Within limits, an increase in temperature results in a shortening of the duration of each stage and consequently of the whole cycle. For instance, the pupal period at room temperature at St. Coombs (Altitude 4,500 ft.) occupied 10 days, and at Passara (Altitude 3,500 ft.) 8 days, whereas it was reduced to 5 days by keeping the pupae in an incubator controlled at 82°F. Larvae cannot survive at temperatures much below 60°F and it was difficult to maintain them at St. Coombs where the room temperature fluctuated between 61 and 77°F.

The last observation affords a reason why the beetles fail to become a pest at elevations above 4,000 feet in Ceylon. The beetles, and more frequently their galleries have been found at higher elevations where the temperature is too low for breeding purposes. For instance, when tea bushes on St. Coombs Estate are pruned borer galleries are sometimes found in the branches but these are usually found to be empty. Female beetles undoubtedly arrive on the estate from lower altitudes and make their galleries but the temperature, particularly at night, is too low for survival, especially for the young.

Adults.—The emergence of a female beetle (Plate 1, C) from the gallery in which she was born affords a suitable starting point

for the life cycle. She is then black and equipped for flight with a pair of membranous wings which are normally hidden below hard chitinous covers (elytra). The male is somewhat smaller and having no membranous wings cannot fly. (Plate 1, B and D).

Although capable of flight she seems to make little use of that power. On the wing she may travel considerable distances when aided by wind and so may reach a bush miles away from the infested area. More usually her journey is a short one, sometimes by flight but more frequently by walking. All she seeks is a suitable stem in which to bore and of these there is no shortage. In the laboratory she will re-enter the stem from which she emerged, at a point a few inches away. At one time it was feared that neglected gardens would become breeding places from which the beetles would invade better cultivated areas. Such fears have proved groundless, though not solely because of the beetles' apparent disinclination to fly.

We must assume that when the female emerges from the parent gallery she is already fertilised and that she carries with her spores of the 'ambrosia' fungus which grew on the walls of that gallery. Reasons for these assumptions will become evident later.

On emergence she loses no time in seeking a new home. While outside a gallery she is unprotected against enemies which cannot reach her when within one. The period elapsing between emergence from the parent gallery till a new one is started is the only time during her life when she is normally liable to their attacks. Also she cannot long survive a dry atmosphere. In the laboratory she would live for 2 or 3 days only on dry blotting paper, but if the paper were wetted, she could be maintained for as long as 15 days. Evidently humid conditions, such as occur within the galleries are essential for her well-being. The drier external conditions, however, cannot be the only stimulus which compels her to bore, as, at least in the laboratory, many females which have emerged naturally or been removed from galleries make little or no attempt to bore another, and males never attempt to make galleries.

Having selected a place for entry the female beetle bores rapidly and will make a tunnel equal to her own length in one hour. She continues her tunnelling for 4 or 5 days cutting into the wood with her jaws and pushing the debris from the gallery with the hind end of her body. The gallery is too narrow to allow her to turn, so any unwelcome visitor is unceremoniously expelled in the same way.

Pre-oviposition.—The interval between her leaving her parent's gallery and her laying the first egg is termed the Pre-oviposition period. As no shot-hole borer beetle has been induced to oviposit outside a gallery where she can be observed the only way to determine this period is by opening galleries of known age to observe their contents. The youngest galleries which King (1937) found to contain eggs were 10 days old. A re-examination of his data shows that of nine 10-day old galleries opened, two only contained eggs, and one of them contained four eggs. I have shown elsewhere (1947) that as many as three eggs are rarely laid on any one day, so it is probable that the female with four eggs began to lay not later than the eighth day after commencing to bore her gallery. On the other hand galleries 2, 3 and even 4-weeks old often contain neither eggs nor young, though the female is alive and apparently healthy. In fact it seems probable that many females do not lay eggs although they make the gallery ready for a family.

We can expect our beetle to lay her first egg about 10 days after we first saw her. She did not spend the whole of the pre-oviposition period in boring, as judging by the absence of fresh wood dust below the entrance, the gallery was completed about the fifth day. Near the end of her gallery she has planted the fungus spores brought with her. The fungus garden probably needs little attention, but it is of the greatest importance that the fungus shall flourish if she is to raise a family.

Incubation period.—Her eggs are small glistening ovoid bodies and she deposits them in a heap near the end of her gallery, adding one each day. The fact that eggs are usually found in heaps usually containing not more than seven eggs has given observers the impression that eggs are laid in batches. The eggs, if kept moist on damp blotting paper, will hatch but the eggs of one heap will not all hatch on the same day. Usually the larvae emerge on successive days, though occasionally two and rarely three eggs will hatch on the same day. On some days no eggs hatch. These observations indicate that normally the female lays one egg per day though she may miss some days or lay two or even three sometimes.

How long she will continue to oviposit and how many eggs in all she may be expected to lay are questions to which precise answers cannot be given. As yet a female has not been induced to lay eggs outside a gallery allowing the process to be seen and the eggs counted, so information regarding family size must be obtained by opening galleries. This question will be considered in greater detail in a later article and it will be sufficient to state here that the largest number of young, including eggs observed in a gallery is 35; normally families are very much smaller, and some females have no young. It is unlikely therefore that our beetle will lay more than 35 eggs over a period of 5 weeks.

The incubation of eggs at the Passara laboratories when the mean room temperature is 73°F takes 7 or 8 days. In an incubator at 82°F. the incubation period is shortened to 5 or 6 days. The previous estimate of 6.9 days for incubation, obtained by indirect methods, is therefore not improbable.

An incubation period of seven days coupled with the fact that the females normally lay one egg per day affords an explanation why the egg heaps rarely contain more than seven eggs. Larger heaps are indicative of abnormal egg laying, and smaller heaps, which are much more frequently encountered, result from irregular oviposition during the previous week.

Larval period.—The newly hatched larva is a small white worm-like object and extremely hungry (Plate I, E). When placed on cultures of the ambrosia fungus *Monacrosporium ambrosium* (Gadd and Loos 1947) they immediately begin to feed ravenously and continue to do so, except for short periods while moulting, until they are full grown and ready to pupate. This fungus occurs naturally on the walls of borer galleries and is undoubtedly transplanted there by the parent females though how or where it is carried is not definitely known. The fact that the insects can be maintained through their whole larval period on pure cultures of the fungus is a clear indication that it forms the main, if not sole, essential food.

The dark purple stain in the tissues around the beetle's gallery is due to this fungus which normally excretes a coloring matter. The fungus extracts its nutriment from the stem tissues, and fruits on the gallery walls giving them a frosted appearance. The larvae feed on the spores. The

importance of the fungus in the insect's economy and the amount and nature of the work to be done before it can be planted in a suitable place for growth seem to rule out the possibility that transfer is entirely accidental.

When the insects are kept in artificial culture the full larval period, from egg-hatch to pupation, is very variable and markedly influenced by temperature. At St. Coombs when the room temperature varied from 61° to 77°F. with a mean daily temperature of 68°F. the shortest larval period observed was 18 days and the longest 33 days. The mean of eight larvae was 23.6 days, and some larvae lived as long as 40 days without pupating. Deaths were very numerous. Better results were obtained when the cultures were kept in an incubator at 77°F or 82°F. At 82°F. the larval period varied from 9 to 19 days ; the mean for 31 insects was 12.4 days which is approximately half of that at room temperature. The larval period previously determined statistically from data of galleries collected and opened at Passara was 15.2 days, which when compared with the above observations appears tolerably correct.

The larval period can be divided into 3 parts separated by moults. The first stage (or instar) is completed about the end of the second day when the larva stops feeding and becomes quiescent. After casting its skin it again becomes active and voracious. The second moult occurs after about the seventh day or later and the final one at pupation on the tenth day or later.

The most critical period in the insect's life appears to occur at the first moult when in artificial cultures deaths are most numerous. Changes in the technique failed to reduce the number materially. In this connection it may be noted that in the earlier investigation dealing solely with data collected from the field it was noted that "only 50 per cent. of the eggs laid develop into adults." The numerous deaths noted in artificial cultures cannot therefore be ascribed solely to faulty technique nor to the absence of maternal care. The experiments show when the deaths are most likely to occur, viz. at the first moult.

Pupal Period.—For one or two days before pupation the larva lies on its back and becomes quiescent. This is usually known as the prepupal period but in this account it has been counted as part of the larval period.

The length of the pupal period varies from 5 days at 82°F. to 10 days at room temperature at St. Coombs *(Circa* 68°F.). Our previous estimate was 7 days which agrees tolerably well with the period ascertained in the Passara laboratories, viz. 8 days.

Two or three days before the adult emerges from the pupal case the mouth parts and eyes become black. The true wings of females, but not the elytra, also become dark coloured, and so at this stage sex can be determined as the males having no true wings do not exhibit this coloration along the body.

Adults.—The adults on emerging from the pupal case are pale yellow except for the eyes, mouth parts and true wings. Colour development in adults raised in culture is slow and at least 5 or 6 days will elapse before the beetles are fully black. As the beetles are black when they leave the gallery it is evident that they remain in it for at least 5 days after emerging from the pupal case. This view is supported by the fact that several young adults are sometimes found together in a gallery.

The male to female ratio of beetles in tea stems is 1:4 or 5 and in castor stems it is probably much wider. Green (1903)

expressed the view that mating occurs within the gallery, and such evidence as there is points to that conclusion. The main difficulty in accepting it is the failure to understand how copulation can occur within the gallery because its diameter is too small to allow one adult beetle to pass another. Also there are no special places of greater diameter or height which might serve as nuptial chambers.

In laboratory cages males are frequently seen walking on the stems and they have been observed to follow young females into galleries recently excavated. It cannot be suggested however that copulation takes place in new galleries as the same objections must be raised to that locality as to the old galleries. Moreover when females fly to a new area the males being without wings cannot follow and so if copulation normally occurs in new galleries such females would invariably be infertile.

Males from castor stems have been observed in the laboratory to excavate shallow chambers adjoining the gallery entrances and to lie in them as though 'in wait.' Not all males do so nor does every gallery entrance have a 'male cavity' adjoining it. These observations suggest that copulation may occur at gallery entrances but such has not been observed. Similar cavities have not been found at gallery entrances in tea stems. Mating has not been observed in cultures and there is doubt that females under those conditions have ever been fertilized.

In the absence of evidence to the contrary we must assume that copulation normally occurs within the parent gallery. Yet the conditions there and the frequency of small families which do not always include a male suggest that many female borers are not fertilised on emergence and consequently have no young. The existence of numerous galleries which do not contain young or eggs is probably to be accounted for by the absence of fertilisation.

The parent female remains mistress of the gallery until all her young have departed. She dies sometimes later but her gallery is never used again for breeding. Each female makes her own gallery and on her death the gallery remains empty.

Life Cycle.—With the emergence of a daughter beetle from her parent's gallery the life cycle is completed. The cycle at 3,000 to 3,500 feet would occupy 6 or 7 weeks made up as follows :—

Pre-oviposition	...	10 days
Incubation	...	7 days
Larval period	...	15 days
Pupae ...	...	8 days
Adult (before leaving gallery)		5 days
Total	...	45 days

Although the eldest of the family may emerge about 6 or 7 weeks after the mother began the construction of her gallery the youngest will not leave till some weeks later, depending on the size of the family and the intervals between egg-laying. By the time the youngest leaves, the eldest female may have a family of her own. In the field young females leave the parent galleries every day and so any increase in the beetle population is a gradual process and not one of marked steps at intervals of 6 or 7 weeks.

LITERATURE

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