STUDIES ON POPULATION DYNAMICS OF THE YELLOW HEADED BORER, *DIRPHYA NIGRICORNIS* OLIVIER (COLEOPTERA:CERAMBYCIDAE), A PEST OF COFFEE IN KENYA.

By

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ABSTRACT

Studies were conducted in coffee plantations in Kenya and under laboratory conditions to determine whether durations and sessions of mating either impeded or enhanced both the ovipositional rate per day and fecundity of Dirphya nigricornis Olivier on susceptible varieties of Coffea arabica L. Stocks of wild and field bred beetles from three districts of Kenya were used in the studies.

Caged pairs of beetles in sex ratio 1:1 installed on distal tips of coffee shoots were in addition used to relate the oviposition behaviour to egg niche location and to elucidate through timing and observations from stop watches the oviposition rhythms if any in the beetle. Variable populations were also initiated and used to establish the mortality factors for the egg, larval, pupal and adult stages of the pest as well as evaluating the efficacy of the braconid, Iphiaulax varipalpis Cary as a biocontrol agent of the pest in Kenya. A series of complementary studies were also conducted to evaluate the actual damage by the larvae to coffee stems and the losses in yield that resulted from their boring. These parameters were critical in understanding the population dynamics of the pest.

Caging of the beetles singly showed that the mating of D. nigricornis influenced its oviposition through the durations (minutes) of mating and the number of times the species mated. Long durations of 280 minutes and six repeated sessions of mating enhanced significantly ($P < 0.05, 0.01, 0.001$) the production of upto 7 eggs per day per female. This led to the maximum fecundities of 21.47 and 29.50 eggs per female of first and second brood beetles, respectively. Short and single matings below 36.41 minutes or 1.30 sessions either impeded oviposition or had minimal influence on it.

The behaviour of the beetles when timed and observed before and during oviposition using 20 x 15 cm wire-mesh cages on coffee tips showed that the ovipositional period lasted 11.3 ± 1.8 minutes. It comprised of a search period of 3.0 ± 0.5 minutes, a gnawing period of 1.0 ± 0.2 minutes, an egg deposition period of 5.0 ± 0.1 minutes, and a sealing period of 2.0 ± 0.3 minutes. Within that time, the females were able to integrate various plant factors such as preferability of the 12 distal internodes, their green colour and girths of 0.9 ± 0.1 cm and the possibility of peeling the bark with least force of approximately 8 - 11 mg/mm^2.

The females when observed and timed both within and between days of oviposition demonstrated that they started ovipositing about the same time during each reproductive day after a constant pause of 22.83 ± 1.19 to 31.17 ± 7.97 hours between days. During each day of oviposition, there occurred two rhythms with eggs laid at seven intervals of < 110.0, 186.0 and 260.5 minutes respectively.

When the occurrence of the egg stage was sampled and categorised per season during the years 1982, 1983 and 1984 in the primary, secondary, tertiary, quarternary and sucker shoots that comprised the coffee canopies at the two sites, this revealed that D. nigricornis constructed single, double, treble, quadruple or other multiples of egg niches. They were predominantly located within 142.0 and 215.0 cm of the mid zones of canopies usually 0.5 to 30.0 cm off shoots but concentrated significantly ($r = -0.44$ to $r = -0.99$) in tip internodes irrespective of shoot category.

The main causes of the fluctuations in the populations of the beetles as assessed under field conditions were namely: brooding, incidence and prevalence of parasites and predators of the larval,

pupal and adult stages as well as the prevalence of abiotic factors. The latter factors also acted on the egg stage.

Brooding produced two different generations which occurred after 351.46 - 354.30 and 586.86 - 588.33 days from every single egg population. The parasites and predators which were recognized and recorded were: Iphiaulax varipalpis Cary, Microplitis sp, Camptotypus (Hemipimpla) sp, Ectopsocus sp, Mirid sp. Dacnodes caffra Dohrn, Pheidole sp. Acantholepis sp, Tapinoma sp, Crematogaster sp, Tetramorium sp and Technomyrmex sp. The incidence of parasitism was low in the larval stage and absent in the pupal and adult stages. Contrarily, there was a trend toward larval, pupal and adult predation.

Field collected samples and specimens of the braconid, I. varipalpis when reared in polyethylene sheet tubes under controlled laboratory conditions of 23.0 C $\pm$ 1.0 at 70% r.h. and used to evaluate its ability to control the beetle in perspex cages showed that while field parasitism was as low as 10.72%, this rose to 56.66% in the laboratory because the parasite detected the hosts very easily in the latter which was minimized in the thick canopies of the plants.

A relationship of the damage to the plant canopy and yield by the boring larvae when evaluated from readings taken of incidence of bores and the amount of destruction by larvae of known ages revealed that the damage occured significantly ($P < 0.001$) when a length of 14.45 cm had been bored by the beetle by killing approximately 2.5 cm of it, but only after 1.45 nodes had completely withered up. This was often the case when at least 16.39 frass bores were visible on the bark. However, economic losses in terms of reduced weights of cherries only occurred when 15.9 cm and beyond of the main stem had been bored.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

1.1.1 Economic value of the coffee crop to Kenya

Since the commercial introduction of coffee (Coffea arabica L) into Kenya at about the turn of this century, numerous local and introduced arthropod pests have become established on it. Fortunately some of these pests are presumably maintained below economic levels by local and imported natural enemies. An example of introduced parasite of the Kenya mealybug became established and its efficacy is a universally plauded biological control success (Le Pelly, 1959, 1968, 1973; Abasa, 1983).

Since its introduction, C. arabica has remained Kenya's most important cash crop (Purseglove, 1968; Choulder, 1972; Rodrigues et al. 1975; Anon., 1980). It is produced and marketed as high quality coffee on the world market. It is estimated that one third (30-40%) of Kenya's foreign exchange earnings comes from coffee sales alone (Rodrigues et al. 1975).

All of this is harvested from total area of about 100,000 hectares yielding above 90,000 tonnes annually (Anon., 1980). This proportion represents 2.0% of global production of coffee as a beverage crop (Rodrigues et al., 1975). It is estimated that coffee farming has raised the economic and social status of not only the

farmers, but also of farm workers and 10% of the entire population through the co-operative movement (Anon, 1980).

1.1.2 Dirphya nigricornis as a constraint to coffee production in Kenya.

Among the insect pests that attack coffee in the field in Kenya, cerambycid beetle larvae belonging to the species Dirphya nigricornis Olivier (Coleoptera: Cerambycidae) is one of the most serious pests of the crop (Le Pelley, 1959, 1968; Abasa, 1983). The pest is usually referred to in the literature as the yellow headed borer beetle (Crowe, 1962). The larvae bore through the wood, which involves tunnelling through the stem pith and vascular systems, rupturing and perforating the bark of branches and stems (Le Pelley, 1973). These activities not only disrupt continuous translocation of nutrition thereby interfering with the normal physiological functioning of the plant, but also lead to direct loss of berry yields (Crowe, 1962).

Unfortunately, the amount of available knowledge on D. nigricornis is sketchy and limited. Detailed knowledge of the biology and ecology of this pest would assist Kenya's coffee industry through the design of appropriate control measures to reduce its damage and increase berry yields.

One reason for lack of information on this pest may be attributed to its sporadic outbreaks, characteristic of

tropical pests. This would tend to discourage thorough investigations which are necessarily long-term enterprises (Wood, 1970).

1.2 REVIEW OF LITERATURE

1.2.1 Identification of D. nigricornis

The yellow headed borer D. nigricornis belongs to the family Cerambycidae in the order Coleoptera. Within this order, the cerambycids have been grouped into the superfamily Chrysomeloidea of the sub order Polyphaga (Crowson, 1967). Below family, the species is one of the 4773 members within the subfamily Cerambycinae (Linsley, 1959).

The distinguishing characteristics of D. nigricornis have been given by Crowson (1967) and Bee et al. (1981) as follows:

- antennae inserted on pronounced tubercles and capable of being reflected backwards over at least two thirds the size of the body;
- three pairs of legs with two tibial spines;
- vestigial maxillary lacinia;
- hairy ovipositor;
- simple tarsal claws; and,
- yellow elegance tinged over a third of basal length of both elytra and the predominantly black posterior abdominal and elytral areas.

1.2.2 Ecology and distribution of *D. nigricornis*

Aurivillius (1912, 1913), Lameere (1913) and Linsley (1936, 1939) reviewed the general ecology of *D. nigricornis* along with other members of its family. Later, Nord (1968), Gray (1972), Beaver (1976), Mathews (1976) and Bee, *et al.* (1981) showed that tropical cerambycids including this species were generally associated with forest ecosystems where they fed on plants as larvae. Besides they attack tree crops, tea, citrus, cocoa, palms, coconuts, coffee and cashew nuts, in particular, among others. Linsley (1959), Crowe (1962) and Le Pelley (1968) were concerned in their studies with the establishment of *D. nigricornis* on plants. They showed that, like other cerambycids, the species invaded plants including coffee from their apical meristems. On the other hand, its close relative, the white borer of Kenyan coffee, *Anthores leuconotus* Pasc. feeds subcortically upon the bark of the main stem (Abasa, 1983).

The pest status of *D. nigricornis* was first recognized by Subramanian (1934) in India and Lepesme and Villiers (1944) in Senegal and then later in Malawi and Kenya (Duffy, 1957). In Kenya, it was first recorded on *C. arabica* (Le Pelley, 1973).

1.2.3 Biological studies on D. nigricornis in Kenyan coffee ecosystems

A sole study by Crowe (1962) on the biology of the pest was conducted on a field population of the pest. He, (Crowe, 1962) investigated the biology of D. nigricornis and showed that females deposited light brown elongate-oval shaped eggs singly under a flap of bark 10cm from the tip of the infected shoot. He did however not ascertain the potential fecundity of female beetles. This parameter and the relative rates of increase were assessed in these studies in order to obtain accurate information to be applied in its control.

1.2.4 Previous studies on population dynamics and damage of D. nigricornis

There is no reported literature on the population dynamics of D. nigricornis in Kenya. The influence of copulation period, on the birth rates of the pest and causes of its mortality have not been elucidated. However, Crowe (1962) recorded Iphiaulax varipalpis Cary (Hymenoptera: Braconidae) and suspected the existence of an undescribed species of Entedon (Hymenoptera:Eulophidae) as the only parasites that caused the general regulation of D. nigrigornis larvae. Their parasitism was apparently confined to the larval stage while similar information for the egg, pupal

and adult stages of the pest was lacking in Kenya as evidenced by a recent reveiw by Abasa (1983). It is further evident from this review that the levels of parasitism and predation by known and unknown enemies of D. nigricornis have not been carefully investigated in Kenya. For example, no studies have been conducted on I. varipalpis. Similarly, the effects of the parasite have not been evaluated to determine its efficiency as an indigenous biological control agent. Such information once obtained would be valuable in designing control strategies for the borer to reduce its damage.

The available information also showed that the impact of D. nigricornis to coffee was not precisely defined to permit the assessment of the status of the pest. There is therefore need to undertake further studies aimed at quantifying precisely the damage caused to coffee by D. nigricornis. In order to achieve this, it became necessary to study several aspects of the relationship of the beetle with its host, coffee. This included studies on the losses of yield caused by the pest in Kenyan coffee agroecosystems.

1.2.5 General objectives of the study

In Kenya, single ovipositions by D. nigricornis(Loc cit) have been recorded and very little information is available on the fluctuations of the pest. The objectives

of this study were:

(i) to identify and study the reproductive characteristics that influence birth rates of *D. nigricornis*;

(ii) to relate the oviposition behaviour to egg niche location in the pest;

(iii) to elucidate oviposition rhymths if any for the beetle;

(iv) to determine the influence of seasons, coffee canopy factors and properties on distribution of egg niches;

(v) to determine the efficacy of *I. varipalpis* as a bio control agent of the beetle, and,

(vi) to determine the exact responses of the coffee canopy to beetle infestation and the relationship with yield components.

The determination of the multiplication of the borer would assess not only how or why its abundance may take a particular form and not the other but also assist in explaining the inherent characters in the species which may lead to particular patterns of such occurrence. The potential fecundity and the relative rates of

increase were assessed in these studies to obtain accurate information to be applied in its control [illegible] survival would also be elucidated. Such information if obtained would be very useful in assisting to determine the population dynamics of D. nigricornis and in designing suitable strategies for its management in coffee agroecosystems.

CHAPTER 2

SOME ASPECTS OF MATING AND OVIPOSITION OF THE YELLOW HEADED BORER, *DIRPHYA NIGRICORNIS* INFLUENCING ITS POPULATION DYNAMICS

2.1 INTRODUCTION

Some of the reproductive aspects such as mating and oviposition, which affect the population dynamics of many coffee insect pests notably *D. nigricornis* in Kenya and lead to their outbreaks have not yet been identified. Such information would explain the dramatic increases in some pest populations that concurrently occur with the expansion of acreage planted to crops (Brown, 1975; Lashomb and Nebeker, 1979). Since such factors may be important in regulating pest populations (Richards, 1960; Richard , 1974; Oh, 1979), it became necessary to investigate and elucidate the mating and ovipositional behaviour of *D. nigricornis* to provide baseline data. Also determined were preference for type of branch infested (Myers, 1967) and the synchronisation of the production of eggs when canopies have abundant and flushy shoots (Morris, 1960; Southwood, 1966; Myers *et al*. 1968; Mayr, 1970). Three experiments were designed to obtain the information.

The two aspects of mating considered to be critical were: (a) (i) the copulation durations; and,

(ii) birth rates of the pest.

On the other hand, four aspects of the ovipositional behaviour of the pest selected for study were:

(b) (i) the behavioural sequence of ovipositing females;

(ii) egg niche size and its effect on infestation levels;

(iii) whether plant tips were synchronized with the egg stage; and,

(iv) the temporal production and harmonies in the diurnal distribution of eggs during oviposition.

Other studies aimed at ascertaining as to whether the pest exhibited any preference for any type of branch and whether the season had any influence on the distribution of egg niches on different coffee varieties attacked.

2.2 MATERIALS AND METHODS

2.2.1 Procedures used in capturing, caging and rearing stock *D. nigricornis* for study

The insects used in these studies came from three generations of wild individuals from the field (heterogenous population) and two resultant brood generations

(homogenous populations). Beetles were from individuals initially collected from fields in Kiambu (Azania, Jacaranda, Kiaora and Rukera), Machakos (Matungulu) and Murang'a (Muri) districts of Kenya. At each collection site, a single block (2.5-3.5 ha.) of coffee of varieties SL28 and SL34 spaced 2.74 x 2.74m was demarcated for sampling. Coffee plants within the sites were examined row by row and any adult insects found were collected.

Field cultures of wild and brood D. nigricornis were established from the collected samples on varieties similar to those from which they were caught in the field. Adults (one female: one male) were placed in large wire mesh cages measuring 20 x 15 cm and installed on susceptible tips of coffee shoots as shown in Figure I. This procedure was complimented by trapping of the insects as they emerged from their holes after pupation. In this case, smaller wire mesh cages (10 x 2.5 cm; Fig. 2) were used to trap emerging adults from different generations. Throughout the period of study on mating and oviposition of the pest, adults of either sex of the insect were separated using different morphological characters of their body sizes and wingspans. In this respect, female beetles were large bodied and robust (2.3 to 2.7 cm), wingspan (3.8-4.2 cm) while the males were small bodied (2.2 to 2.6 cm) and had a shorter wingspan (3.6 to 3.9 cm).

During the dissection of the dead female beetles to count the number of unlaid oocytes, both chorionated and unchorionated ones were determined on the basis of their appropriate colour, shape and configuration.

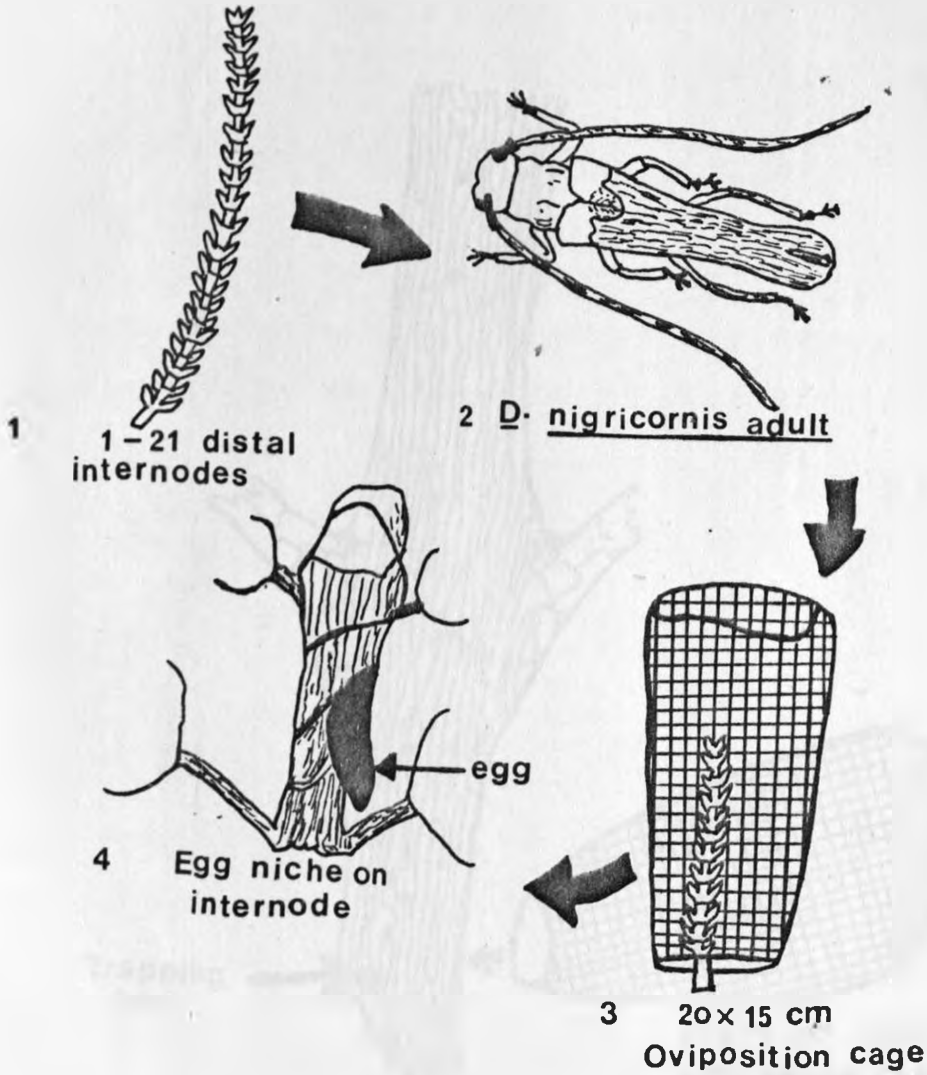


Fig. 1. Diagrammatic representation of mating and oviposition cage (Relative size)

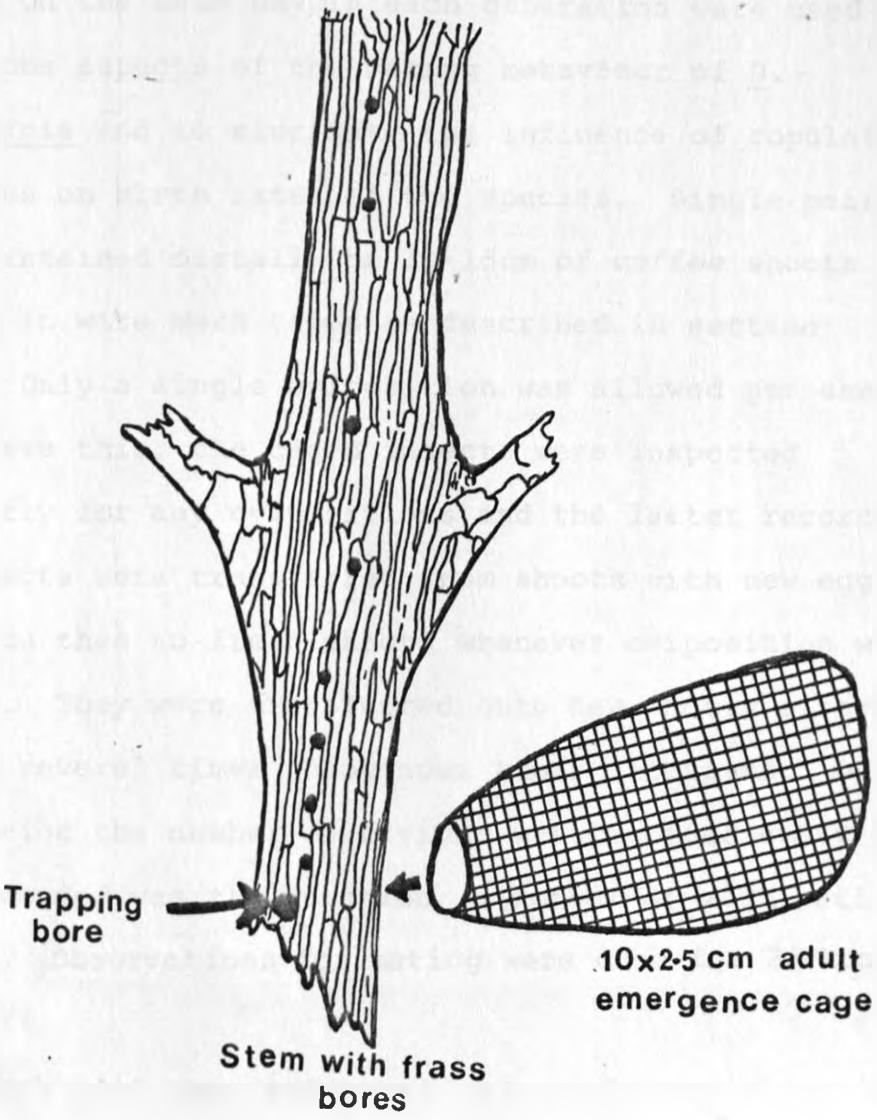


Fig. 2. Diagrammatic representation of wire cage for trapping singly each emerging D. nigricornis adult.

2.2.2 Mating aspects and birth rates of *D. nigricornis*

Fifteen, eight and three pairs of unmated adults of wild, first and second broods, respectively, that had emerged on the same day in each generation were used to study some aspects of the mating behaviour of *D. nigricornis* and to elucidate the influence of copulation durations on birth rates of the species. Single pairs were maintained distally on 10-15cm of coffee shoots *in situ* in wire mesh cages as described in section 2.2.1. Only a single oviposition was allowed per shoot. To achieve this, the caged insects were inspected frequently for any ovipositions and the latter recorded. The insects were transferred from shoots with new egg niches on them to fresh shoots whenever oviposition was noticed. They were transferred onto new shoots either once or several times throughout their lifespans. During this period the number of matings was recorded every day. Also recorded was the duration (minutes) of each mating session. Observations for mating were done for 24 hours each day.

Each pair was designated as a replicate of all the insects. Correlations were calculated between the oviposition rate per day and fecundity and three parameters of mating, namely:

(i) total period of mating;

(ii) number of times mated; and,

(iii) mean duration per mating

The relating of mating to oviposition was to elucidate whether the former process enhanced or impeded oviposition and fertility in the species.

After eggs had been laid, their fate was assessed daily. Subsequently, the development of the pest was monitored to establish its generation periods. The data gathered was used to calculate periods of survival, fecundity, rates of increase, gross and net reproductive rates of the species.

The fecundity of the insect was determined by dissecting each adult female at the end of its lifespan under a binocular microscope (x10). The number of eggs each female had previously laid was summed up with the unlaid oocytes to establish fecundity. Potential fecundity and egg viability were estimated through percentage calculations.

2.2.3 Oviposition behaviour and its relation to egg niche location and diel rhythms in the yellow headed borer, Dirphya nigricornis

A series of field observations was conducted in which the activities of female borers were recorded before and during oviposition. Ten mature adults belonging to the first generation produced on coffee in the field were mated and confined individually in cages at the tip of shoots of coffee plants (section 2.2.1). Each coffee shoot tip consisted of 21 internodes,

starting from the coffee shoot primordia. Pre-ovipositional and ovipositional activities of the beetles were followed closely and assigned to one of four activity categories, namely:

(i) physical search by tarsi and vision;
(ii) gnawing with mandibles
(iii) egg deposition; and,
(iv) egg sealing by ovipositor

Each activity was individually timed by stop-watch (Model: Smiths, Shockproof) and recorded. This was continued until death of the female.

As soon as a beetle was moved to a new shoot, the length and width of each egg niche was measured immediately after it had been formed. For this study, ten new shoots were measured. Each tip included in the cage was classified in three ways:

(i) by the number of internodes it contained
(ii) by its colour; and,
(iii) by the peelability of its bark

The later was tested on the 12 distal and nonsnapping internodes per shoot at each position by making an artificial egg niche. The five categories of shoots involved were primary, secondary, tertiary, quarternary and suckers. At each internode position an incision identical to the egg niche constructed by the beetle was made and a small portion of the bark was raised with a scalpel. A string was then tied to the bark at one end and the other

end was fastened to an analytical balance (Sartorius, accurate to 0.1 mg). The shoot was pulled gently until its bark just started to peel and the force (mg/mm^2) effecting adherence of the peel was estimated. This value was taken to represent the force used by the beetle to split the bark while constructing the egg niche.

To establish whether the beetle responded to the girth of the shoot as an element in choosing an ovipositional site, a sample of 100 shoots taken from each of the four varieties (French Mission, SL34, SL28 and Caturra) were each measured to obtain the girth at the point where the beetle constructed the egg niche. Data obtained for girth was then tested for its correlation with field infestations of D. nigricornis. Regressions were calculated to relate the number of egg niches of field infestation in the four varieties during the long- and short-rains seasons in Kenya to the girth.

Also investigated was the degree to which the length of internal green tissue of tip primordia could facilitate entry by hatching beetle larvae. Different coffee tips were split with a scalpel. The length of the undifferentiated tissue from tips was estimated under a dissecting microscope (x10) and recorded.

Using mated pairs of ovipositing, wild and field bred D. nigricornis beetles (Section 2.2.1), the hours of ovipositions and the intervals (minutes) between

ovipositions occurring the same day (intraday) were determined by clocks (Model: Fauren-Leuba-Jaz S.A) and stopwatches. For each day of observation during the study, the time of termination of oviposition for the day was recorded. The intervals between oviposition days maintained overnight were determined and recorded as interday periods (hours). If no oviposition occurred until death of the female beetles, the elapsed periods between the terminal oviposition and death were not used to elucidate the diel rhythms if any in the production of eggs by different female beetles.

To elucidate whether the beetle possessed a diel cycle during the distribution of its egg niches on the different shoots, the temporal production and distribution of its eggs within and between days was analysed. The number of eggs laid throughout its ovipositional period as recorded:

(i) relative to canopy temperatures;
(ii) position of eggs; and,
(iii) day of oviposition was used.

2.2.4 Effects of coffee canopy factors and seasons on distribution of egg niches

The two sites used in these studies were Rukera and Jacaranda. The varieties grown there were French Mission (FM) and SL34 respectively (section 2.2.1). At each site,

single blocks (1.75 - 2.5 ha) of coffee were demarcated and used for sampling. The plants at Rukera were capped while those at Jacaranda were uncapped. Although the plant spacing (2.74 x 2.74 m) at Rukera and Jacaranda was similar, the actual plant populations were uneven being approximately 3281 and 2323 coffee canopies respectively. These canopies were surveyed seasonally throughout the period, 1982-1984.

The canopy factors that were studied were determined on the above named varieties and on 8 additional clones namely: Caturra, SL28, Purparescens, KS series A, Geisha hybrid, Kit 83, M48 and a single cross E565 x Blue Mountain.

The determination of the effects of the coffee canopy and season, if any, that could influence the fluctuations of D. nigricornis was confined to the egg stage. The egg stage was used as a measure of the adult response to coffee canopy during infestation each season as it was sedentary.

During sampling, egg occurrence was categorised as either single, double, treble, quadruple or other multiples continued upto maxima of the fashion of infestation encountered. Five types of coffee branches namely: Primary, secondary, tertiary, quarternary and sucker shoots were considered.

The length (cm) of each of the internodes 1-12, which was taken to be a probable factor attracting and accommodating the beetle during oviposition (section 2.3.2) was measured. The physical composition of each internode was assessed to ascertain if it favoured construction of egg niches by the beetle. To achieve this each of the internodes was cut and after labelling, they were weighed before being dried in the oven (Model: Memmert) at 150^{o}C for 48 hours. They were then reweighed and percentage dry matter and moisture content calculated.

To determine the preference of the pest for bark thickness of a particular texture per internode, four cross sections of each internode position were prepared, and the thickness (mm) of the bark measured by an eye-piece micrometer. These parameters were related to percentage occurrence of niches constructed by the pest.

The main non plant factor that was assessed for its influence, if any, on population fluctuations of D. nigricornis was season of oviposition. The occurrence of the egg stage was surveyed during the long and short rainy seasons for three consecutive years. During sampling, all canopies were searched and an absolute level of infestation of the plants recorded. Estimating of all egg niches for each season was accomplished within a fortnight. Data was gathered as either infestation or reinfestation out of 3281 and 2323 canopies, according to the census of each canopy throughout the study period.

Data from the survey on distribution of egg niches was analysed for the different seasons without pooling. To adjust the variability in the population of the beetle, possibly due to being located on a single canopy, every infested plant was assigned a value of one and all multiple niches if any expressed as fractions for the plant before being summed to establish incidence.

To determine how the shoots affected egg niche distribution, each niche found on the coffee host, the location of the egg relative to the shoot tip was measured (cm) and recorded. Vertical heights (cm) from the ground to points on different branches where egg niches were constructed were measured. The aim of this was to ascertain if D. nigricornis preferred shoots at some specific height for ovipositing. The total length (cm) from ground level over the portions of the main stem and branches to points where egg niches were located were also measured. The total length found was correlated with vertical heights to demonstrate whether the female beetles synchronised the points at which they oviposited with the larval habitat irrespective of how the coffee was cultured.

The other physical characteristics of the canopy considered in the study were the length of internodes, their dry matter, moisture content and bark thickness. These were assessed to ascertain the extent, if any, to which they determine egg niche location.

Overall incidence of egg niches was established by percentage transformation of the census data. An analysis of variance was performed on the transformed data before applying Duncan's multiple range test (Duncan, 1955)

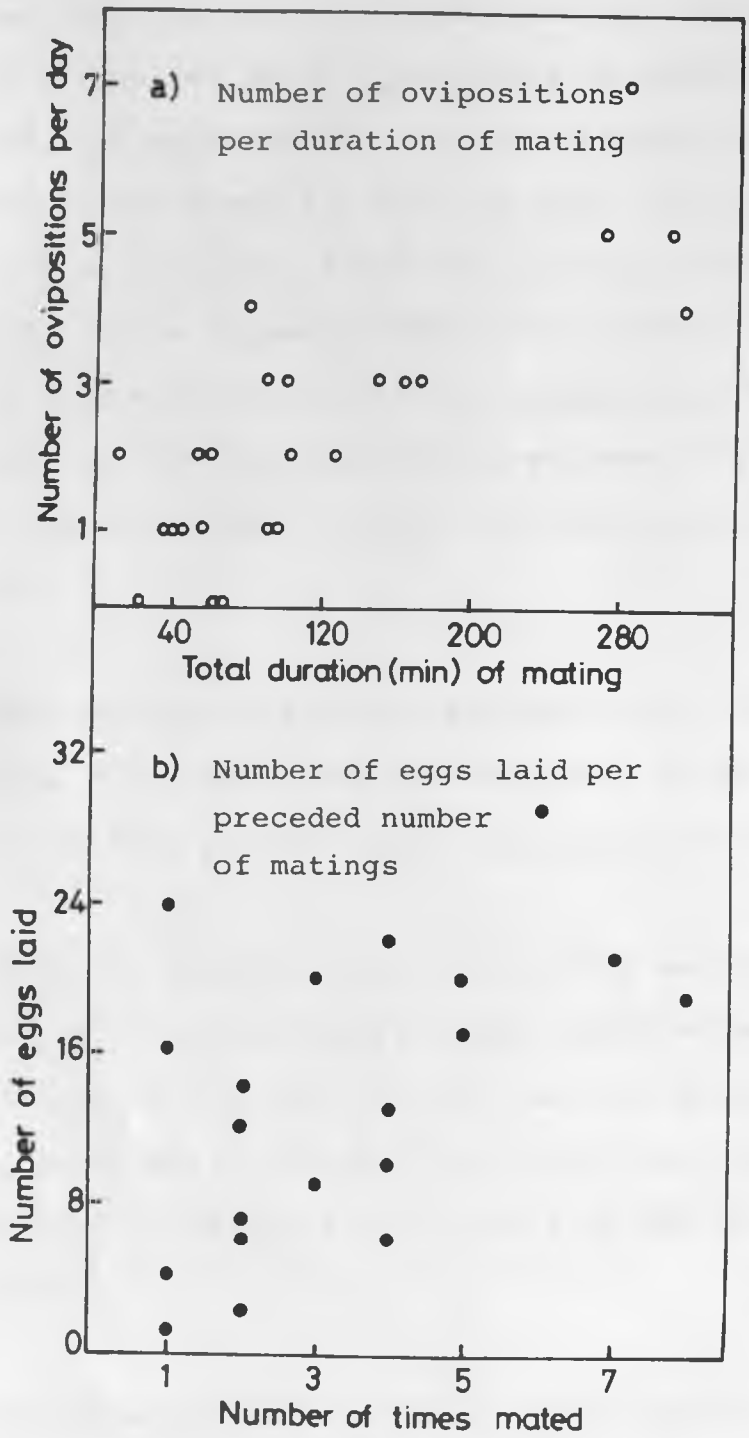
2.3 RESULTS

2.3.1 Mating aspects and birth rates of D. nigricornis

Mating of D. nigricornis influenced its oviposition per day through the durations of mating and the number of times the species mated. The inter-relationship of the above parameters is shown in Figure 3a which indicates that approximately 7 eggs were laid as a result of a duration of 280 minutes of copulation. **Figure 3b** shows that a maximum fecundity of 29 eggs per female often resulted when 6 mating sessions had been completed.

The reproductive potential of the pest seemed to be enhanced when mating was sustained above 36.41 minutes often in repeated matings of more than 1.30 (Fig. 3b). A female beetle hardly laid a single egg unless these thresholds were attained. This showed that while long and repeated copulations enhanced production of many eggs, short and single ones either impeded oviposition or had minimal influence on it.

Fig. 3. Effects of duration (minutes) and number of matings on oviposition by D. nigricornis.



A linear relationship was found between the duration (minutes) and frequency of mating and the ultimate number of eggs oviposited by D. nigricornis on coffee (Table 1). The number of eggs laid per day were either significantly correlated ($r = 0.98$, $P < 0.05$) or very highly correlated ($r = 0.68$ to $r = 0.95$, $P < 0.001$) with the total duration of mating. This suggested that short intervals of mating did not adequately inseminate D. nigricornis females. This was true for all the three pest generations studied. It was also true when the data for these populations were combined.

The oviposition rate per day was highly correlated ($r = 0.85$, $P < 0.001$) with the frequency of mating that accompanied this process in D. nigricornis (Table 1).

While the duration and frequency of matings affected oviposition, the mean duration per mating affected egg productivity ($r = 0.98$, $P < 0.01$) only in first or second brood populations. However, the latter was not as critical in enhancing oviposition in the pest as the former two parameters.

The presented data in Table 1 also indicate that the fecundity of females was significantly correlated ($P = 0.05$) with the mean duration of mating if the beetles belonged to a wild population. It further showed

that the frequency and mean duration of mating was correlated ($P \leq 0.001$) with daily oviposition rate of *D. nigricornis*, irrespective of the generation of populations.

When oviposition ended, all the developmental stages (egg, larval, pupal and adult) in the species of the beetle introduced additional variations as depicted in Table 2. It is shown in Table 2 that the amplitude and average level of the survival and mortality between the stage of the beetles for different broods were variable between the generations. For instance, egg survival was high with low mortality while larval survival was still high (63.4%) despite of incurred mortality of approximately 24.5%. However, it was evident that mortality was highest (36.6%) during the pupal stage and thus leading subsequently to drastic reductions in adult population.

The generation from which the beetles emerged had a pronounced effect on almost all the parameters that were studied (Table 3). Mean lifespan was 1.73 and 5.67 days longer in females than in males of either first or second brood, respectively. The generation span of females was 232.0 days longer for the second brood than for the first brood.

Table 1. Correlation coefficients for two measurements of reproduction (oviposition rate per day, total fecundity) versus three measurements of coitus (no. times mated, mean mating duration, total mating duration) for different populations.

Population generation observed	d.f	Number of times mated	Mean duration per mating	Pooled duration (min) of mating
		Oviposition rate per day		
Second	1	0.98*	0.99*	0.98***
First	6	0.95***	0.97***	0.44NS
Wild	13	0.68***	0.26NS	-0.27NS
Combined	24	0.82***	0.88***	0.03NS
		Fecundity		
Second	1	0.85*	0.96NS	-0.42NS
First	6	0.43NS	0.36NS	-0.42NS
Wild	13	0.40NS	0.45*	0.19NS
Combined	24	0.63***	0.64	-0.03NS

Probabilities: *, P = 0.05, **, P = 0.01, ***, P = 0.001; NS, not significant at any of the probability levels.

Table 2. Life table for three generations of D. nigricornis reared under field conditions on coffee in Kenya.

Generation	Total No.	No. surviving	No. dying	Survival (%)		Mortality (%)	
				Real	Apparent	Real	Apparent
			(i) Egg stage				
Field	143	121	22	84.6	84.6	15.4	15.4
First	133	115	18	86.5	86.5	13.5	13.5
Second	53	49	4	92.5	92.5	7.5	7.5
Total	329	285	44	263.6	263.6	36.4	36.4
Mean	109.7	95	16.7	87.9	87.9	12.1	12.1
			(ii) Larval stage				
Field	121	65	56	45.5	53.7	39.2	46.3
First	115	97	18	72.9	84.3	13.5	15.7
Second	49	38	11	71.7	77.6	20.8	22.4
Total	285	200	85	190.1	215.6	73.5	84.4
Mean	95	66.7	28.3	63.4	71.9	24.5	28.1
			(iii) Pupal Stage				
Field	65	38	27	26.8	58.5	18.9	41.5
First	97	54	43	40.6	55.7	32.3	44.3
Second	38	7	31	13.2	18.4	58.5	81.6
Total	200	99	101	80.6	132.6	109.7	167.4
Mean	66.7	33.0	33.6	26.9	44.2	36.6	55.8
			(iv) Adult stage				
Field	38	22	16	26.8	58.9	11.2	42.1
First	54	38	16	40.6	70.4	12.0	29.6
Second	7	3	4	13.2	42.9	5.7	57.1
Total	99	63	36	80.6	172.2	28.9	128.8
Mean	33.0	21.0	12.0	26.9	57.4	9.6	42.9

The differences between the first and second brood generation were more apparent when the intrinsic rate of increase ($Log_e\ l_x m_x$) was computed on daily basis as this factor expressed changes in both lifespan and in reproduction. The rate of increase was 21.0% more for first brood compared to second (Table 3). It is shown in Table 3 that the reproductive period was almost the same for the two generations, even though the pre- and post- reproductive periods were marginally different.

When the number of eggs laid per female as simulated by mating was added to the number of residual oocytes that were found by dissecting the females at the end of oviposition, the data obtained for potential fecundity was as presented in Table 4. Data for the actual fecundity indicated that female D. nigricornis laid individually no eggs and either deposited single or several to many eggs upto a maximum of 21-29 eggs. The number of eggs laid represented a fertility rate of approximately 32.6, 61.5 and 51.5% for wild, first and second brood beetles, respectively. This showed that the more eggs laid above this percentage of the total fecundity for the species, the fewer the oocytes were left over. This was apparent even if most oocytes were chorionated and matured and were ready to be laid (Table 4).

Table 3. Statistics on adult survival days and birth rates of two brood generations of D. nigricornis reared under field conditions on coffee in Kenya.

Statistics	Definition/ Formula	Application in these studies	Females		Males	
			1st	2nd	1st	2nd
Pre-reproductive span	Days preceding mating/oviposition	Recorded	1.38	1.67	2.0	3.33
Reproductive span	Days of mating/ Oviposition	Recorded	5.88	5.0	3.22	4.0
Post reproductive span	Days after mating/ oviposition	Recorded	6.38	9.69	5.0	4.0
Fecundity	Average number of eggs laid per female during lifespan	Recorded	21.47	29.50	-	-
GRR, gross reproductive rate	Number of female births produced by a female during her maximum lifespan $GRR = \{ \; M_x$	Recorded and calculated	16.56	17.56	-	-
rm, intrinsic rate	Instantaneous rate of progeny produced per generation per beetle $\{^{\infty} Log_e \; lxmx = 1$ $x = 0$	Calculated by iteration	0.0001243 (1.243^{-4})	0.0000977 (9.77^{-5})	-	-
λ, finite rate	Number of times the beetle population multiplies itself in a generation, $= e^{rm}$	Calculated	1.0001	1.0002	-	-
R_o, Net reproductive rate	Average number of female offspring produced per female over entire lifespan $R_o = \{ \; lxmx$	Calculated	18.49	28.65	-	-
T, generation time	Average days from egg to egg through development	Recorded	359.93	591.86	357.0	593.33
Lifespan	Average days alive	Recorded	11.4	14.17	9.67	8.50

Table 4. Fecundity and fertility of D. nigricornis eggs for wild, first and second brood females.

Parameter of oviposition	Wild		First		Second	
	Range	Mean	Range	Mean	Range	Mean
Number of eggs laid	0-24	6·70	6-21	16·60	2-29	17·60
Number of chorionated oocytes	0-13	7.90	7-14	9·30	10-13	11.30
Number of unchorionated oocytes	0-15	1·70	0-4	0·60	0	0·0
Potential fecundity	7-32	16·30	20-33	26·50	15-40	29·0
Fertility (Number of eggs laid as percentage of potential fecundity	0.0-75.0	32·60	30.0-73.10	61·60	13.30-72.50	51·50
n		13		8		3

n represents the number of female beetles used to determine fecundity and fertility.

2.3.2 Oviposition behaviour and its relation to egg niche location and diel rythms in the yellow headed borer, Dirphya nigricornis

The female of D. nigricornis preceded the construction of an egg niche by walking back and forth on the tip for 3.0 ± 0.5 min (all values are ±S.E.). During this activity the mandibles were held perpendicular and parallel to the long axis of the searched shoot. In 99% of the cases this behaviour was followed by construction of an egg niche. Once a site had been chosen, the searching female paused and gnawed an egg niche in the tip. This consisted of making successive bites on two parallel lengths along the internode and one width perpendicular and adjacent to it to 'open' the bark. This lasted 1.0 ± 0.2 min. After forming the egg niche the female deposited an egg beneath the bark flap formed by the U-shaped incision. This was accompanied by curving of the ovipositor proximal to the peeled bark and by aligning the body and ovipositor to coincide with the open end of the egg niche. It inserted the egg lengthwise in 5.0 ± 0.1 min and then sealed the sides to form a slit; this latter activity took 2.0 ± 0.3 min.

The whole process of locating an ovipositional site, constructing an egg niche, depositing an egg and sealing the sides of the egg niche lasted 11.3 ± 1.8 min. D. nigricornis laid its eggs in a non random fashion as

presented in Tables 5a and 5b. Data showed that the beetles laid mainly on distal internodes 1-12 as shown in Tables (5a and 5b). This incidence occurred irrespective of the type of coffee shoots and season (long- or short-rains) of infestation. Throughout the study period, the degree of shoot preference was tertiary > primary ≥ secondary > sucker > quarternary (Tables 5a and 5b). Incidence was predominant on immature internodes, as compared with mature ones beyond internode 13.

D. nigricornis gnawed egg niches which were 5.0 ± 0.4 mm long and 3.7 ± 0.3 mm wide. When the number of egg niches was regressed against either size of the egg niche, the abundance of the egg niches was negatively correlated to their widths ($r = 0.85$), which meant that size was not a limiting factor in the initiation of infestation by this pest.

Egg niches were very abundant in green internodes, abundant in brown and rare in soft white ones (Table 6). Thus, the pest located a decreasing number of egg niches, as the distance from the distal point of each shoot category increased.

Table 5a. Absolute number of egg niches of D. nigricornis on different coffee shoots relative to internode position, during the long-rains season (March to May) in Kenya.

Internode position	Shoot type				
	Primary	Secondary	Tertiary	Quarternary	Sucker
	(Number of eggs)				
1	11	2	11	0	1
2	38	17	36	0	8
3	62	32	78	2	13
4	49	33	83	2	3
5	45	20	86	2	2
6	38	22	73	1	1
7	33	34	63	2	1
8	38	19	31	0	0
9	25	15	27	1	0
10	18	17	23	0	0
11	20	11	9	0	0
12	15	14	10	1	0
13	9	4	8	0	0
14	4	3	5	0	0
15	3	3	2	0	0
16	2	3	2	0	0
17	1	4	3	0	0
18	2	0	2	0	0
19	2	0	1	0	0
20	2	0	1	0	0
21	0	0	0	0	0
Mean	19.85	11.00	26.38	0.52	1.38
±S.E	4.15	2.74	6.72	0.17	0.70

Internode positions 1-6 were green, 7-10 were brown, 11-12 were soft white and 13-21 were of other colour (Data were pooled for 3 years, 1982-1984).

Table 5b. Absolute number of egg niches of D. nigricornis on different coffee shoots relative to internode position, during the short-rains season (October and November) in Kenya.

Internode position	Shoot type				
	Primary	Secondary	Tertiary	Quarternary	Sucker
	(Number of eggs)				
1	8	14	6	6	1
2	13	11	14	2	5
3	18	22	28	4	11
4	18	13	38	3	6
5	18	20	39	3	3
6	6	24	41	3	1
7	20	12	22	0	0
8	15	6	17	0	0
9	9	9	11	0	0
10	7	5	7	0	0
11	4	5	3	0	0
12	5	5	3	0	0
13	5	1	7	0	0
14	4	3	4	0	0
15	0	1	1	0	0
16	1	3	1	0	0
17	0	3	1	0	0
18	0	0	3	0	0
19	1	1	2	0	0
20	2	0	2	0	0
21	0	0	0	0	0
Mean	7.33	7.52	11.90	1.00	1.28
±S.E.	1.50	2.67	2.97	0.38	0.37

Internode positions 1-6 were green, 7-10 were brown, 11-12 were soft white and 13-21 were of other colours. (Data were pooled for 3 years, 1982-1984).

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Table 6. Effects of internode colour and distance from primordia on the number of egg niches of D. nigricornis in different types of coffee shoots.

Colour	Internode position	Distance from primordia (cm)	Egg niches per coffee shoot					
			Shoot type					
			Primary	Tertiary	Secondary	Quarternary	Sucker	Total
			Long-rains season					
Green	1-6	0.1-7.0	243	367	126	7	28	771
Brown	7-10	7.1-9.0	114	144	85	3	1	347
Soft white	11-12	9.1-11.0	35	19	25	0	0	79
			Short-rains season					
Green	1-6	0.1-7.0	83	166	82	21	27	379
Brown	7-10	7.1-9.0	35	57	32	0	0	124
Soft white	11-12	9.1-11.0	10	6	10	0	0	26

To raise the flap of the bark beneath which the egg was laid, the pest would require significantly (P = 0.01) different forces (Table 7). The mean force estimated to represent this activity was 13.30 ± 0.52, 12.58 ± 0.51, 12.16 ± 0.57, 11.83 ± 0.38 and 11.80 ± 0.33 mg in secondary, quarternary, tertiary, sucker and primary shoots, respectively. The bark found beyond the 12th internode either snapped or was difficult to peel, thus deterring any egg niche construction.

Mean girth at internodes where egg niches were located was 0.90 ± 0.11 (range 0.3-1.5) cm (Table 8). This parameter was not significantly correlated with the abundance of D. nigricornis egg niches. Thus, it did not explain a significant amount of the variance in the abundance and distribution in coffee plantations. This was explained by the length of green and undifferentiated to just differentiated primordial tissue in a tip (Table 9). This tissue extended to 9.0, 7.0, 4.2, 3.6 and 3.3 cm in sucker, primary, secondary, tertiary and quarternary tips, respectively. These portions of the tips had 98.2, 94.0, 68.1, 62.2 and 93.3% of the total egg niches deposited on each shoot category, respectively.

During the oviposition, it was observed that the eggs were deposited on the plants from 08.10 to 18.50 hours throughout the reproductive period of D. nigricornis (Table 10). The temporal production and distribution

Table 7. Calculations of F ratios from the determined force (mg/mm^2) required to peel off the bark on internodes of coffee plants to prepare a niche.

Internode position	Force measurements determined per shoot type				
	Primary	Secondary	Tertiary	Quarternary	Sucker
			(mg/mm)		
1	9	9	8	9	9
2	11	11	9	10	11
3	13	13	12	11	12
4	11	13	11	12	11
5	12	14	12	12	11
6	12	13	12	13	12
7	12	13	13	13	12
8	12	14	13	13	12
9	12	15	14	14	12
10	12	15	14	14	12
11	13	15	14	14	14
12	13	15	14	15	14
Mean	11.80	13.30	12.16	12.58	11.83
±S.E.	0.33	0.52	0.57	0.51	0.28

Analysis of variance of the forces

Source of variation	d.f.	Sum of squares	Mean squares	F ratio
Total	59	167.65	-	10.21*
Shoot type	4	19.07	4.76	10.21*
Internode position	11	128.05	11.64	24.92*
Error	44	20.53	0.46	

*Significance of forces at 0.01% probability.

Table 8. Relationship between girth at site of oviposition by D. nigricornis and percent incidence of egg niches on four coffee varieties.

Girth (cm at site of oviposition	Percent of egg niches per variety			
	French Mission	SL34	SL28	Caturra
0.3	10.0	0.0	0.0	1.6
0.4	20.0	0.0	0.0	0.0
0.5	0.0	0.0	0.0	4.9
0.6	10.0	0.0	9.1	4.9
0.7	20.0	3.8	18.2	13.1
0.8	30.0	15.4	9.1	23.0
0.9	10.0	23.1	27.3	21.3
1.0	0.0	23.1	27.3	18.0
1.1	0.0	30.8	0.0	8.2
1.2	0.0	0.0	9.1	1.6
1.3	0.0	0.0	0.0	0.0
1.4	0.0	0.0	0.0	1.6
1.5	0.0	3.8	0.0	0.0
Comparative correlation coefficients (r) to incidence in four varieties	0.24 NS	-0.02 NS	0.07 NS	-0.05 NS

NS = Not significant. Mean girth (cm) at site of oviposition ± S.e = 0.9 ± 0.11 .

Table 9. Primordia in tip internodes of coffee shoots which carried large numbers of *D. nigricornis* egg niches.

Type of shoot	Length (cm) of green primordia from the tip of the shoot (mean ± S.E)	Number of egg niches
Primary	7.0 ± 1.0	520 (553)
Tertiary	3.6 ± 0.2	533 (804)
Secondary	4.2 ± 0.4	280 (411)
Quarternary	3.3 ± 0.2	28 (30)
Sucker	9.0 ± 1.0	55 (56)

Values in parentheses represent the total number of egg niches per shoot category.

of eggs in the period indicated two hourly rhythms. The initial rhythm started at 0900 hours with low oviposition (Table 10). It rose sequentially to maximum level after 1400 hours. The next rhythm started at 1500 hours and peaked at 1740 hours. This synchronized with temperature changes from 18.0°C to 30.0°C (Table 10), suggesting that the endogenous rhythms work in combination with exogenous conditions of climate during oviposition.

Due to these rhythms, the eggs were laid at a maximum of seven varying intervals each day (Table 11a). Table 11a also shows that the intervals between two consecutive ovipositions were initially either short (31.0-89.33 minutes) or long (111.0-172.0 minutes). The next oviposition intervals were still either short (40.5-110.0 minutes), long (143.0-186.0 minutes) or very long ones beyond 260.5 minutes (Table 11a). The third oviposition intervals were mostly short or long to very long. These observations suggested that probably the ovaries of the pest were able to release eggs at harmonised intervals on different days of oviposition.

While ovipositing, the ageing of female beetles seemed to have no effect on intervals between eggs. Thus, the periods that elapsed between ovipositions appeared to be uniform for a series of ovipositions for several individual insects of any similar age (Table 11b). This suggested a probable harmony in egg production by the species. Thus, as one ovary released a mature egg

Table 10. Oviposition rhythms of D. nigricornis relative to hours of day and coffee canopy temperatures.

Time of oviposition (hrs)	Number of ovipositions	Number of reproductive days involved	Ranges of canopy temperatures at three periods (hrs)		
			900	1200	1500
810-831	7	5	18.0-20.0°C		
944-955	3	2			
1005-1040	8	4			
1100-1150	10	5			
1200-1240	10	4		25.5-27.5°C	
1400-1442	26	7			
1500-1540	9	4			27.5-30.0°C
16.00-17.00	8	3			
1800-1850	2	2			

Table 11a. Frequency of oviposition intervals (minutes) for the eggs produced by D. nigricornis females within the day of oviposition for wild (W), first (F) and second (S) brood populations.

Ranking of intervals (Min)	First			Second			Third			Fourth			Fifth			Sixth			Seventh		
	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S
6.0-7.0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
16.0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
22.0-23.0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0
31.0-39.0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	0	0	0	1	0	0	0
40.5-48.75	3	3	0	1	1	1	0	1	0	1	0	0	0	0	2	0	0	0	0	0	0
50.0-57.33	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
60.5-69.0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
73.2-79.0	0	1	1	0	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0
83.0-89.33	0	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90.5-95.0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
101.67-110.0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0
111.0-116.0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
125.17	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130.0-130.5	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
143.0-145.67	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
157.75-158.8	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
165.0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
172.0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
186.0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
196.0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
205.0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
220.0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
260.5-26.0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
293.0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

First to seventh represent position of interval in the sequence of ovipositing D. nigricornis beetles. Zeros represent no occurrence of interval in the position of oviposition in the generation.

the other one did not. As soon as the ovary not previously engaged in oviposition initiated the release of its oocyte, the reverse occurred to the twin ovary within the day of oviposition.

The ability by the beetle to lay after a constant pause of several hours between days was observed (Table 12). The eggs were released after 22.83 ± 1.19 to 31.17 ± 7.97 hours throughout the period of experimentation (Table 12). However, variability in the intervals existed between the consecutive days of oviposition when intervals often as wide as 48.03 or even 63.15 hours elapsed before any egg was laid. Thus, the beetles started ovipositing about the same time each reproductive day presumably linked to a diel cycle of ovipositing activity (Table 12).

The evidence for the ability of the species to exhibit a diel cycle of ovipositing activity seemed to reside in the logical number of ovaries and their oocyte cycles. The beetle was found through dissections over time to possess two ovaries each of which contained several to numerous oocytes (Fig. 4).

Table 11b. Effects of reproductive days of *D. nigricornis* females on intervals (minutes) between consecutive ovipositions for wild (W), first (F) and second (S) brood generations.

Ranking of intervals (Min)	Day 1			Day 2			Day 3			Day 4			Day 5			Day 6			Day 7			Day 8		
	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S	W	F	S
22.67-29.83	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34.43-35.67	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
48.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
54.0-58.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
61.38-69.0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0
73.0-77.25	0	0	0	1	1	1	0	2	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
81.67-89.0	1	0	0	2	1	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
93.0-97.67	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
101.50-106.0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1
114.75-119.50	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0
134.25-136.33	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
142.5	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
150.75-157.0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
168.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
182.0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0
190.0-199.0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0
238.0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0

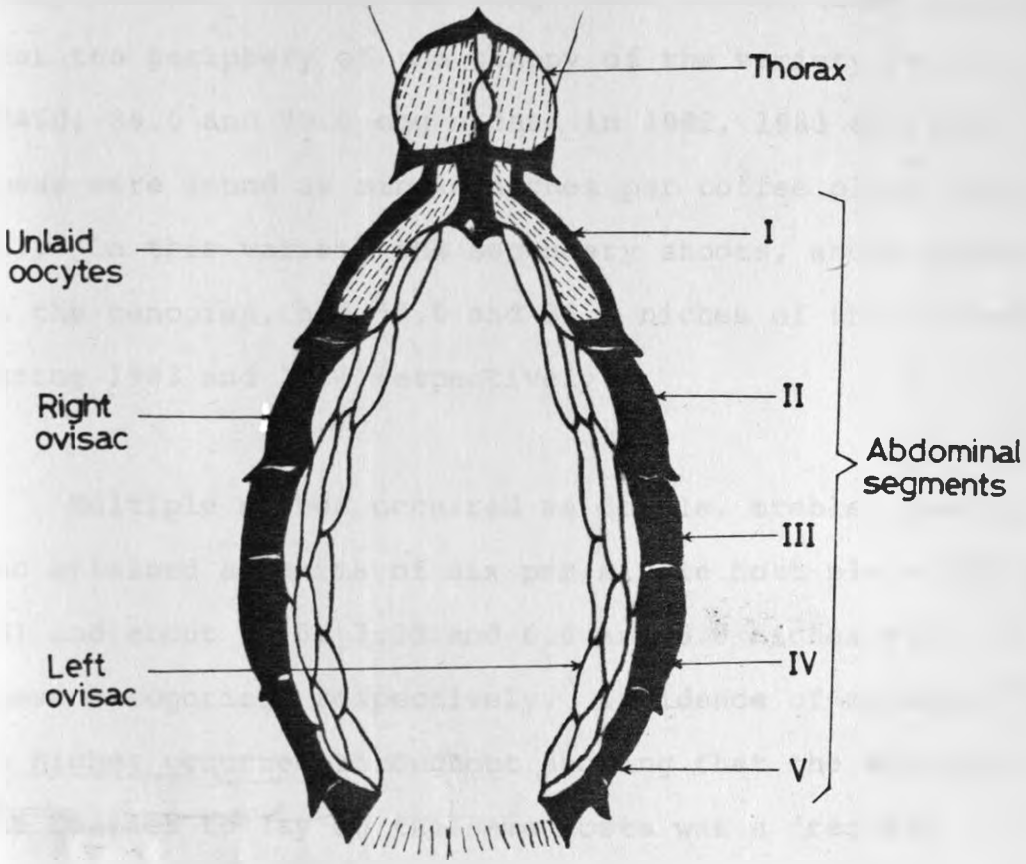
Zeros represent no occurrence of the interval during the day in the generation.

Table 12. The intervals (hours) between terminal and initiation of ovipositions between days for wild, first and second broods of *D. nigricornis* females.

Female	Interval (hours) during days (2-9) of oviposition subsequent to day one.							
(a)	Wild beetles				(hrs)			
	2	3	4	5	6	7	8	9
1	41.17	18.67	0.0	0.0	63.15	0.0	0.0	0.0
2	39.52	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	14.42	32.83	0.0	48.03	23.38	48.0	0.0	0.0
4	18.58	0.0	49.28	19.08	14.50	41.50	29.50	0.0
5	23.25	20.50	0.0	35.0	0.0	0.0	0.0	0.0
6	19.20	25.87	21.92	21.0	23.08	16.17	0.0	0.0
7	21.83	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	20.47	20.54	0.0	0.0	0.0	0.0	0.0	0.0
9	19.92	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	19.02	22.67	16.75	0.0	0.0	0.0	0.0	0.0
11	23.14	15.33	19.08	15.33	18.0	19.0	0.0	0.0
(b)	First brood beetles				(hrs)			
1	20.04	22.26	18.26	21.35	19.22	25.28	0.0	0.0
2	20.04	22.33	18.26	12.35	19.22	23.23	0.0	0.0
3	22.42	15.17	17.43	28.24	0.0	0.0	0.0	0.0
4	21.14	21.28	17.44	21.4	15.37	0.0	0.0	0.0
5	18.54	19.0	0.0	0.0	0.0	0.0	0.0	0.0
6	16.46	20.31	17.15	20.12	0.0	0.0	0.0	0.0
7	0.0	17.14	22.01	15.18	19.44	17.19	0.0	0.0
8	15.29	15.30	15.38	22.03	16.35	22.35	0.0	0.0
(c)	Second brood beetles				(hrs)			
1	22.46	17.49	20.04	16.57	37.31	14.38	22.05	17.22
2	13.22	21.14	14.10	0.0	0.0	0.0	0.0	0.0
3	24.40	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Zeros represent either death of the ovipositing female or lack of any oviposition on the day.

Fig. 4. Diagrammatic representation of the arrangement of oocytes in the two ovisacs of D. nigricornis x 10 (ventral view).



Not drawn by tube, oocytes / ovisacs and female genitalia greatly enlarged.

2.3.3 Effects of coffee canopy factors and seasons on distribution of egg niches.

The egg stage was not distributed evenly in the different branches of the coffee canopy throughout the study period. During the long rains the tertiary branches near the periphery of the canopy of the variety FM had 174.0, 89.0 and 79.6 egg niches in 1982, 1983 and 1984. These were found as single niches per coffee plant (Table 13). On this variety the secondary shoots, about midway in the canopies, had 55.0 and 35.0 niches of this category during 1983 and 1984 respectively.

Multiple niches occurred as double, treble, quadruple, and attained a maxima of six per single host plant (Table 13) and about 32.5, 7.33 and 6.0 and 3.0 niches were in these categories, respectively. Incidence of multiplicity in niches occurred throughout showing that the ability by the beetles to lay on the same hosts was a frequent activity. Although this was the case, invariably occurrence of niches on quarternary, primary and sucker shoots rarely exceeded 17.0, 1.0 or 0.33 single, double or treble niches, respectively. This showed that the pest did not prefer the quarternary branches on the periphery of the canopy and the sucker branches closest to the main stems.

When the situation in the variety SL34 was considered with respect to the infestation in the long rains, it was shown (Table 13) that the primary shoots possessed 54.0, 62.0 and 163.0 egg niches in 1982, 1983 and 1984, respectively. In this variety, the highest number of multiple niches (26.0) belonged to the double niche category. A single canopy sustained up to six niches on the variety SL34 in 1984 during which the sucker shoots had 5.0 and 0.33 single and treble niches.

During the short rains, tertiary shoots of the variety FM carried 176.0, 137.0 and 41.0 egg niches of the pest in the years 1982, 1983 and 1984,respectively as shown in Table 14. In this season, the secondary and sucker shoots of coffee were attacked to a higher level than quarternary and primary shoots and that upto five multiple attacks per single host plant were recorded. The data in Table 14 also showed that both primary and secondary shoots of coffee variety SL34 were about equally infested by D. nigricornis. During the same period neither single nor multiple niches were associated with quarternary and sucker shoots.

Data (Tables 13 and 14) gathered during this study indicated that while egg niches occurred singly per shoot they did not do so exclusively. Often the pest constructed more than one niche on similar shoots of host plants during the same season.

Table 13. Comparative incidence of egg niches in two varieties of coffee infested by D. nigricornis in three long rainy seasons, 1982-1984.

Category of egg niche	Primary shoots		Secondary shoots		Tertiary shoots		Quarternary shoots		Sucker shoots	
	FM	SL34	FM	SL34	FM	SL34	FM	SL34	FM	SL34
i) Long rains 1982 (total number of niches)										
Single egg niche	17.0	54.0	1.80	6.0	174.0	0.0	7.0	10.0	0.0	0.0
Double egg niche	0.0	8.5	3.0	0.5	29.0	1.0	0.5	0.0	0.0	0.0
Treble egg niche	0.33		0.67	0.0	6.0	0.0	0.33	0.0	0.0	0.0
Quadruple egg niche	0.0		4.5	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Six egg niche	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0
ii) Long rains 1983										
Single egg niche	14.0	62.0	55.0	33.0	89.0	38.0	1.0	1.0	0.0	0.0
Double egg niche	0.5	7.0	7.34	1.50	12.16	1.0	0.0	0.5	0.0	0.0
Treble egg niche	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
iii) Long rains 1984										
Single egg niche	1.0	163.0	35.0	51.0	79.0	7.0	7.0	0.0	10.0	5.0
Double egg niche	0.5	26.0	3.0	10.17	6.0	0.5	1.5	0.0	0.0	0.0
Treble egg niche	0.0	6.67	0.67	0.67	0.33	0.67	0.0	0.0	0.0	0.33
Quadruple egg niche	0.0	1.25	0.0	0.75	1.0	0.0	0.0	0.0	0.0	0.0
Six egg niche	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Niches counted on the same host plant during any one season formed a particular niche category where more than one egg niche occurred, then fractions were introduced by classifying each egg niche per type of shoot infested during the season per host plant before summation.

FM denotes the variety French Mission.

Table 14. Comparative incidence of egg niches in two varieties of coffee infested by *D. nigricornis* in three short rainy seasons, 1982 - 1984.

Category of egg niche	Primary shoots		Secondary shoots		Tertiary shoots		Quarternary shoots		Sucker shoots	
	FM	SL34	FM	SL34	FM	SL34	FM	SL34	FM	SL34
i) Short rains 1982 (total number of niches)										
Single egg niche	5.0	27.0	22.0	55.0	176.0	0.0	2.0	0.0	7.0	0.0
Double egg niche	0.0	2.5	2.0	0.5	26.0	0.0	0.0	0.0	1.0	0.0
Treble egg niche	0.0	0.0	0.0	0.0	2.67	0.0	0.0	0.0	0.67	0.0
Quadruple egg niche	0.0	0.0	0.0	0.0	1.0	0.0	0.25	0.0	0.0	0.0
ii) Short rains 1983										
Single egg niche	7.0	57.0	69.0	15.0	137.0	1.0	15.0	0.0	20.0	1.0
Double egg niche	1.5	2.5	12.17	3.0	20.5	0.0	3.0	0.0	3.0	0.0
Treble egg niche	0.0	0.0	1.67	4.5	2.01	0.0	0.33	0.0	0.0	0.0
Quadruple egg niche	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Five egg niche	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
iii) Short rains 1984										
Single egg niche	5.0	12.0	9.0	41.0	1.0	1.0	0.0	0.0	2.0	0.0
Double egg niche	0.0	2.0	2.5	0.50	7.0	0.0	0.0	0.0	0.0	0.0
Treble egg niche	0.0	0.0	0.0	0.0	0.33	0.0	0.0	0.0	0.0	0.0

Niches counted on the same host plant during any one season formed a particular niche category. Where more than one egg niche occurred, then the fractions were introduced by classifying each egg niche per type of shoot infested during the season per host plant before summation.

FM denotes the variety French Mission.

The pest population would probably fluctuate if the pest failed to concentrate most of the eggs in shoots which were neither tertiary nor primary ones which appeared to be most preferred.

The portion of the canopy that carried the highest percentage of egg niches was confined to the tips of all categories of shoots. This was the young and tender portion of the canopy shoots usually between 0.5 to 30 cm off the tips of the shoots as shown in Table 15.

Data showing that egg niches were distributed unevenly at different heights of the canopy is presented in Appendix 1. This showed that the zones of the canopies found approximately between 142 and 215 cm above ground level were the most preferred (Appendix 1). The shoots in the top and bottom zones of the canopy attracted little or no infestation. Heights of capped and uncapped canopies of coffee above ground level that were liable to infestation by the beetle were significantly correlated with the accumulated inter canopy branch lengths ($r = 0.99$, $P < 0.001$) (Appendix 2). Capping coffee plants put approximately 186.6 cm at risk while leaving them uncapped placed 215 cm at risk. This finding demonstrated that D. nigricornis had an inherent ability to locate egg niches on the plants that provided adequate supply of the wood to support the larvae.

Table 15. The location (cm) of D. nigricornis egg niches on different shoots of coffee relative to the tips from the varieties, French Mission (FM) and SL34 during 1982.

(i) Long rains

Category of shoots	French Mission				SL34			
	Range (cm)	Mean ± S.E.	Egg niches	Percentage	Range (cm)	Mean ± S.E.	Egg niches	Percentage
Tertiary	0.5-24.0	11.7±0.4	255	82.8	3.5-25.0	9.8±0.3	56	81.2
Secondary	1.0-24.0	9.3±0.7	46	14.9	7.0-14.0	11.1±1.4	5	7.2
Quarternary	9.0-24.0	9.0±1.5	3	1.0	6.0-14.0	11.0±1.5	6	8.7
Primary	7.5-10.0	10.8±1.6	2	0.6	6.5-12.0	7.5±0.5	2	2.9
Sucker	7.5-15.0	11.0±0.7	2	0.6	0	0		0
Total			308				69	

(ii) Short rains

Tertiary	1.5-30.0	8.7±0.3	227	83.2	0.0-20.0	6.0±1.5	2	2.6
Secondary	2.0-15.0	7.5±0.3	25	9.2	4.0-6.0	6.0±2.2	6	7.7
Quarternary	1.5-10.0	4.2±1.7	5	1.8	0	0	0	0
Primary	2.0-8.0	5.5±0.8	7	2.6	1.0-14.0	4.5±0.3	70	89.7
Sucker	2.0-12.5	7.1±1.1	9	3.3	0	0		0
Total			273				78	

The data on quantitative properties of coffee tips are presented in Appendix 3. Internode length, percentage dry matter, moisture content and bark thickness differed significantly ($P < 0.001$) between varieties and internode positions. Therefore each internode position was a different entity from the other for both varieties French Mission and SL34 considered.

By analysing the tertiary shoots, which sustained the highest infestation as a model it was indicated that the dry matter, moisture content, bark thickness and internode lengths of shoots varied progressively from the tip-most internode and internode 12 (Appendix 4). The variations in these properties synchronised with 11.8, 79.2 and 9.0% of the egg niches at 1st, 6th and 12th internodes of tertiary shoots, respectively.

The level of canopy infestation by D. nigricornis was as presented in Table 16. It was low during the long rains and hardly exceeded 5.84 and 8.21% in the varieties FM and SL34, respectively. Even during the short rains, coffee infestation was still low. During these seasons approximately 6.35 and 1.56% of the coffee plants in the varieties FM and SL34 were attacked, respectively. The data (Table 16) indicated that infestation did not fluctuate annually. Only minimal significant difference ($P < 0.05$) was detected between varieties, while attack for the seasons was uniform.

Table 16. Comparative levels of coffee canopy infestation by D. nigricornis determined for two coffee varieties in different seasons, 1982-1984.

Period	Number of canopies infested		Percentage infestation	
	(Long rains)			
	French Mission	SL34	French Mission	SL34
	(No)		(%)	
1982	242	82	7.38	3.53
1983	170	126	5.18	5.42
1984	163	364	4.74	15.67
Totals	575	572	17.53	14.62
Means	191.67	190.67	5.84ab	8.21b
	(Short rains)			
	(No)		(%)	
1982	243	0.0	7.41	0.0
1983	296	85	9.05	3.66
1984	76	24	2.32	1.03
Totals	615	109	18.76	4.69
Means	20.5	36.33	6.25b	2.56a
S.E.			1.37	
L.S.D. (P = 0.05)			4.54	

Mean values across and down % columns followed by same letter represent similar levels of infestation per two varieties according to Duncan's multiple range test.

Table 17. Canopy reinfestation by D. nigricornis determined for two coffee varieties in different seasons 1982-1984.

Period	Number of canopies reinfested		Percentage reinfestation	
	French Mission	SL34	French Mission	SL34
	(No)	(Long rains)	(%)	
1983	22	0	12.94	0.0
1984	16	11	9.82	3.02
Totals	38	11	22.76	3.02
Means	19.0	5.5	11.38ab	1.52a
	(No)	(Short rains)	(%)	
1982	14	0	5.76	0.0
1983	31	3	10.48	3.53
1984	2	2	2.63	2.35
Totals	47	5.0	18.87	5.88
Means	15.67	2.50	6.29ab	2.94a
S.E.	1.09			
L.S.D. (P = 0.01)	5.75			

Mean values across and down % columns followed by the same letters represent similar levels of reinfestation per two varieties according to Duncan's range test.

Similarly the percentage level of reinfestation of the plant canopies in the two varieties was low throughout the study period, although the number of plants at risk every season was significantly higher ($P<0.001$) for the variety FM than SL (Table 17). It was therefore concluded from these observations that the infestation and reinfestation phenomena demonstrated lack of involvement of any deterrent stimuli that rendered already attacked canopies unacceptable for subsequent attack.

2.4 DISCUSSION

The mating habits of D. nigricornis beetles on coffee plants which regulate oviposition were attainment of critical durations of time during coitus through a multiplicity of copulations. The frequency and duration of mating fluctuated considerably with different generations. Perhaps this type of mating phenomenon is widespread in Cerambycids. The red oak beetle Enaphalodes rufulus Haldemann, has an analogous ability of repeated copulations (Donley, 1978). Oviposition resulted only after females had mated for long durations and was attained after several subsequent copulations. As a result, the average daily oviposition rate was low and was not prolonged.

Although this may be the situation for many other insect species, some comparative thresholds on mating in insects appear to suggest that multiple mating

activities tend to produce a superflous effect on egg production. In some insects, many matings may impede the production of eggs as well as their viability thus affecting population increase (Fisher, 1958; Hamilton, 1967; Petit and Ehrmann, 1969; Richard, 1974; Wiley, 1974; Oh, 1979). However, all insects with sexual reproduction do engage initially in invariable sessions of mating most of which not only preclude oviposition but also complement other factors such as the weather and the genetics of the species which equally can influence ovipositional activities (Hunter Jones, 1960; Schlager, 1960; Clark and Sheppard, 1962; Parker, 1970a, b, 1974; Trivers, 1972).

Seemingly, greater variations in reproduction pertained to the birth rates (GRR = $\sum m_x$ and $R_o = l_x m_x$) (Birch, 1948). The calculated values on these parameters were similar for the second brood compared to the first brood. Since both GRR and R_o are measures of the total fecundity, these results can probably explain the capacity for D. nigricornis to compensate and perpetuate its progeny for the long periods of development the broods undergo in the field. Differences in birth rate could also be explained by variations in temperature during the two generations which invariably varied.

The oviposition sequence, as described here consisted of a site-seeking phase, in which vision and

feeling are probably used, and finally the oviposition event. The searching phase is decisive as to the choice of the most favourable location for the eggs which a female will ultimately lay. It is possible that during the walking and searching of the tip internodes, the beetles felt the shoot in such a way that, as soon as the tips were large enough, the search ceased. As soon as the female paused at the selected sites, the peeling of the flap of bark was initiated and accomplished quickly, within one minute. Delcomyn (1985) has elucidated the tact of walking by insects in order to make decisions. The current observations tended to support the view that ovipositional site decisions by D. nigricornis involved walking to determine the shoot girths using the tarsi.

Judging from the long time of association the pest has had with coffee it can be argued that the pest has developed mechanisms by which it defined and infested coffee tips. One of these is probably the colour of the tip internodes. Green internodes were the most heavily infested in each season as compared with those of any other colour irrespective of shoot type. This observation is in good agreement with that of other authors who showed that many phytophagous insects, including beetles, were invariably attracted to their hosts by the latter's colour (Brown, 1975; Mitchell, 1975; Mathews, 1976; Maxwell and Jennings, 1980; Khaemba, 1980; MacDonald and

McInnis, 1985).

Another possible reason why the pest attacked the tip internodes is that they were easy to cut and the bark is raised with the mandibles. This contention was confirmed in experiments which showed that the bark at the distal end (positions 1 and 2) of the tip internodes required significantly ($P = 0.05$) less force to peel than the bark on internodes at positions 5 or 6 and beyond (8-11 vs 13-15 mg/mm^2), respectively. Only few egg niches were located between internodes 13 and 21, probably because the bark there was comparatively difficult to peel and snapped, thus requiring not only excessive force but extreme care, a combination that could not be attained by the biting activity, which was limited to 1 min. However, the features which make it easy for boring pests to attack host plants depend on many plant properties and are common in many plant species (Nord, 1968; Grimble et al. 1969). Some of these features can be explained by the hypothesis of minimal force, peelability and probably bark thickness (Lashomb nad Nebeker, 1979; Maxwell and Jennings, 1980).

The other observation made in our studies worthy of consideration was the shape of egg niches established by D. nigricornis females on coffee twigs. These were mainly U-shaped and nearly rectangular. The factors, if any, that governed the establishment of egg niches

of that shape by the pest were not elucidated. In all past reports most species of Cerambycids used their mandibles solely to construct egg niches of various, but precise shapes (Lashomb and Nebeker, 1979). Often the niches are horse-shoe or shield-shaped, scarred, slit, or galled up (Myers, 1967; Nord, 1968; Grimble et al. 1969; Bin, 1972; Kobayashi, 1977). Judging from the current findings and past reports, it could be concluded that the shapes of egg niches varied among different Cerambycids presumably depending on the host plants involved and the diel cycles of oviposition in the pest.

Among the diel cycles during oviposition in D. nigricornis was a time pattern in which the egg laying activities were sequentially distributed during the ovipositional period both within and between days. The problem of temporal production and distribution of eggs is ecologically important and often represents endogenous rhythms which combine with exogenous ones in many insect orders (Labeyrie, 1978). The data suggested that D. nigricornis rhythms were probably a result of interactions of time of day, the variation in canopy temperatures as the external cues and the state of oocyte maturation within the two ovaries of the pest. The intervals between ovipositions were relatively uniform which suggested that there was little intra-specific (within female) variability in the species

throughout the period of oviposition and female ageing. This phenomenon regularly occurs in many other animals (Labeyrie, 1978; Rogers and Randolph, 1985).

A rare phenomenon of oviposition that may be linked to time is the occurrence of synovigenicity in insects. Syme (1974) defined this as the synchronisation of ovigenesis with oviposition. Thus, if no eggs were laid during an interval of time, then none was matured; if many eggs are laid then more are matured rather quickly, even synchronously. Whether this occurred in the species was not elucidated. The data gathered seemed to suggest that there could be simultaneity during the oviposition of D. nigricornis eggs whereby the ability to release eggs in a specific pattern was partially resident in its twin ovaries.

D. nigricornis showed a strong ovipositional preference for primary and tertiary shoots. This was peculiar in view of the fact that on the basis of the architectural arrangement of the coffee canopy, quarternary branches are the outermost (Ombwara, 1968). Because of this it was regarded that they were the first portions of the canopy the pest got in contact with and the beetles would therefore initiate more egg niches on them than on any other portion of the canopy which was not the case.

D. nigricornis females on some occasions performed multiple ovipositions on each of the five types of shoots examined. The reason for this rather strange ovipositional behaviour was not immediately established. However, Myers (1967), Nord (1968), Grimble (1969), Grimble et al. (1969), Grimble and Knight, (1970) in their studies of cerambycids, Saperda inornata Say, Saperda concolor Le Conte and Oberea schaumi Le Conte, all of which are pests of Aspen in Michigan, reported analogous multiplicities.

A large proportion of D. nigricornis beetle egg niches were initiated on the first 12 tipmost internodes of shoots of different varieties of coffee during each season. It was considered that these internodes provided favourable food resources to the beetles. Similar findings have been highlighted in reviews of Morris (1960), Richards (1960), Varley and Gradwell (1960) and Southwood (1966). Preference by a pest for a given host or its part seems to be based mainly on two factors: adaptation and genetic constitution (Mayr , 1970). The alignment of niches of D. nigricornis along the tips of coffee shoots is apparently an efficient adaptation which places young progeny in tender tissues with extremely low dry matter, as soon as they were produced. This is a common phenomenon in insect host plant relationship (Dethier, 1970; House, 1961; Maxwell and

Jennings, 1980; Delcomyn, 1985).

In addition, it was revealed in these studies that infestations were concealed at specific heights of the canopy. This is in agreement with observations by Grimble *et al.*, (1969) and Lashomb and Nebeker (1979) who recorded higher incidence of bark beetle egg niches mainly in mid-canopies of Aspen suckers. The ability by the beetles such as *D. nigricornis* to infest their hosts with a marked degree of precision suggested the existence of some types of population regulation as those reported by Varley and Gradwell (1970). However, changing of canopy structure through capping would significantly alter the mode of attack by the beetles on the stem. This could further explain part of the fluctuations in the populations in nature.

CHAPTER 3

EFFECTS OF BROODING ON FLUCTUATIONS OF FIELD POPULATIONS OF *DIRPHYA NIGRICORNIS*

3.1 INTRODUCTION

Among the factors that may influence the fluctuations of insect pests such as *D. nigricornis* with extensive boring habits are periods of development (Nord, 1968). The elucidation of these factors would assist in making decisions aimed at augmenting levels of management of the pest through the exploitation of the detected weak links in the factors studied. Reported here are investigations which were conducted to gather this information. Investigated were the effects of brooding and developmental periods as related to sex on population fluctuations of *D. nigricornis* and the use of the egg stage to determine the population trend in the species.

3.2 MATERIALS AND METHODS

3.2.1 The sites and samples used in the studies

The beetles used in these studies to elucidate the effects of brooding on the fluctuations of the pest

were obtained from sites and varieties described in section 2.2.1. Beetles were reared using methods identical to those already described. Jacaranda site was used more extensively than the rest in the studies because of close location to laboratory research facilities. The site was approximately at an altitude of 1608 m, on latitude 1^{o} 06'S and longitude 36^{o} 45'E

3.2.2 Effects of brooding

In order to elucidate the influence of brooding, if any, on the fluctuations of D. nigricornis, single infestations for each shoot were started following procedures described earlier (section 2.2.1). Using these infestations, the changes in the populations of the beetles were assessed from egg incubation through hatching, within tunnel development of the larvae and pupae to adult emergence. The effects of sex on beetle developmental periods was elucidated by relating the sex of the emerging adult to its previous developmental history.

Larval survival and development within the tunnel which was evidenced by the ejection of frass was assessed on weekly basis up to pupation. Evidence of pupation was obtained from the presence of an enlarged terminal bore which acted as an exit hole for the adult instead of the

smaller frass bores. The day the enlarged bore was noticed was recorded and taken as being the day of commencement of pupation. The duration (days) of pupation was the period taken by the pupae to transform into adults which were trapped in cages (section 2.2.1) as they emerged.

All the beetles that emerged within 12 months were sexed and assigned to the first brood generation of the pest. If the niches did not produce adults within one year, those adults that later emerged were assigned to the second brood generation. Five stems were dissected to determine occurrence of prepupal or pupal stages, if any at fortnightly intervals throughout the brooding period of the pest. The experiment was repeated four times during the period, 1982-1984.

During the initiation of the generations used throughout the studies, the population of eggs was used to establish the trends in the fluctuation of the population of the species. Population trends were worked out for four successive generations. The trends of these generations were calculated from the egg population ratios for the species i.e. the number of eggs laid daily to the number of those laid on previous day. A comparative determination of the total number of eggs per female as another measure for population

change was assessed using 23, 8 and 3 female beetles for wild, first and second brood generations, respectively.

3.3. RESULTS

3.3.1 Effects of brooding

Brooding, the ability for a species to produce different generations from the eggs laid during the same season occurred in D.nigricornis. This phenomenon was continuous throughout the study period as evidenced by Table 13.

Survival of the different stages in the field for these populations and the ones that emerged from them was very variable and dramatic (Table 18). Compared to the original egg population (100.0%), drastic fluctuations occurred throughout the rest of the stages of development. To develop from egg to adult, the populations varied by 9.1-73.4, 11.2-93.0, 1.4-37.1% for the stages of wild, first and second brood, respectively (Table 18).

Data showing that sex of beetles did not affect egg incubation is contained in Tables 19a and 19b. While eggs destined to be male beetles took 22.5 ± 0.4 days to hatch those destined to be females took 22.6 ± 0.4 days. These periods were not significantly ($P > 0.05$)

Table 18 The changes in the number and percentage fluctuations of *D. nigricornis* due to brooding over generations.

Description of stage and its history of origin		Number	Percentage of the new brood	Percentage of original egg number
(i)	Eggs from original wild (Fo)	143	100.0	100.0
	Larvae	105	73.4	73.4
	Pupae	65	45.4	45.4
	First brood adult of original (F1)	25	17.5	17.5
	Second brood adult of original (F2)	13	9.1	9.1
(ii)	Eggs laid by (F1) adults	133	100.0	93.0
	Larvae	109	83.0	76.2
	Pupae	97	72.9	67.8
	First brood of (F1)	38	28.6	26.6
	Second brood of (F1)	16	12.0	11.2
(iii)	Eggs laid by (F2) adults	53	100.0	37.1
	Larvae	45	84.9	31.5
	Pupae	38	71.7	26.6
	First brood of (F2) adults	5	9.4	3.5
	Second brood of (F2) adults	2	3.8	1.4

The original population (Fo) therefore fluctuates by produced F1 and F2 as varieties of the same population which also brood to produce new F1 and F2 each generation.

different indicating that sex had no influence on incubation period. The development of the larval stage lasted 251.0 - 281.0 days. On the other hand, larvae destined to be male beetles took 259.3 ± 2.0 days while those destined to be female ones took 260.7 ± 2.9 days, a 1.4 day and insignificant ($P > 0.05$) difference between the larval periods attributed to their sex. As in the case of incubation period of eggs sex did not influence larval development period.

Tables 19a and 19b also show that the duration of the pupae for male beetles was 69.9 ± 1.8 days while pupation for female beetles lasted 71.1 ± 3.8 days. Female beetles emerged simultaneously after 354.3 ± 1.4 days and the males after 351.3 ± 2.7 days, respectively. The sex of the beetles did not significantly ($p < 0.05$) vary the developmental periods.

Development periods for second brood beetles are shown in Tables 20a and 20b. The major difference was the occurrence of a pre-pupal stage (Plate 1) between the larval and pupal stages which lasted 129 days for females and 130 days for males. Thereafter pupation proper occurred after 91-105 days, leading to a longer developmental period of 582-593 days (Tables 20a and 20b). It could therefore be concluded (Tables 20a, 20b) that the brooding phenomenon introduced fluctuations in

Table 19a. Duration of the development of D. nigricornis emerging as first brood generation when raised from eggs destined to develop into females (days).

	Incubation period of eggs	Development within the tunnel		Total duration
		Larva	Pupa	
		(Days)		
	22	275	50	347
	22	273	53	348
	22	259	70	351
	20	273	62	355
	24	252	78	354
	23	256	77	356
	25	251	82	358
	23	256	81	360
	23	256	81	360
Range	20-25	251-275	50-82	347-360
Mean	22.7	260.7	71.1	354.3
± s.e	0.4	2.9	3.8	1.4
C.V. %	6.0	4.0	17.0	2.0

S.e. = Standard error

C.v. = Coefficient of variation

Table 19b Duration of the development of D. nigricornis emerging as first brood generation when raised from eggs destined to develop into males (days).

	Incubation period of eggs	Development within the tunnel		Total duration
		Larva	Pupa	
		(Days)		
	24	253	64	341
	24	253	64	341
	25	253	63	341
	25	258	59	341
	22	258	64	342
	23	255	71	349
	23	257	70	350
	21	254	76	351
	25	253	74	352
	21	268	70	354
	20	258	76	354
	21	271	62	354
	22	259	74	355
	21	281	80	382
	21	259	82	362
Range	20-25	253-281	62-82	341-382
Mean	22.5	259.3	69.9	351.5
± s.e.	0.4	2.0	1.8	2.7
C.v. %	7.6	3.0	1.0	3.0

s.e. = Standard error

C.v. = Coefficient of variation

the parent population. For either of the broods, the pupa emerged into an adult through the transformation depicted in plate 2.

Prior to the fluctuations that resulted from brooding, the egg population of the pest fluctuated initially from generation to generation as shown in Figure 5. In figure 5 the rate of increase of the pest is represented by the greatest tangent to the curve of the ratio plotted against the day of oviposition and shows that D. nigricornis would increase in the absence of mortality factors. These rates of increase varied from 2.5 to 6.5 for different egg populations.

The alternative measure of the fluctuations in the egg population of D. nigricornis using wild, first and second brood generations gave the different trends in egg populations presented in Table 21. Table 21 shows that the variability in the mean number of eggs per female which were 6.2, 16.6 and 17.7 for wild, first and second brood generations, respectively. This showed that the ability by females to lay more eggs accounted for increase in subsequent populations and that first and second brood generations increased by 2.6 and 2.8 fold over the wild ones. The rates depicted by the increase were analogous to the lowest limits, established through the tangetial method.

Table 20a Duration of the development of D. nigricornis emerging as second brood generation when raised from eggs destined to develop into females (days).

	Incubation period of eggs	Development within the tunnel			
		Larva	Prepupa	Pupa	Total duration
			(Days)		
	21	338	129	91	582
	22	338	129	96	585
	24	338	129	96	587
	24	338	129	96	587
	25	338	129	101	592
Range	21-25	338	129	91-101	582-592
Mean	23.4	338.0	129.0	96.4	586.9
± S.e	0.5	0	0	1.2	1.1
C.v. %	8.0	0	0	3.0	10

S.e. = Standard error

C.v. = Coefficient of variation

Table 20b Duration of the development of D. nigricornis emerging as second brood generation when raised from eggs destined to develop into males (days).

	Incubation period of eggs	Development within the tunnel			
		Larva	Prepupa	Pupa	Total duration
			(Days)		
	21	337	130	96	586
	23	337	130	96	587
	24	337	130	96	587
	24	337	130	96	587
	24	337	130	96	588
	25	337	130	105	593
Range	21-25	337	130	96-105	586-593
Mean	23.3	337.0	130.0	97.5	588.0
I S.e	0.6	0	0	1.5	1.0
C.V %	6.0	0	0	4.0	0.5

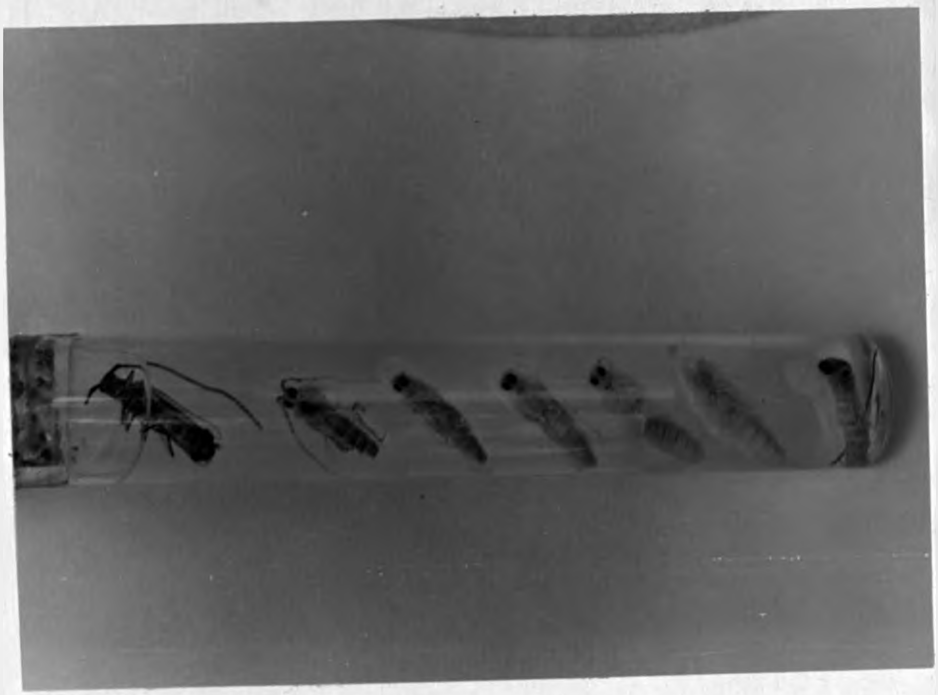
S.e. = Standard error

C.v. = Coefficient of variation

Plate 1

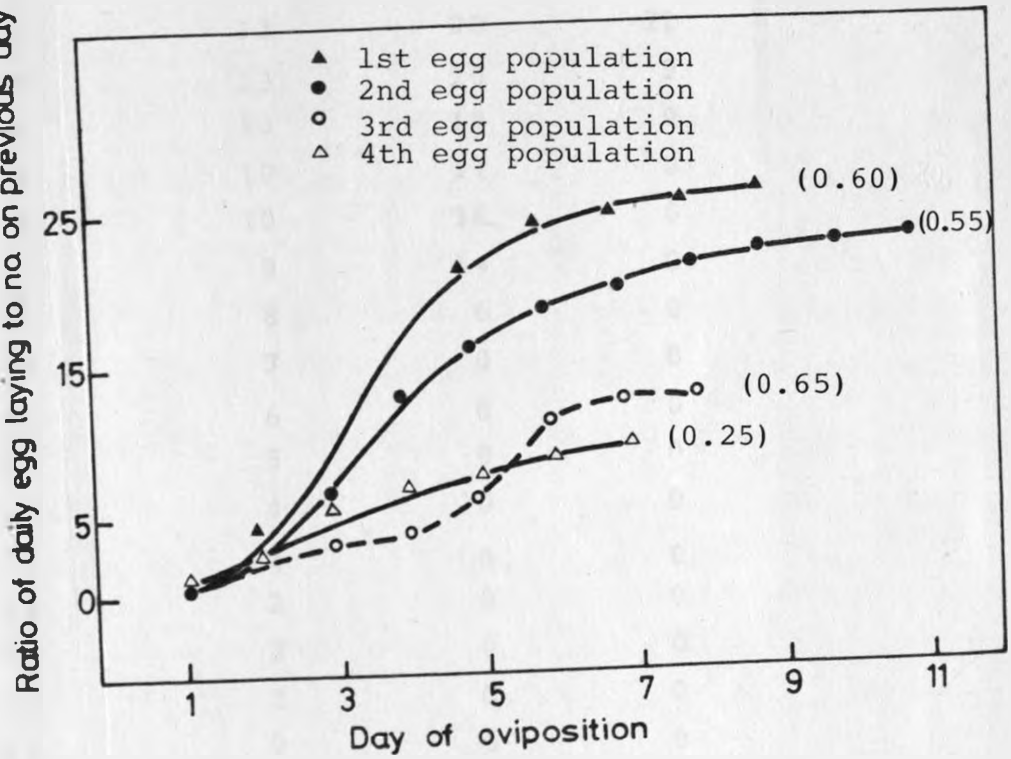
Prepupa of D. nigricornis beetles.

Plate 2



The transformation of the D. nigricornis pupal stage into the adult stage.

Fig. 5. Ratio of egg laying per day to laying previous day, for succeeding days of oviposition.



Values in brackets are maximum slopes of each population.

Table 21 The total number of eggs per female as a measure of population trend for three brood generations of *D. nigricornis*.

Female observed	Generation broods involved		
	Wild	First	Second
	(No. of eggs/female)		
1	25	21	29
2	13	20	22
3	13	20	2
4	13	19	0
5	10	17	0
6	10	16	0
7	9	14	0
8	8	6	0
9	7	0	0
10	6	0	0
11	5	0	0
12	4	0	0
13	4	0	0
14	2	0	0
15	2	0	0
16	2	0	0
17	2	0	0
18	2	0	0
19	2	0	0
20	1	0	0
21	1	0	0
22	1	0	0
23	1	0	0
Total fecundity	143	133	53
Mean number of eggs per female	6.2	16.6	17.7
S.e.	1.2	1.7	8.1
n	23	8	3

Zero values indacate that no females were involved in recording.

This incidentally showed that the two parameters are equally reliable indices as measures of estimating population fluctuation in the species.

3.4 DISCUSSION

The factors that may account for variability in the population of the pest are many and varied. A significant character of D. nigricornis development is brooding which created two generations within 18 months from every single generation initiated each season. Studies on American cerambycids have demonstrated a similar phenomenon of brooding on Aspen suckers that eggs laid in a single season often resulted in beetle populations which emerged differently over a period of one to four subsequent years (Myers et al., 1968; Nord, 1968). Brooding in D. nigricornis ensures that at least four generations resulted out of the two seasonal infestations that occur in Kenyan coffee ecosystem. This is contrary to earlier observations in which a single infestation was noticed during each year (Crowe, 1962; Le Pelley, 1968). Because the broods occurred far apart, they got exposed to a wide variety of numerous factors that caused variabilities in the population. This suggested that survival of D. nigricornis was considerably reduced by natural mortality, lowest at the egg stage and highest prior to adult emergence.

It was therefore likely that young females contributed substantially to the population compared to aged ones.

It was apparent that brooding was a challenge to our current control tactics, as a fraction of the infestation remained quiescent in prepupal stage. Such a stage would not be controlled by physical control methods advocated by Crowe, (1962) and Ombwara, (1968) as they are designed for actively boring larvae. Apparently these authors were not aware of the existence of the second brood generation.

CHAPTER 4

LIFE TABLES AND MORTALITY FACTORS OF *DIRPHYA NIGRICORNIS* IN COFFEE FIELDS IN KENYA.

4.1 INTRODUCTION

A thorough understanding of the factors regulating population density of *D. nigricornis* was regarded as being essential in a management control strategy of the pest in Kenya. The objectives of the studies reported here therefore were to identify and quantify field mortality factors in order to elucidate their significance in natural control of the beetle in coffee ecosystems. It was apparent from the survey of literature (Chapter I) that no such work had been undertaken whereby field changes of this pest from the egg through adult stages had been determined. Therefore no ecologically sound management control strategies for the pest could be advocated in the absence of the above information.

Studies to derive life tables and mortality factors of *D. nigricornis* in coffee agroecosystems were conducted in a single plot of coffee in the facilities of the Coffee Research Station, Ruiru. The work was undertaken bearing in mind the contributions of Varley and Gradwell (1970)

in Britain. Based on their pioneering experiences, they suggested that life tables could be derived for a species such as D. nigricornis only from an intensive study of the population of the pest in one place of any ecozone. However, before undertaking such a study, all the factors involved need to be recognized and identified in the first instance (Bin, 1972: Leston, 1973; Varley and Gradwell, 1970). This initial approach was followed before elucidating D. nigricornis survival with and without some of the mortality factors.

4.2 MATERIALS AND METHODS

4.2.1 The identification and quantification of natural mortality factors operating on the eggs, larvae, pupae and adults of D. nigricornis in coffee fields.

The purpose of this part of the study was to recognize the parasites and predators of the larvae, pupae and adults of D. nigricornis from natural infestations.

Sampling of the larval and pupal stages was confined to individual rows and was performed at the sites similar to those from which the adults used in the mating and oviposition studies of Chapter (2) were collected. The larvae of the pest were initially spotted by the presence of withered tips. All infestations found in the 5th plant of each sampled row

were severed monthly and placed in perspex cages (60x45x45 cm) in the laboratory for capture of any parasitic and predatory agents that emerged over a period of 21 days. The pupal stage was sampled annually from January to March and July to September and infested portions of coffee held for 21 days in separate cages from those of the larval instars to capture parasitic and predatory agents.

The insects were sorted out as they emerged and stored in 60% ethanol for identification and reference. After every 21 days, each cavity was dissected open, examined under the microscope and the nature of death described. A general description of the agents found was not prepared.

In the studies to quantify mortalities, egg niches were established as before (Chapter 2, section 2.2.1), each on its own coffee plant of the variety SL34 growing on study area of 0.75 ha. Observations on each of them were started as soon as they became established. Mortality factors in all the developmental stages of D. nigricornis were identified, quantified by counting and recording the number of individuals involved out of the total egg numbers laid at the start of the experiment. These were then used to construct life table budgets and to identify key mortality factors for the generations of the pest.

The experiments were conducted in two stages from 6 April 1982 to 2 April 1983 and from 22 November 1982 to 26 November 1983. During each of the studies, a total of 49 for the first experiment and 45 egg niches for the second experiment were used. Each was treated as a separate generation.

The mortality factors in the egg stage were investigated as described below. The ovipositional behaviour of D. nigricornis female was observed during the forming of each egg niche. The number of eggs that were crushed by the ovipositor and abdominal stroke during the sealing of egg niches were counted and recorded. Cases of egg crushing were identified either by the presence of copious discharge of clear fluid of the crushed egg or by complete crumbling of the external morphology of the egg niche. A second mortality of the egg was attributed to accidental dislodging of the egg due to poor sealing of the niche.

During the preparation of each niche by D. nigricornis each individual was timed and its oviposition duration recorded following the procedures stated in Chapter 2 (section 2.3.2). All eggs that dropped on the same day they were oviposited or thereafter within two days were attributed to hastened ovipositions. Similarly, all the eggs that were positioned in leaf petioles and laid

across the length of the egg niches were recorded as mislocated. Their fate was followed and recorded throughout their incubation period or until they dropped. All the eggs that were not completely covered were recorded as having been inadequately sealed.

From the moment eggs were laid they were observed daily until hatch. The environment around the niches was described whenever there were collections of rain water droplets or morning dew. Cases of mortality that resulted out of this phenomenon were estimated by counting empty egg shells or crumbled to flattened egg niches prior to hatching.

At the termination of the observation period which was pegged at 25 days as demonstrated previously by the results of Chapter 3, all eggs that had failed to hatch were counted. This mortality was attributed to inviability or infertility.

The presence of a minute frass bore on the surface of the niches were used to count and record the number of larvae initially produced. Thereafter at intervals of one week, each tunnelling larva was examined. By placing a mark with a blue paint at the frass bore that had been newly constructed each week, it was possible to follow the events involved. The first mortality factor during the larval stage was attributed to failure

by the larvae of D. nigricornis to make more than one frass bore. The second mortality factor was identified as being misorientation by the larvae which bored in the internode tissues progressing towards the growing point which immediately dried up. The third mortality factor of the larvae of D. nigricornis, was identified as parasitism. This mortality factor was ascertained by capturing and identifying all those hymenopteran species that frequented the bored portions of the coffee branches and stems.

All the larvae of D. nigricornis that failed to continue boring were presumed to have suffered parasitism or predation from the effects of hymenopterans identified. Additionally, the entire length of the bored portion of the coffee was examined in situ weekly. The purpose of this was to identify the types of cocoons or other evidence of the presence of parasites especially I. varipalpis.

A fourth and a final mortality factor during the larval stage was attributed to perishing of the larvae as a result of failing to bore through lignified node junctions and accidental breakage of the coffee branches. This last category of mortality was assessed directly by the difference between the number that pupated relative to the total larvae which suffered identified mortalities.

Pupal mortality factors were determined by using the proportion of the larval population that survived the collective mortality factors operating from hatch of eggs to pupation. In this case, the number of pupae that were parasitized and those that were preyed upon were counted after splitting open their tunnels in the field to expose and examine them *in situ*. Additionally the ant species that were associated with these cavities were collected and identified by experts at the British Museum. The other mortality factors were attributed to undetermined causes within coffee tunnels. In this category were diseases and other unkown factors of the pupae and their habitats. These were determined as the difference between those pupae for which mortality had been assigned to already identified factors from the total number of the cases involved for the stage.

During the emergence period only two mortality factors were identified and assessed. The first mortality factor was failed emergence of *D. nigricornis* pre-pupal stage if the pest belonged to the second brood. The second mortality was due to predation by formicid ants in which case only wings, head crania and exoskeleton remains of the pest were found within tunnels.

From the adult *D. nigricornis* that emerged at the termination of the observation period, the sex ratio

was determined so as to permit its assessment as a mortality factor of the pest.

The following additional studies, were undertaken whereby most of the exogenous mortality factors that had been identified as affecting D. nigricornis in the previous studies (section 4.2.1) could be minimised or excluded artificially. This was done with a view to determine whether such treatment of the pest population would enhance its survival.

These studies would also elucidate on the probable role played by the natural mortality factors. Pairs of D. nigricornis beetles used in these studies were obtained from the field as previously described (Chapter 2). Egg niches on several coffee plants were established employing techniques described in (Chapter 2). As before each coffee plant was allowed to carry only a single egg niche. The experimental plot was the same as the one used in the previous studies reported in section 4.2.1. Egg niches were examined daily for 25 days and any of them found flooded were immediately dried.

After the incubation period, the total number of eggs of D. nigricornis that hatched were counted, recorded and percentage survival calculated relative to the initial number of egg niches recorded at the start

of the experiment. As soon as the larvae hatched they were protected from their parasites and predators by means of an insect proof sleeve cage (100 x 30 cm) which was installed on the infested branches (Plate 3)

To exclude parasitic and predatory agents that inhabit the stem, the basal portions of coffee stems of infested plants were painted with a solution of Dieldrin 18% M.L. Additionally, parallel bands of the insecticide were applied on infested branches taking care to avoid frass bores and pupation chambers constructed by the pest.

Plate 3: The sleeve cage employed in excluding predators and parasites from branch boring larvae of *D. nigricornis*.

4.3 RESULTS

4.3.1 The identification and quantification of natural mortality factors operating on the eggs, larvae, pupae and adults of D. nigricornis in coffee fields.

Four and two major groups of parasites and predators, respectively, emerged from the larva and pupa stages of D. nigricornis. In all the samples of either stage of the pest, occurrence of parasitic and predatory agents was variable but generally higher in the larval stage than the pupal stage. Of a total of 35 samples examined only seven of them yielded a braconid of the genus Microplitis (Hymenoptera : Braconidae). Two of the samples gave rise to heteropteran Ectopsocus sp (Heteroptera : Ectopsocidae). A single sample gave rise to an Ichneumonid wasp in the genus Camptotypus (Hemipimpla sp.) (Hymenoptera : Ichneumonidae) These were taken to be new records of parasites and predators of the pest besides I. varipalpis which prevailed in most samples

The Mirid sp (Heteroptera : Miridae) was also reared from one of the samples but could not be named at the British Museum. On a single occasion a solitary female earwig, Dacnodes caffra (Dohrn) (Dermaptera) was recovered.

Larvae preyed upon were represented by remains of mere head crania and wings. Those killed but still unconsumed were dark brown carions. Parasitized larvae especially by I. varipalpis were skeletal and crusty.

A definitive identification of the agents found in this part of the study revealed that braconids occurred in 20% of the infested coffee shoot samples from the field. Parasitic ichneumonids (2.8%), ectopsocids (5.7%) and mirids (2.8%) were scanty and found only occasionally throughout the study. A corresponding occurrence applied to the sole dermapteran found.

According to the data obtained D. nigricornis habitats were invaded by six different formicid ants. These were Pheidole, Acantholepis, Tapinoma, Crematogaster, Tetramorium and Technomyrmex spp (Hymenoptera: Formicidae). The occurrence was abundant (40%) to very abundant (72%).

The results of this part of the study, demonstrated that D. nigricornis mortality resulted out of many agents. The agents belonged to a variety of species. Some may be efficient while others may not on their own provide adequate levels of control.

Several of the identified mortality factors affected the survival of the egg, larval, pupal and adult stages of D. nigricornis. Data that express which factors and to which magnitude each one operated are presented in Tables 22a and 22b for the period 6 April 1982 to 2 April 1983 and 22 November 1982 to 26 November 1983, respectively.

It was apparent from Table 22a that three mortality factors operated on the egg stage. It was revealed that eggs were lost due to their being laid in petioles and dropping prior to hatch (2.04%), partially sealed and exposed to accidental drop (2.04%) and water flooding and dehydration of the oviposition sites (8.16%) (Table 22a). This represented a total egg mortality of 12.24%.

At eclosion, it was shown that 4.08% of the larvae failed to produce frass bores (Table 22a). Table 22a also shows that 6.12% of the larvae died due to misorientation in excavating their habitats. It was further shown (Table 22a) that 4.08% of the larve were preyed upon by two formicid ants Pheidole sp and Tapinoma sp. (Hymenoptera:Formicidae). Data in Table 22a also shows that while 6.12% and 10.20% of the larvae were parasitized by the Ichneumonid Camptotypus (Hemipimpla sp.) (Hymenoptera : Ichneumonidae) and I. varipalpis respectively, about 10.20% of the larvae were equally lost through branch breakages. The overall larval mortality in this experiment was 40.81% (Table 22a).

During pupation, 8.16% of the pupae were preyed upon by two species of formicid ants, Pheidole sp and Acantholepis Sp (Hymenoptera : Formicidae) (Table 22a). It was also evident from the data gathered that about

26.53% of the pupae failed to emerge due to their inability to enlarge exit holes, diseases and other unknown causes (Table 22a). In this experiment, it was estimated that 4.08% failed to emerge as they belonged to the second brood generation. The total loss during the pupal stage was approximately 38.77%.

Data in Table (22a) also demonstrated that all the individuals which emerged were males. Therefore the sex ratio was rather drastic as it was not even. The generation total loss was approximately 91.81%.

Similarly, during the second experiment it was apparent that only two mortality factors acted on the eggs. All the eggs were adequately sealed (Table 22b). At eclosion, data (Table 22b) shows that the same mortality factors operated except that the larvae were preyed upon by a third species of ants, Technomyrmex spp. In this experiment I. varipalpis was the sole parasite recorded. Branch breakages led to a substantial (11.62%) loss in the larvae.

During pupation, it was shown that an additional species of the formicid ants, Tetramorium spp. (Hymenoptera: Formicidae) preyed upon 6.67% of the pupae (Table 22b). No additional factors were elucidated. The overall mortality was 88.13%.

Table 22a: Life table for a single generation of *D. nigricornis* from 6th April, 1982 to 2nd April, 1983.

Age interval (x)	Mortality factor (dxf)		Number d ying during each stage (dx)	Apparent mortality (100qx as % lx)	Real mortality (dx as % of egg lx)
EGG (49)*	(a)	Eggs in petioles, dropping before hatch	1	1.04	2.04
	(b)	Partially unsealed eggs dropping	1	2.04	2.04
	(c)	Eggs killed due to flooding of egg niches	4	8.16	8.16
Total egg Mortality			6	12.24	12.24
LARVA (43)*	(a)	Failure to make bores at the egg niches	2	4.65	4.08
	(b)	Accidents, misorientation	3	6.97	6.12
	(c)	Killed by formicid ants (*Pheicole* and *Tapinoma* spp)	2	4.65	4.08
	(d)	Killed by hymenopterans *Camptotypus*	3	6.97	6.12
		I. varipalpis	5	11.62	10.20
	(e)	Accidental breakages	5	11.62	10.20
Total larval mortality			20	46.48	40.80
PUPA (23)*	(a)	Eaten by formicid ants (*Pheidole* and *Acantholepis* spp)	4	17.39	8.16
	(b)	Failed to emerge after pupation, diseases, other	13	56.52	26.53
	(c)	Second brood generation	2	8.70	4.08
Total pupal mortality			19	82.61	38.77
ADULT (4)*	(a)	Sex ratio of males/ females 4:0			
Generation total loss					91.81

* Value in brackets denotes number of individuals at the start of the experiment for each stage (lx)

Table 22b. Life table for one generation of D. nigricornis from 22nd November, 1982 to 26th November, 1983

Age interval (x)	Mortality factor (dxf)	Number dying during each stage (dx)	Apparent mortality (100qx as % lx)	Real mortality (dx as % of egg)
EGG (45)*	(a) Eggs mislocated on niche, dropping before hatch	1	2.22	2.22
	(b) Eggs killed due to flooding of egg niches	2	4.44	4.44
	Total egg mortality	3	6.66	6.66
LARVA (42)*	(a) Failure to make bore at egg niches	5	11.63	11.11
	(b) Accidents, misorientation	9	21.43	20.0
	(c) Killed by formicid ants (Pheidole, Tapinoma and Technomyrmex spp.)	3	7.14	6.67
	(d) Killed by hymenopteran (I. varipalpis)	2	4.76	4.44
	Total larval mortality	19	44.96	42.22
PUPA (23)*	(a) Killed by formicid ants (Pheidole and Tetramorium spp.)	3	13.04	6.67
	(b) Failed to emerge after pupation, diseases, other	8	34.78	17.78
	(c) Second brood generation	5	21.74	11.11
	Total pupal mortality	16	69.56	35.56
ADULT (8)*	(a) Sex ratio of males/females 1:1			
	Generation Total loss			84.44

*Value in brackets denotes number of individuals at the start of the experiment for each stage (lx)

The data (Tables 22a and 22b) were processed further by the key factor analysis method in order to identify the stage and mortality factor which led to population changes in the field. The analysis showed that the most critical developmental stages of the pest during which mortality caused drastic population changes were the larval and the pupal stages (Table 23). The killing power of mortality factors during the larval and pupal stages were 0.26665 and 0.3798, respectively (Table 23). The corresponding value for the egg stage was 0.04335 (Table 23) which was quite low. This clearly indicated that more deaths occurred during the larval stage followed by the pupal stage. On the other hand there were very few deaths occurring during the adult stage. The findings showed that the factors causing variabilities usually affected the pest during the larval and pupal stages, although the population was unregulated initially during the egg and adult stages.

Table 24a and 24b summarises the data on levels of survival of D. nigricornis when some of the mortality factors were excluded. It is shown that minimising egg mortality increased the viability of eggs from 90.43% to 97.92% and only 2.08% of the eggs did not hatch. Table 24a also shows that out of 47 larvae that hatched 36 (75.0%) of them survived and only 11 (22.92%) died.

Table 23. Key factor analysis for all stages of D. nigricornis in two generations (a and b).

Stage	Mortality factors	Generation mortality a	Generation mortality b	Total	Mean
Egg	K_1				
	K_2				
	K_3				
	$Ke=K_1-K_3$	0.5067	0.030	0.0867	0.04335
Larva	K_4				
	K_5				
	K_6				
	K_7				
	K_8				
	K_9				
	$KL=K_4-K_9$	0.2718	0.2615	0.5333	0.26665
Pupa-Adult exit	K_{10}				
	K_{11}				
	K_{12}				
	$K_{pa}=K_{10}-K_{12}$	0.7596	0.4586	0.7596	0.3798
Generation mortality $KG = K_e + KL + Kpa$		1.0881	0.7501	1.8382	0.9191
Generation survival (Sa) =		0.0816	0.1778	0.2594	0.1297

Egg = Ke	Larvae=KL	Pupa to Adult exit = Kpa
K_1 leaf-petiole egg	K_4 Failure to bore	K_{10} Predation
K_2 poor seal of egg	K_5 Accidents 1	K_{11} Failure to bore to exit by young beetle
K_3 Flooding/dehydration/desiccation	K_7 Parasitism 1	K_{12} Second brood
	K_8 Parasitism 11	
	K_9 Accidents 11	

The killing power of the factors in a stage was obtained by the summation of log differences of each factor that acted prior to the next factor.

Table 24. Survival of P. nigricornis beetles in the experiment in which mortality causes were excluded or minimised (a) as compared to those in which the factors operated freely (b).

(a) Factors excluded or minimised.

Stage	Number involved	Number dying	Number surviving	Percentages Mortality A	Mortality R	Survival A	Survival R
Eggs	48	1	47	2.08	2.08	97.92	97.92
Larvae	47	11	36	23.40	22.92	76.60	75.0
Pupae	36	4	32	11.11	8.33	88.89	66.67
Adults	32	0·0	0·0	0·0	0·0	0·0	0·0
Total Generation Survival	0·0	16	32	0·0	33.33	0·0	66.67 66.67

(b) Factors not excluded or minimised

Stage	Number involved	Number dying	Number surviving	Percentages Mortality A	Mortality R	Survival A	Survival R
Eggs	94	9	85	9.57	9.57	90.43	90.43
Larvae	85	39	46	45.88	41.49	54.12	48.94
Pupae	46	34	12	73.91	36.91	26.09	12.77
Adults	12	0·0	0·0	0·0	0·0	0·0	12.77
Total Generation Survival	0·0	82	12	0·0	87.23	0·0	12.77 12.77

A = Apparent mortality = $\frac{\text{(Number dying)\%}}{\text{(Number involved per stage}}$

R = Real mortality = $\frac{\text{(Number dying)\%}}{\text{(Number of eggs laid)}}$

Data was based on pooled data for two experiments

Where no mortality factors had been excluded (Table 24b), egg and larval mortality values of 9.57% and 41.49% respectively occurred. The data presented (Table 24a, 24b) showed further that 66.67% of the larvae pupated and emerged into adults when water, parasites and predators operating on them were excluded. On the other hand when mortality factors were left to operate naturally, survival was about 12.76%. It was therefore concluded from these observations that enhanced emergence as a result of the exclusion of some of the mortality factors occurred. This demonstrated that there was potential in using some of the mortality factors with an ability to regulate the pest population.

4.4. DISCUSSION

The trend of mortality on all stages of the pest showed that several factors other than parasitism and predation acted on them. The factors were variable and were density independent on immature and young adult stages in nature. Mispositioning of eggs in their niches on coffee shoots does enhance the egg mortality in this species. According to past literature (Myers, 1967; Nord, 1968; Loc. at.) a well constructed cerambycid egg niche must have a definitive shape. When this does not occur, mortality should ultimately follow.

According to the data, distribution of the eggs in the appropriate internode was crucial since leaf petioles were subject to physiological shedding. This is easily enhanced by the reaction of the host to activities such as biting the bark to form a niche. Hastened ovipositions did suggest that D. nigricornis was often unable to integrate successfully its orientation to sites where its niches would be favoured. This does invariably occur in nature (Dethier, 1970) unlike in the present study in which coffee as hosts were freely available.

Among the identified egg mortality factors according to the past records involving relatives of D. nigricornis were no egg, egg inviability and egg desiccation (Grimble, 1969: Grimble et al., 1969; Grimble and Knight, 1970). Where ovipositions lacked it implies disruption of the cerambycid's labour process. In which case all the pre-niche activities if any were wasted. There was no evidence to suggest that this frequently occurred in D. nigricornis.

The cover and edges of egg niches of cerambycids have been observed to curl and wither following their construction (Grimble et al., 1969). The reasons as to why this happens have not been explained by past workers. The probable causes as observed in the current studies were invariably manifestations of rainfall droplets, dew and their drying up.

Whenever the rainfall droplets and morning dew flooded D. nigricornis egg niches prior to their being dried up , several phenomena appeared apparent. If the niches were underneath the shoot surfaces, the flooded ones were probably dehydrated by solar heat in addition to gravitational drainage. Such drainage created hydraulic forces around the egg. Then as the thin bark covering the egg niche dried and curled the dynamism of the resultant microenvironment probably crumbled the eggs. A related phenomenon of curling of the egg niches has been recorded but not explained by Grimble et al., (1969).

As with egg mortality there was large variation in percentage parasitism and predation of D. nigricornis during the larval and pupal stages. The general trend of parasitism did not increase with larval instars. In previous studies on parasites and predators of cerambycids Bin (1972); Grimble (1969); Grimble and Knight (1970); Kobayashi (1977) and Raske (1973a, b) found that larval parasitism was prevalent while predation was scanty. Observations recorded during these studies showed that parasitism and predation on the larval stages of the pest were equal. The aforementioned workers found at no time any single agent which singly accounted for the effective control of the species they studied. They however attributed the highest incidence of parasitism to braconids and Ichneumonids. For example, the North

American cerambycids, S. inornata, S. concolor and O. schaumii were occasionally parasitised by Enderus lividus Ashmead (Eulophidae) but regularly by Iphiaulax eurygaster Brulle, Cenocoeduis sanquineiventris Ashmead, Meterons cognatus Muesebeck and Bracon n. sp. None of these parasites were recorded during the current studies. However it was demonstrated that larval parasitism did result from two related braconids, namely I. varipalpis which was augmented by a second braconid Microplitis sp. The former belongs to the same genus Iphiaulax like the American I. eurygaster. Consequently either species could be exploited under conditions foreign to it to find out whether they can establish and control the different cerambycids. The larval stages of the pest was also attacked by an ichneumonid, Camptotypus sp., which was most likely synonymous to Crowe's (1962) unidentified endoparasite of D. nigricornis.

These studies showed that ants are major predators of D. nigricornis in Kenya. Their role as the ultimate predators of insect pests is not peculiar to coffee as reported in these studies. Leston (1973) and Taylor (1977) demonstrated the probable significance of the ant-mosaic and the limitation of pests and disease of tropical tree crops.

The data showed that the population varied away from equilibrium during the pupal stage when survival was enhanced due to protection. It apeared that the role of natural enemies such as the mirid bug which was not named could be playing a crucial role in the regulation of this pest.

CHAPTER 5

THE BIOLOGY AND BEHAVIOUR OF *IPHIAULAX VARIPALPIS* CARY (HYMENOPTERA : BRACONIDAE) AS A PARASITE OF *DIRPHYA NIGRICORNIS*

5.1 INTRODUCTION

The feasibility of controlling the yellow headed borer *D. nigricornis* by the braconid parasite *I. varipalpis* Cary has not been amply demonstrated in Kenya. Wood borers have not been solely controlled by braconids for a long time. For example, the braconid *I. eurygaster* is not a reliable method for beetle control in America and Canada (Grimble, 1969; Grimble *et. al.*, 1969; Grimble and Knight, 1970). No explanation has been provided for this failure. A good understanding of the biology and behaviour of *I. varipalpis* would help to ultimately understand its role and potentiality as a control agent for the pest. Such an evaluation should necessarily precede attempts to introduce natural enemies of any pest which is a target of classical biological control (Huffaker and Messenger, 1976). It also helps to understand host discrimination if any (Van Lenteren, *et. al.*, 1978).

The development of a rearing method and adequate information on the fecundity of a parasite is basic to the initiation of biocontrol. If these locally occurring parasites were able to control the borer on its own, steps would be formulated to augment

and enhance its action in coffee. This study considered in some details some aspect of the biology of I. varipalpis as a parasite of D. nigricornis. The parasite I. varipalpis acts only on the larval stage of D. nigricornis. It is not known whether I. varipalpis is uniformly active on the host throughout the long development period of the D. nigricornis larvae in the field.

5.2 MATERIALS AND METHODS

5.2.1 Determination of the biology, parasitic behaviour and efficacy of I. varipalpis as a parasite of D. nigricornis larvae

D. nigricornis infested branches were collected from six sites: Jacaranda, Rukera, Muri, Kiaora, Azania and Matungulu. At each site, 1-2 hectares of coffee variety SL 34 aged about 20 years old and above were selected for sampling. The samples were collected from individual rows and all infestations found in the fifth plant of each row taken. It is not known whether I. varipalpis is uniformly active on the host throughout D. nigricornis larval developmental period.

Branches were severed 20-30 cm below the basally visible frass bore-hole and transferred to the laboratory. In the laboratory the entire bored length of the shoot was stripped of leaves prior to being examined under a binocular microscope, for the presence of I. varipalpis cocoons'.

Whenever cocoons were found, shoots were placed in rearing tubes measuring 30-60 cm long and 2.50 cm diameter made from polyethylene sheet(Plate 4). The ends of the tubes were sealed loosely by cotton wool to facilitate aeration. The rearing laboratory conditions were 23.0^{o}C± 1.0 at 70% r.h. The tubes were examined daily for the emergence. I. varipalpis females were killed and dissected under a microscope (x 10) and the number of oocytes in their ovaries established. The purpose of this was to determine the potential fecundity of the braconid. Additionally, the length (mm) of their ovipositor was measured and recorded. These data would be used to establish whether the length of the ovipositor played any role in the accessibility of D. nigricornis to the parasite.

Experiments were also designed to study how the I. varipalpis parasitized D. nigricornis. To investigate this aspect, newly emerged adult parasites were introduced into perspex cages (30 x 25 cm) in single pairs (sex ratio 1:1). They were fed on diluted honey on cotton wool. Live and active larvae of the pest within their tunnels were presented to adults of I. varipalpis. The parasites were then observed closely to record ovipositor probing into frass boreholes made by the borers presented. The frequency and interval of ovipositor insertions were timed and recorded. The period of observation lasted the entire lifespan of the pair of parasites from day 1 to day 28.

Plate 4: The tubes employed in rearing of *I. varipalpis*.

The duration of the pre-oviposition, oviposition and post-oviposition periods (days) were monitored from the same specimens throughout. Durations of the development from the start of the parasitization through to emergence of adults was established.

5.3 RESULTS

5.3.1 Determination of the biology, parasitic behaviour and efficacy of *I. varipalpis* as a parasite of *D. nigricornis* larvae

Data obtained from field samples are shown in Table 25. The Jacaranda, Kiaora and Azania samples yielded no braconids during this study. Field parasitization was dismally low in nature. It ranged from 5.56% to 14.29% for samples obtained from three sites: Muri, Rukera and Matungulu. This meant that on average the level of parasitism was 10.72% ± 1.47 only. Throughout the sites the parasites were found early in the season of host attack, which coincided with onset of rainy seasons. As the pest larvae developed parasitism was scanty on its later instars.

About 3.43 ± 0.69 parasitoids emerged per *D. nigricornis* larva during 15.43 ± 4.57 days after sampling. It was therefore concluded from the data obtained that *I. varipalpis* was either gregarious or it superparasitized its host. Upto six individuals (Plate

5a) of the braconid pupated in a white cocoon of approximately 4.18 ± 0.41 cm long. The cocoons (Plate 5b) consited of chambers with each of them being occupied by an individual pupa.

The number of oocytes in each female I. varipalpis was high (Fig. 6). The braconid had a high potential fecundity of approximately 323 oocytes. The ovipositor measured about 5.07 ± S.e. mm long. It was concluded from these observations that the braconid had an ovipositor which ensured accessibility of D. nigricornis larvae boring within tunnels.

Data obtained on the durations of various developmental stages are shown in Table 26a. Eggs laid by I. varipalpis invariably hatched into larvae after 7.0 ± 0.25 days. The larval stage lasted 6.60 ± 0.24 days. Pupation took another 12.0 ± 1.0 days. It was evident that although this braconid was capable of initiating several generations on a single generation of the larval stage of the beetle, the sole pest stage that is susceptible to attack by I. varipalpis, this did not occur in the field.

The estimated periods for pre-oviposition, oviposition, post-oviposition and lifespan (days) for I. varipalpis are shown in Table 26b. Females of I. varipalpis attained

Table 25. Emergence times and number of I. varipalpis attacking larvae of D. nigricornis at Muri, Rukera and Matungulu coffee estates.

Site	Duration (days) emergence after host collection	Adult parasitoids emerging per shoot	Larval parasitism
Muri (n=13)	14	6	7.69
(n=18)	7	3	5.56
(n=7)	7	2	14.29
Rukera (n=10)	14	6	10.0
(n=7)	42	3	14.29
Matungulu (n=8)	12	2	12.50
(n=2)	12	2	12.50
Range 2-18	7-42	2-6	5.56-14.29
Means 9.29	15.43	3.43	10.72
± 1 S.e. 1.92	4.57	0.69	1.47

Bracketed values represent the number of individual stems in the samples

Plate 5a: A photograph showing three (arrowed) newly emerged I. varipalpis from a single larva of D. nigricornis.

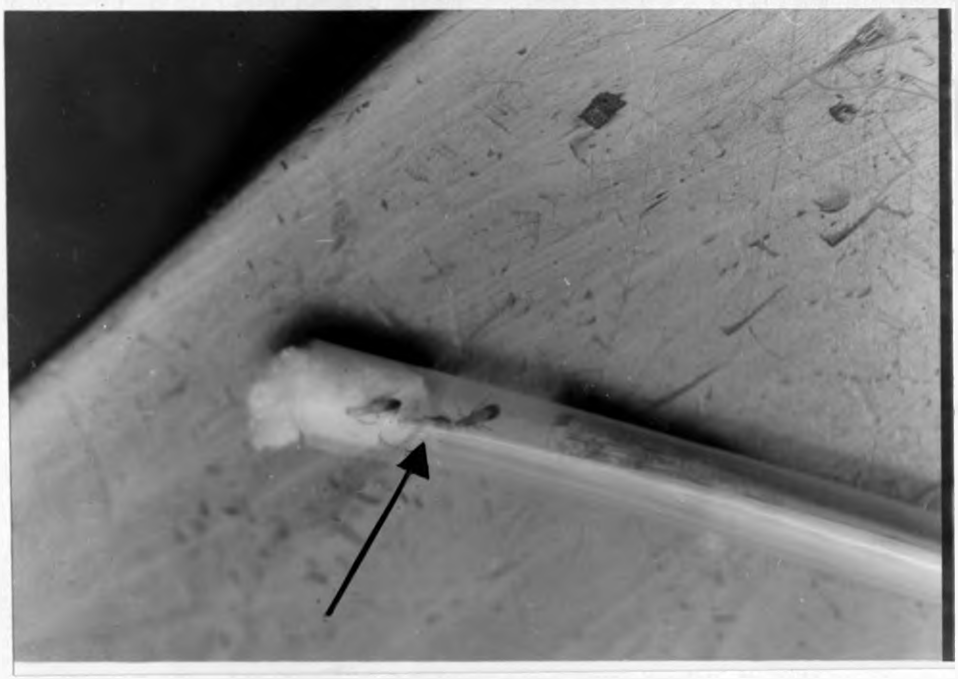


Plate 5b: Pupal cases of I. varipalpis cocoons showing distinct chambers.

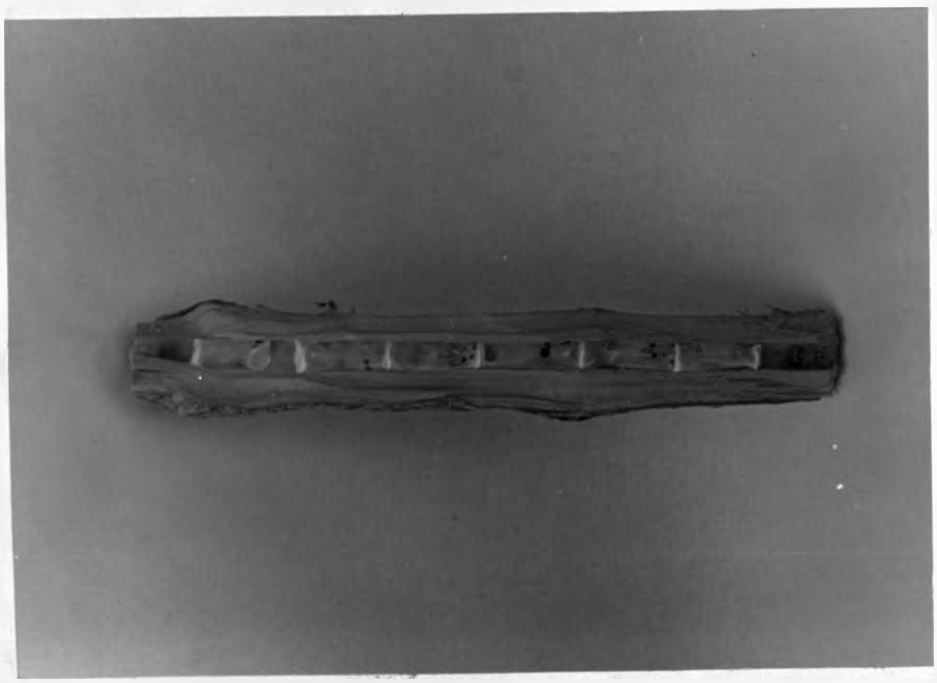
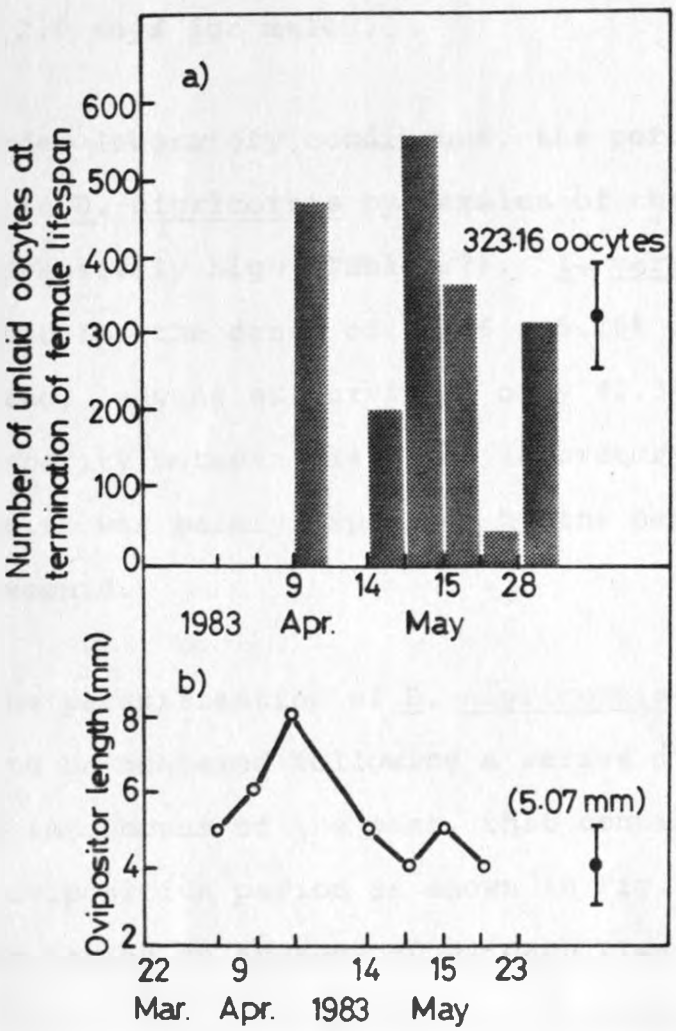


Fig. 6. Parasitic potential of Iphiaulax varipalpis determined from oocyte number and ovipositor length.



oviposition (Pre-oviposition period) after 11.0 days following emergence. Thereafter they had potential to parasitise D. nigricornis larvae for 15.0 days (oviposition period). Following this they survived for 3.0 more days (post-oviposition period). The overall lifespan was 28.01 ± 1.0 days for females and 14.0 ± 2.0 days for males.

Under laboratory conditions, the percentage parasitism of D. nigricornis by females of the braconid was impressively high (Table 27). I. varipalpis accounted for the death of 57.66 ± 5.16% of D. nigricornis presented, leaving as survivors only 42.34 ± 5.16%. The disparity between field and laboratory levels of parasitism was mainly explained by the behaviour of the braconid.

The parasitization of D. nigricornis larvae was found to be achieved following a series of ovipositor probes into bores of the pest, that continued over the adult oviposition period as shown in Fig. 7a. The process lasted on average 90.0s each time. It could extend upto 1020 s (Fig. 7b). I. varipalpis thus does parasitize larvae of D. nigricornis rather briskly each time. Perhaps short probing periods do not result in oviposition. Prior to the 10th day of oviposition when the parasites attained the highest rate of probing, the process is punctuated by 3 phases of oviposition activity spread over 2-6 days.

Table 26a. Developmental periods from egg to adults of I. varipalpis.

Stage	Duration (days)
Egg	7.0 ± 0.25
Larva	6.60± 0.24
Pupa	12.0 ± 1.0
Adult	18.0 ± 0.50

Table 26 b. Duration (days) of I. varipalpis survival in the cages.

Period	Duration
Pre-oviposition (Pre-parasitic)	0.0 - 11.0
Oviposition (Parasitic)	16.0 - 24.0
Post oviposition (Non parasitic)	25.0 - 28.0
Lifespan (Females)	28.0 ± 1.0
Lifespan (Males)	14.0 ± 2.0

Table 27. Colonization potential by I. varipalpis adult female on D. nigricornis larvae in several coffee portions under laboratory conditions.

Parasitization period (days)	Live larvae presented	Number of larvae attacked	Real percent mortality	Survival per experiment
5	14	6	42.86	57.14
8	18	12	66.67	33.33
8	13	8	61.53	38.47
6	14	8	59.59	40.41
Range 5-8	13-18	6-12	42.86-66.67	33.33-57.44
Mean 6.75	14.75	8.50	57.66	43.34
±ls.e 0.75	1.11	1.26	5.16	5.16

Fig. 7a. Effects of age of Iphiaulax varipalpis on its parasitization, n = 10.

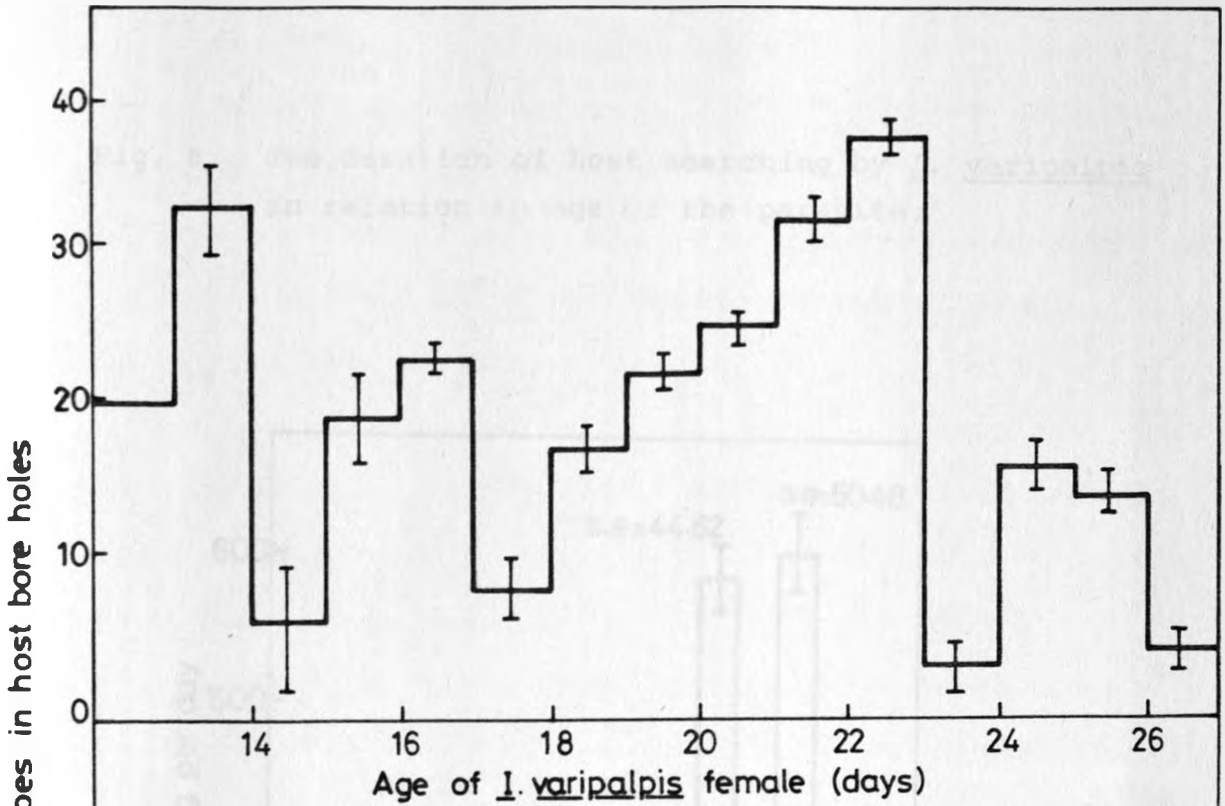


Fig. 7b. Duration of I. varipalpis during parasitization of D. nigricornis larvae, n = 10.

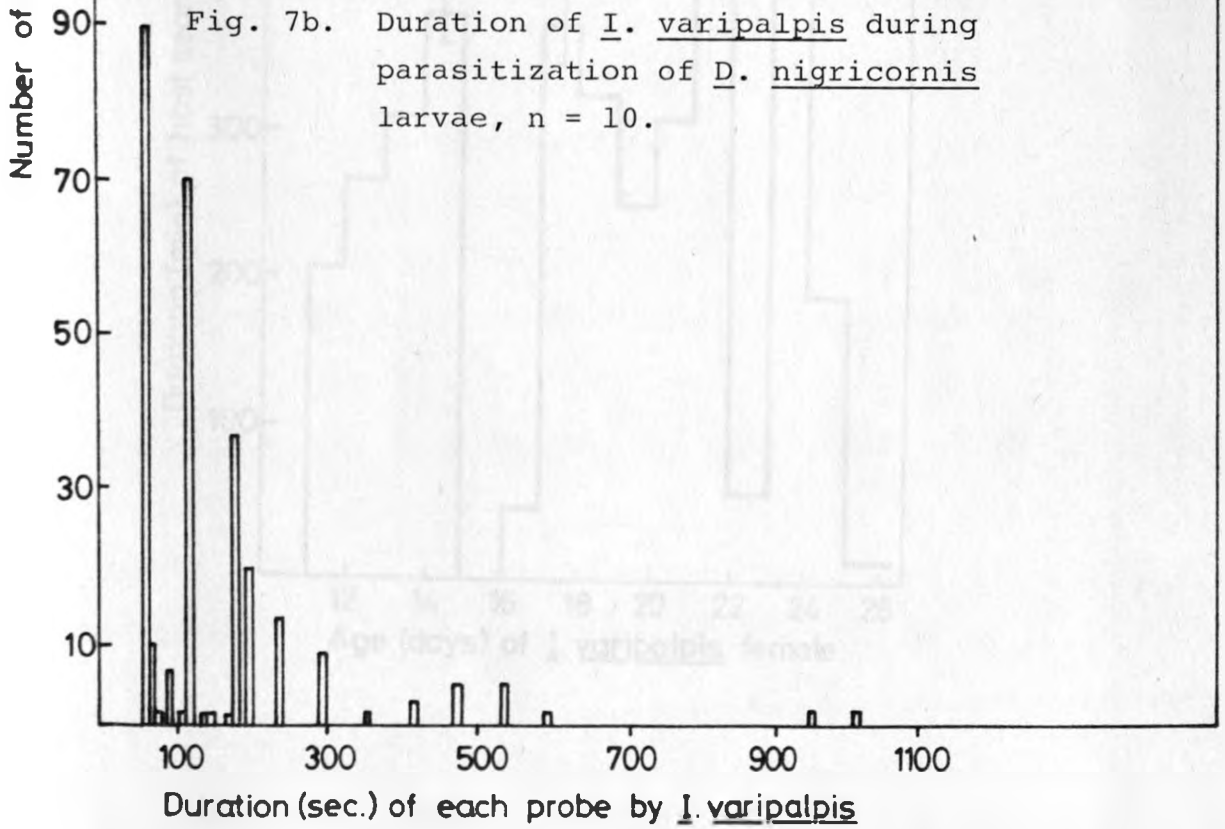
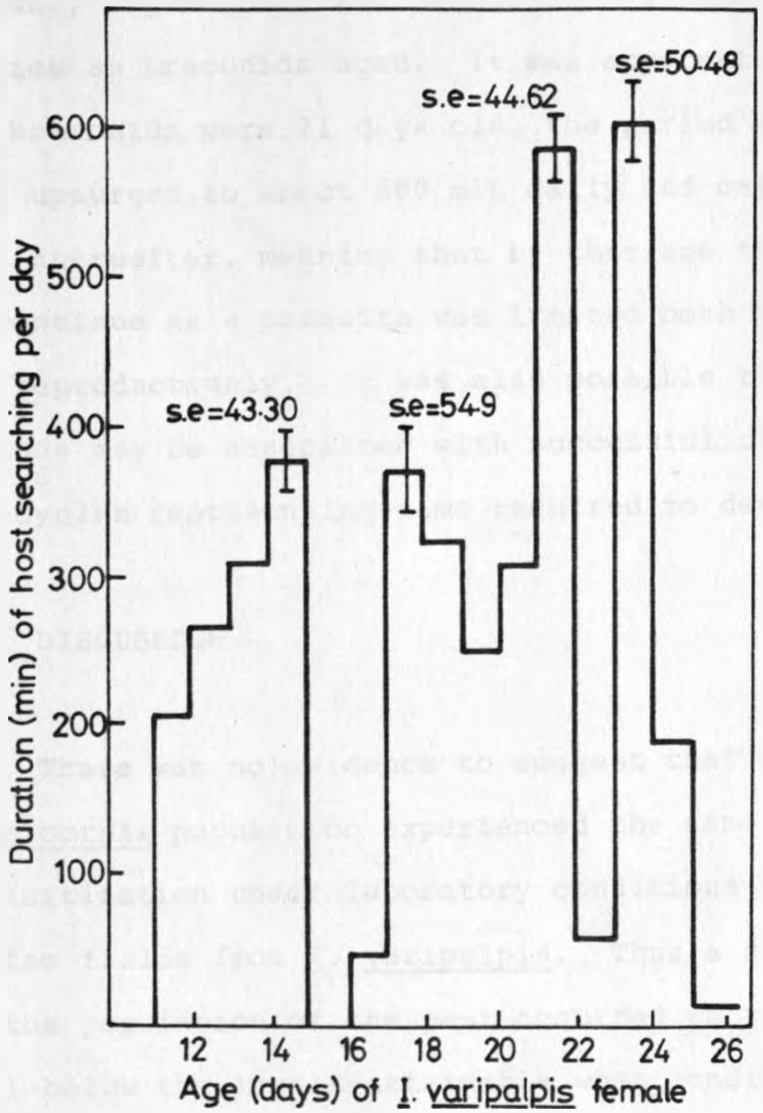


Fig. 8. The duration of host searching by I. varipalpis in relation to age of the parasite.



When adults of I. varipalpis were about 12 days old, they spent accumulatedly about 200 min probing (Fig. 8). This rose to 380 min daily when they attained the age of 14 days. At advanced ages when little or no parasitization occured, the period taken was approximately 30 min per day. The reduction in the parasitic activity probably represented the exhaustion of eggs from the ovaries as braconids aged. It was apparent that when the braconids were 21 days old, the period of parasization upsurged to about 600 min daily and ceased 2-5 days thereafter, meaning that by that age the ability to continue as a parasite was limited both physically and reproductively. It was also possible that the longer periods may be associated with successful oviposition, the cycles representing time required to develop eggs.

5.4 DISCUSSION

There was no evidence to suggest that the D. nigricornis population experienced the same level of parasitization under laboratory conditions and in coffee fields from I. varipalpis. Thus a slow reduction in the population of the pest occurred in the field well below the levels attainable when conditions are ideal as in the laboratory. Success in laboratory breeding (Van Lenteren et. al., 1978), variable abundance in all localities, lack of information on its occurrence by previous workers (Crowe, 1962) and undetectable

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occurrence or absence in 50.0% of the sites used during this study suggested that the braconid required specific environmental requirements for its survival.

The data of this study were generated from laboratory evaluations of I. varipalpis obtained near optimal conditions for food (D. nigricornis), space, shelter and the absence of competition. Obviously, in nature, parasitic searching prior to detecting the hosts is variable in result especially when the host becomes scarce (Tanigoshi and McMurty, 1977). The data gathered indicated, however, the potential ability of I. varipalpis to overtake low populations of D. nigricornis larvae. The reason then why I. varipalpis does not strongly repress the field populations of D. nigricornis today could be purely its inability to search, detect and colonize the hidden larvae of the pest within canopies and cavities of the coffee plant. The coffee plant, although serving as a host to D. nigricornis, often contained single attacks only on any of the categories of shoots of the plant. The attacks occur least at canopy peripheries.

The braconid as an important biological control agent for the pest parasitized gregariously and reproduced abruptly. Presumably this is an adaptation to some peculiarity of its ecology. It is unproven but quite possible that I. varipalpis takes advantage of a single

D. nigricornis once found in nature to place a great amount of its progeny in that host (loc. cit.). This is a regularly occurring phenomenon among parasitic insects (Hassell, 1966, 1968, 1969 a, b; Hassell and Varley, 1969; Huffaker and Kenneth, 1969; Varley and Gradwell, 1970).

Apparently I. varipalpis did not fully discriminate the hosts it had already parasitized. It therefore qualified as a super parasite. This behaviour is a common feature with many parasitic insects (Smith and Debach, 1942; Van Lenteren, et. al., 1978). These authors were of the opinion that the inability to discriminate parasitized hosts from unparasitized ones was a serious disadvantage to the species concerned in spreading their progenies. They also considered that at species level, the habit indicated specialisation to aggregate their progenies which therefore ultimately enhanced survival.

Natural enemies, such as I. varipalpis, if they were to control populations of D. nigricornis, would require certain characteristics. They would have to keep pace with the immense coffee canopy and the long range dispersal of their host if any. Additionally, they have to be but not invariably host specific (Miller, 1980; Ehler and Miller, 1978). It is not certain whether the parasite investigated was host

specific. The likelihood is that it was monophagous as it only attacked D. nigricornis larvae while the egg, pupal and adult beetle stages were not susceptible.

CHAPTER 6

EVALUATION OF COFFEE CANOPY DAMAGE BY *DIRPHYA NIGRICORNIS*

6.1 INTRODUCTION

Economic thresholds for insect pests on crop plants can be developed by evaluating each factor that contributes to yield loss (Taylor and Bardner, 1970). One of these factors for infestations of the stem borer, *D. nigricornis* on coffee is the larval canopy damage potential. This damage considered in combination with other factors, such as larval excretion (House, 1961) and the capacity of the plant to compensate for insect damage (Taylor and Bardner, 1970) could provide the biological basis for establishing action thresholds.

However, there is need to first undertake quantitative studies of the pest-induced feeding stress on coffee during its larval development and elucidate how this affects yield components. Unknown also are the exact responses of the coffee canopy to beetle infestation and the relationship with yield components as well as the sex of the larvae of the pest relative to its excretion during development. A study to more fully determine the effect of boring during larval development, on potential damage and yield per larva for the pest was therefore conducted.

6.2 MATERIALS AND METHODS

6.2.1 Evaluation of damage

The beetle infestation used in these studies was started using the caging and pairing techniques of the insects from the field stock as described in chapter 2 (Section 2.2.1). Infestations were initiated singly on stems of susceptible variety SL34 grown within coffee fields of (1 ha) that received no insecticide treatments throughout the study. After eclosion, the boring activity of the larva was followed throughout its span of development.

Symptoms of boring were detected and estimated as the number of bore holes over the time. The observations were made daily throughout the period of larval survival. Each larva was used as a replicate in a completely randomised design. Days of damage and the construction of perforations were recorded and intervals between the most recent bore measured relative to the bore previous to it. Paint was used to mark the advance in the boring ability of each beetle larva throughout. The observations were maintained and terminated at the pupation of each larva.

Using the same insects, the incidence of symptoms on branches and stems was assessed to determine whether beetles bored them to the same extent in nature. The external arrangement of the bores on the branches and stems were enumerated and classified using a chart on intervals (cm) of interbore distances developed for this purpose. The classes fitted the following descriptions. The numerous close perforations (= 100 bore holes and above) , many close perforations (= 40 - 100 bore holes), several to

sparse perforations (= 10 - 30 bore holes), sparse to rare perforations (= 1 - 4 bore holes) and rare to no perforations (= 0 bores). These descriptions represented the damage categories which are easily discerned visually from which a threshold level could emerge.

Since the symptoms were based on the branch and stem parts of the plants, entire canopies of coffee at cropping stage were used in subsequent studies to assess damage on them and estimate reduction in yield. To ascertain if any relationship existed between the extent of damage caused to vegetative parts of coffee plants by the larvae of D. nigricornis and their age, single infestations of the pest were initiated on tips of susceptible coffee variety, SL34, which is commonly grown by Kenyan farmers. A total of 37 D. nigricornis larvae were used. When the larvae hatched their rate of boring using frass bore construction as a parameter was determined at intervals of 20 days throughout their larval development which lasted about 260 days. Recorded also were the accumulated bored lengths of stems and branches and the quantity of nodes and internodes that withered and dried up. Correlations were calculated between the age of the boring larvae and the forementioned parameters of the plant.

Additionally, the amount of larval frass ejected when the larvae of D. nigricornis were bred on the test variety was collected in paper funnels which were changed at weekly intervals throughout the larval development period. The collected frass was then dried up for 12

hours at 50°C in the oven (Memmert model) before being weighed to estimate direct loss of coffee plant wood through wasteful larval excretion.

Emerging adults of D. nigricornis were trapped in wiremesh sleeve cage (1.0 x 2.5 cm) installed over the last frass hole constructed by the last instar larval stage before pupation. Adults caught were then sexed and related to the amount of frass each individual produced during its larval development. This procedure helped to elucidate the role, if any, of sex in the ultimate degree of damage caused through frass excretion.

The purpose of the other part of the studies reported here was to establish the exact relationship between coffee canopy responses due to infestation by D. nigricornis and components of yield. Only one test variety, SL34, was used in these studies. The canopies of twenty plants selected for the studies were physically divided into three categories of partition for modelling as follows:

(i) Bottom Canopy Partition (BCP): this was the canopy formed by branches below the last basal frass bore,

(ii) Mid Canopy Partition (MCP): this represented the portion of the canopy formed by branches in the tunnelled portion of the main stem; and,

(iii) Top Canopy Partition (TCP): this was the portion

of canopy formed by branches above the topmost frass bore holes made on the main stem by D. nigricornis larva.

Branches forming each plant canopy were sequentially numbered from the basal to the topmost branch. At the same time their positions on the main stem were determined by measuring the length (cm) of the stem between ground level and the basal point of each branch. For each branch in all the three canopy partitions the quantities of its nodes, pinheads, berries, flowerbuds and leaves were counted intact with Tally counter through the season of coffee cropping. The number of frass intact bores constructed in the MCP was also recorded.

In the current studies measurements (cm) of positions of branches (H) in the canopy and all components of yield assessed were related by an arithmetic progression, similar to that used by Hammond and Pedigo (1982) in their studies, as follows:

(i) HI, HI + 2 ... HI + n; and

(ii) CI, CI + 2 ... CI + n where:

HI = stem length (cm) between ground level and basal branches at the start of BCP, MCP and TCP;

HI + 2 = accumulated stem length (cm) between ground level and the first and second

basal branches at the start of BCP, MCP and TCP;

CI = number of nodes, pinheads, flowerbuds, berries, leaves and frass bores found on the first basal branch at the start of BCP, MCP and TCP;

CI + 2 = number of nodes, pinheads, flowerbuds, berries, leaves and frass bores found at the level of two branches at the start of BCP, MCP and TCP; and

CI + n = number of nodes, pinheads, flowerbuds, berries, leaves and frass bores found on the topmost branches of BCP, MCP and TCP.

Data accumulated for weights of harvested berries from each of the three partitions were assessed using the arithmetic progression outlined above. Canopy partitions were treated as three blocks with branches used as replicates to facilitate statistical analysis of the data. Data assembled for each of the parameters studied were transformed to logs to base 10 so as to stabilize their variances before calculating their regression equations to ascertain if there were any canopy responses to infestation by D. nigricornis and the relationship of these responses and the ultimate quantity of berry yield obtained.

6.3 RESULTS

6.3.1 Evaluation of damage

The abundance of bores on the plants of cv SL34 averaged 24 bores at 31 days after infestation (Table 28). Bore perforation then increased by 14.7, 9.0 and 2.1 bores for each additional 30, 31 and 30 days of infestation, respectively. The larvae did not perforate the plants continuously. The rate of bore hole formation was highest initially and it reduced progressively for 153 days after the infestation (Table 28). Thereafter, there was a drastic decline in the production of frass bores which remained constant from approximately 184 days to 232 days (Table 28). This showed that all the bores that the pest had previously constructed were used for excretion for several days prior to the construction of any additional bores. Thus bore abundance was not a parameter that could be used to elucidate damage independently.

Table 29 gives data on the interbore intervals (II) found on the branches and stems of cv SL34. During the study, plant growth continued and no dead plants were recorded which suggested sustained growth of the infested plants. Generally, the II fitted all the classes of the descriptions evaluated. The numerous close perforations were positioned less than 1.2 cm apart (Table 29). The highest percentage of the intervals between the branches and stems was approximately 39.9 and 34.8%, respectively.

These were spaced predominantly 0.5-0.8 cm apart. Many close perforations prevailed in 4.7 to 11.8% of all the intervals measured and were < 2.0 cm apart. The sparse, very sparse, sparse to rare, rare to no perforations were minimal on the branches but were occasionally found on the main stem (Table 29). This suggested that the interbore distances were determined by the degree of wood lignification which ought to be higher in the stems than the branches. It was concluded that perhaps concern to control the larvae ought to be focussed on the ones that made the intervals closely as the larvae that produced bores at wide intervals did not extensively perforate the bark and thus disrupt the translocation of the plant nutrients.

The regression relating the damage caused by D. nigricornis on coffee stems and branches by its tunneling activities throughout its larval development on cv SL34 of coffee is presented in Table 30. It is revealed in Table 30 that high correlation ($r = 0.99$; $n = 13$; $P = 0.001$) existed between larval age (days) of D. nigricornis and the length of the portions of stems and branches of coffee tunnelled. Likewise bored stem portions that withered and dried up ($r = 0.98$), the rate of boring of branches and stems ($r = 0.98$) and the number of nodes that dried up ($r = 0.99$) were highly correlated ($p = 0.001$) with the age of the pest (Table 30). It was concluded from the analyses presented (Table 30) that damage caused by the larvae of D. nigricornis aggravated as they increased in age.

Table 28. The rate of bore hole formation by *D. nigricornis* on the variety SL 34 (n=45)

Days of boring	Accumulated number of bores	Average bores made per day	Bores made by each larva
31	1078	0.7	24.0
61	1742	0.6	38.7
92	2146	0.5	47.7
122	2244	0.4	49.8
153	2380	0.3	52.8
184	2404	0.2	53.4
212	2411	0.2	53.5
232	2417	0.2	53.7

Table 29. The external expression of frass bores of equal distances between them on branches and main stems of the cv SL34.

Interbore distance (cm)	Number of frass bores		Percentage of frass bores	
	Branches	Stems	Branches	Stems
0.1-0.4	349	111	26.4	18.5
0.5-0.8	527	209	39.9	34.8
0.9-1.2	252	97	19.1	16.1
1.3-1.6	66	71	5.0	11.8
1.7-2.0	62	48	4.7	8.0
2.1-2.4	15	10	1.1	1.6
2.5-2.8	19	8	1.4	1.3
2.9-3.2	9	12	0.6	2.0
3.3-3.6	5	3	0.3	0.5
3.7-4.0	7	3	0.5	0.5
4.1-4.4	2	2	0.1	0.3
4.5-4.8	4	0	0.3	0.0
4.9-5.2	0	5	0.0	0.8
5.9-6.2	1	1	0.1	0.1
6.3-6.6	0	1	0.0	0.1
6.7-7.0	1	4	0.1	0.6
7.3-7.6	0	1	0.0	0.1
7.7-8.0	0	1	0.0	0.1
8.1-8.4	0	1	0.0	0.1
9.3-9.6	0	1	0.0	0.1
9.7-10.0	0	1	0.0	0.1
10.3-10.8	0	3	0.0	0.5
11.9-12.2	0	1	0.0	0.1
12.3-12.6	0	1	0.0	0.1
16.3-16.6	0	1	0.0	0.1
18.3-18.6	0	1	0.0	0.1
19.7-20.0	0	1	0.0	0.1
21.9-22.2	0	1	0.0	0.1
n	55			

Table 30. Correlation equations and co-efficients between the ageing (0-260 days) of D. nigricornis and damage to coffee plants.

	Damage parameters	Equations	Co-efficients and significance
i)	Bored stem or branch length	$Y=-14.45+0.53x-0.004x^2$	0.99***
ii)	Withered and dried up stem	$Y=-2.50+0.43x-0.0007x^2$	0.97***
iii)	Accumulated number of bores	$Y=-16.39+0.49+0.00004x^2$	0.98***
iv)	Number of nodes dried up	$Y=1.45+0.11x-0.0001x^2$	0.99***

The relationships of the components assessed (Table 30) were apparently curvilinear (Figs. 9-12). This observation suggested that the extent of tunnelling by D. nigricornis larvae attained a certain specific dimension before significant (P = 0.05) damage could be caused to branches and stems. From derived equations (Table 30 and Figs. 9-12), this dimension was represented by every 14.45 cm of length of the stem or branch bored by D. nigricornis. This was further associated by 2.5 cm portion of stems killed by the pest which led to loss of quantity of 1.45 nodes. However, this became the case only when the pest constructed at least 16.39 frass bores since its hatching.

Evidence collected during the current studies showed that female larvae excreted about 25% more frass (16214.91 ± 1105.61 mg) than did the male larvae (12067.90 ± 500.75 mg) (Appendix 5). These excretions were spread over slightly different periods being, approximately 34.29 ± 0.74 weeks for larvae destined to be females and 32.78 ± 0.62 weeks for those destined to be males. It was concluced from these observations (Appendix 5) that rather than the duration of boring, sex of the larvae accounted to a large extent for the quantity of frass produced and therefore the ultimate degree of loss of wood caused.

The bulk of frass excreted consisted of crude fibre (56.31%) followed by cellulose (46.30%) and Lignin (10.76%) (Table 31). All the components were largely undigested compared to the wood of the stem (Table 31).

Fig. 9. Effect of age of tunnelling beetle larvae on bored length.

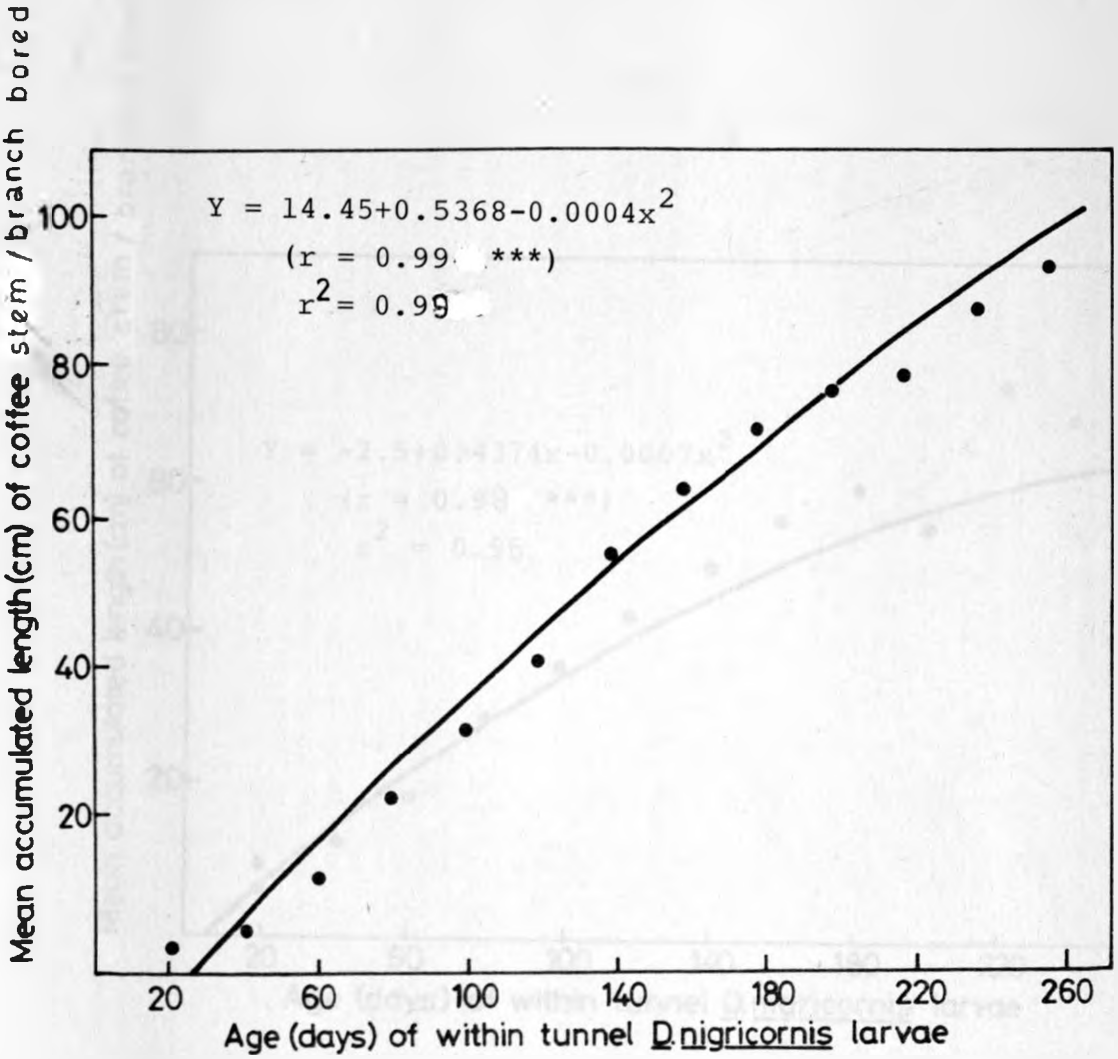


Fig. 10. Effect of age of tunnelling larvae on senescing length.

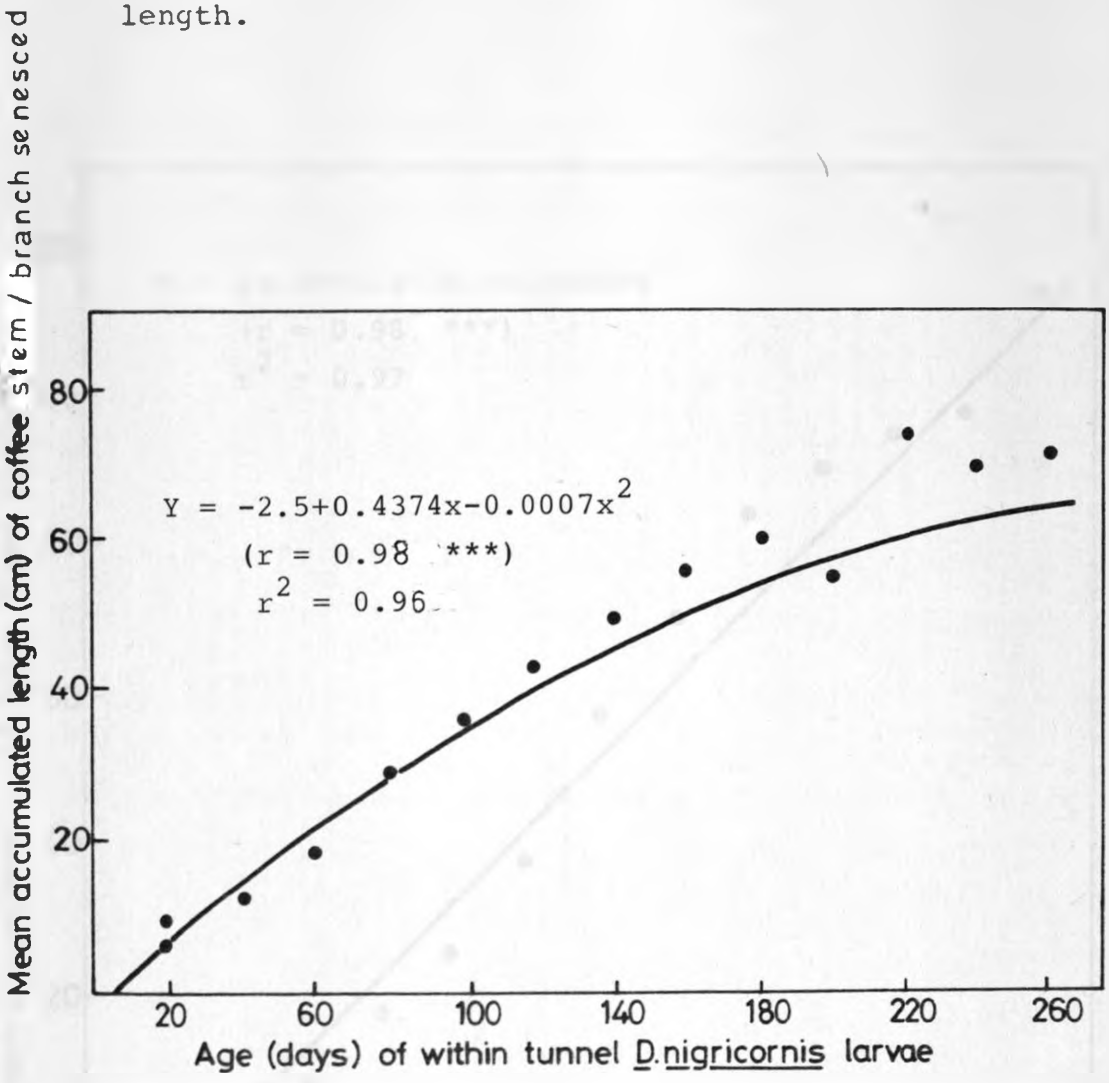


Fig. 11. Effect of age of tunnelling larvae on accumulation of frass bores.

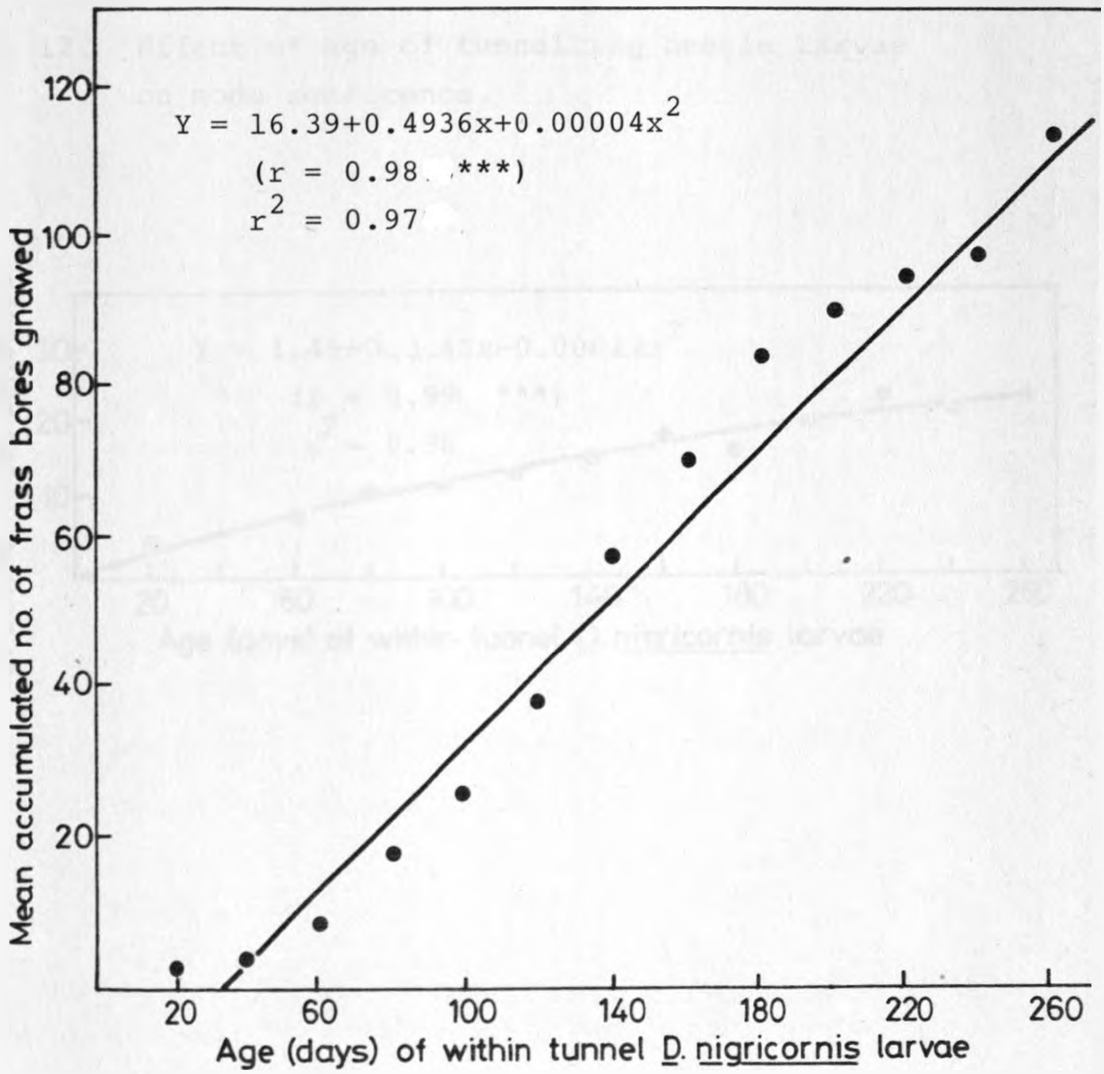
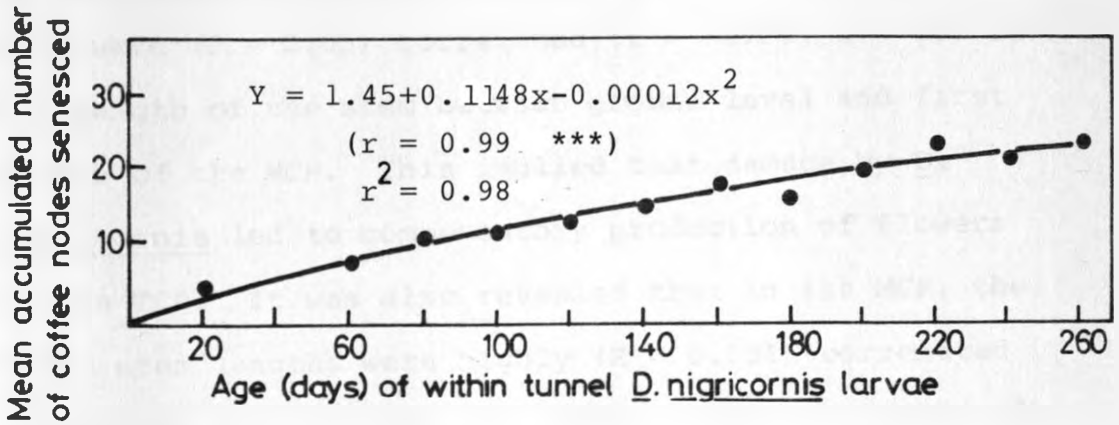


Fig. 12. Effect of age of tunnelling beetle larvae on node senescence.



Other organic compounds found in frass were traces of phenolic, uric acid and aldehyde groups.

Presented in Table 32 are regression equations depicting the relationship between branch position measurements above the ground level and components of coffee yields. It is evident (Table 32) that the length of the stems that postorally gapped branches in BCP were not correlated with flowerbuds. In MCP the length of the bored portion of the stem and the number of flowerbuds were ($P = 0.05$) correlated ($r = -0.28$; $n = 57$) to the length of the stem between ground level and first branch of the MCP. This implied that damage by D. nigricornis led to compensatory production of flowers in the TCP. It was also revealed that in the MCP, the bored stem lengths were highly ($P = 0.001$) correlated ($r = 0.84$; $n = 57$) with the number of leaves (Table 32). This indicated that stem boring by D. nigricornis stimulated defoliation.

Additionally, data collected showed that significant ($P = 0.05$) correlation existed between the lengths of the stems bored and the quantities of pinheads ($r = 0.29$; $n = 49$) produced in the TCP (Table 32). This was further evidence showing that damage in MCP by D. nigricornis stimulated compensatory growth in yield components in the TCP.

Table 31. The magnitude of major components of frass excreted by D. nigricornis larvae compared to the undigested stem.

Components	Percentages	
	Stem of cv SL34	Frass
Crude fibre	73.70	56.31
Cellulose	58.10	46.30
Lignin	11.81	10.76

Other organic compounds found in the frass were traces of phenolic, uric acid and aldehyde groups.

According to the data presented in Table 32, the notation (X) formed the height upon which the yield parameters depended. The constants for leaves, berries, pinheads and flowerbuds represented the logs of the minimum lengths that must exist between canopy partitions in order for each parameter to vary significantly (P = 0.05, 0.001) in a linear fashion. The positive constants of most of the variables assessed pointed to the existence of reciprocal effects, although these were quite small. It was therefore established that there existed a capacity for a certain minimum quantity of the stem that had to incur some boring by D. nigricornis in order to cause damage which reciprocated with partitions of the canopy. This implied that there was compensation and reduction of each of the category of canopy partition to the next and vice versa.

Data gathered on yields (weights) of berries showed that tunnelling of the stems and branches by D. nigricornis significantly depressed yields in the BCP and MCP (Tables 33a, 33b). Similarly there was a significantly high (P = 0.01) correlation between the number of frass holes and depression of yields (Tables 33a, 33b).

Thus despite the existence of small gaps between branches in BCP, MCP and TCP which caused variability in yield parameters, the actual weights of coffee berries were reduced by the destructive effects of D. nigricornis when huge portions (Table 33b) of the stems in the MCP was bored. This provided further evidence in support of

Table 32. Regression equations relating the transformed data for flowerbuds, pinheads, berries and leaves to the length of the main stem in three partitions of coffee canopies.

Partition of canopy	Components of yield involved	Regression equations	Regression Co-efficient (r)	Level of signif. for each component
A				
Pretunnelled	1) Flowerbud numbers	Y=1.05-0.05x	-0.01, n=49	NS
Bottom partition	2) Pinhead numbers	Y=2.85-1.19x	-0.29, n=49	*
of Canopy (BCP)	3) Berry numbers	Y=-0.39+0.89x	0.20, n=49	NS
	4) Number of leaves	Y=0.89+0.40x	0.11, n=49	NS
B				
Tunnelled	1) Flowerbud numbers	Y=1.11-0.57x	-0.28, n=57	*
Mid partition	2) Pinhead numbers	Y=0.06+0.56x	0.20, n=57	*
of Canopy (MCP)	3) Berry numbers	Y=0.24+0.66x	0.18, n=57	NS
	4) Number of leaves	Y=-0.04+0.99x	0.84, n=57	***
C				
Post tunnelled	1) Flowerbud numbers	Y=1.07-0.33x	-0.21, n=97	*
Top partition	2) Pinhead numbers	Y=1.87-0.76x	-0.39, n=97	***
of Canopy (TCP)	3) Berry numbers	Y=1.37+0.23x	-0.21, n=97	*
	4) Number of leaves	Y=0.17+0.13x	0.09, n=97	NS

NS = No significant effect of effective length between branch position and lowest affected or unaffected length of the canopy and the component considered.

* = Significant effect (P = 0.05)

** = Highly significant effect (P = 0.01)

*** = Very highly significant effect (P = 0.001)

Table 33a. Regression equations relating data on the actual weights of harvested coffee berries to the postoral length of the main stem in three partitions of coffee canopies.

Partition of Canopy	Regression equation	Regression co-efficient (r)	Level of significance
Pretunnelled bottom canopy partition (BCP)			
a) Effect of length	Y = 179.13 + 0.70x	0.15, n = 108	NS
Tunnelled mid partition of canopy (MCP)			
a) Effect of length	Y = 214.68 - 1.94x	-0.34, n = 72	**
b) Effect of bores	Y = 222.85 - 2.1x	-0.36, n = 72	**
Post tunnelled top of Canopy (TCP)			
a) Effect of length	Y = 118.19 - 0.28x	-0.10, n = 122	NS

NS = No significant influence on weights of berries occurred that could be attributed to the tunnelling of the stem by D. nigricornis (P = 0.05).

* = Significant reduction resulted by boring of D. nigricornis on berry weights (P = 0.05).

** = Highly significance reduction resulted by boring of D. nigricornis on berry weights (P = 0.001).

Table 33b. Effects of the length (cm) of the partition and number of frass bores on yields (gm) of coffee.

Bored length/stem	Frass bores/length	Yield/stem
7.2	6.9	298.4
15.9	17.8	262.1
25.6	25.9	106.8
32.9	38.2	124.5
46.2	37.8	76.3
56.0	56.2	68.9
63.0	59.4	49.5

the earlier finding that reciprocal effects existed between the extent of boring by D. nigricornis and yields of coffee. Significant (P = 0.01) reduction in yields was experienced only when the tunnelled portions of the stem reached 15.9 cm and beyond. This was regarded as the critical degree of damage. The practical implication of this finding is that control measures are called for before the critical degree of stem damage is caused to avert economic losses of coffee yields.

6.4 DISCUSSION

There are a number of possible explanations for the relationship of larval development to damage demonstrated here. However, three are more probable than the others. One is the probable limiting effect that the variation in branch and stem size has that is attendant with increased lignification and solidness on the pest (Guthrie, 1975; Gallum et. al., 1975; Ratcliffe and Oakes, 1982). Most of the damage observed was the result of perforating bores closely (4.2 cm) by all instars of the larvae within 122 days after infestation. The limitation on perforating the branches and stems by larvae of the pest may not have been so much a matter of preference for either part of the plants as of their inability to penetrate and rupture more mature stem than the branch.

The other explanations pertained to effects of the pest. D. nigricornis larval boring adversely affects

both canopy sustenance and yield components. Age-induced excavation increased significantly (P = 0.001) the rate of withering of branches, internodes and nodes of coffee plants. The feeding of the pest synchronized with the entire health of the canopy which could not be considered negligible. This association did account for why relatives of the pest damage timber (Donley and Worley, 1976) whose production depends on the intactness of plant canopies free of frass bores.

Actual wood destruction was also largely due to wasteful excretion and partial digestion of ingested wood. It has been established in a number of other cases that feeding by insects causes injury by not only reducing productivity but also by the actual biomass removed and its estimated use (Taylor and Bardner, 1970). Other than providing nutrition (Dethier, 1970; House, 1961) to D. nigricornis larvae during development, female borers required probably more feeding to differentiate sexually, this accounting for the need to excrete about 25-fold excess frass as compared to the males and thus failing to utilise efficiently consumed wood.

The established yield loss model presented in this analysis represents the actual estimate of the canopy responses to infestation and damage by D. nigricornis and is an improvement over derived polynomial yield loss situations. The model has the advantage that losses caused by stem borers other than the one studied on a number of perennial crops could be compared directly by

using physically determined height constants of canopy partitions. For coffee yield components, the constants for berries, leaves, pinheads and flowerbuds were variable. The constants represent the damage threshold that would relate productivity to bored portions of stems long before a crop-pest response curve does attain any apex even if the relationship was sigmoidal (Taylor and Bardner, 1970). The degree of damage reciprocates by about a third, which parameters can either be compensated or reduced depending on which canopy partition they accrue in. They are minimal in the bottom of the canopies and highest in the top ones, indicating the existence of either additive or depressive ability of the non-perforated portions of the stems to perform physiological functions that cater adequately for enhanced productivity. This is a commonly occuring phenomenon (Taylor and Bardner, 1970).

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

The results obtained by caging (sex ratio 1:1) of D. nigricornis singly on coffee shoots showed that the females deposited almost the full compliment of its eggs. This was attributed to the fact that coitus in this beetle lasted for a long time resulting in many eggs being fertilized and subsequently being laid.

If the females have been adequately supplied with viable sperm, multiple copulations may be disadvantageous to them. They could better invest their time in searching for hosts or ovipositing This is vital because it has been established that for many insects, each female competed with others for ovipositional sites, and the female that produced the greatest number of progeny is the superior competitor (Gordh and Debach, 1978). Perhaps this type of mating phenomenon is widespread in cerambycids, because one other stem borer the red oak cerambycid , Enapholodes rufulus (Haldemann) has the same mechanism of repeated copulations, Donley (1978).

Mating characteristics have come to be considered as adaptations affecting a species survival in different environments. These characteristics usually cover mating

behaviour, mating habits such as monogamy, polygyny and polyandry, mating preference (Petit and Ehrmann, 1969; Richard, 1974) and sex ratio (Fisher, 1958; Hamilton, 1967). In some cases these mating characteristics have been found to be important in regulating population numbers (Wynn-Edwards, 1962; Wiley, 1974). Apparently the mating-oviposition process in D. nigricornis accounted for the ability in this species to multiply. In this species the oviposition intervals were probably linked to the timing of sperm exhaustion and the next copulation. The timing of sperm exhaustion may influence the time of repeated copulation which may occur in adult life (Oh, 1979).

It was apparent from these studies that the survival of D. nigricornis was not only determined by the number of oocytes produced by the females but also by its distribution in time. Data collected showed that females oviposited few eggs per day for over two weeks. Labeyrie (1978) emphasized that this behaviour was critical to survival of any insect species. The reason he gave for this was that it could enable the species concerned to overcome any periodic hazards if there were any in the habitat. This suggestion was supported by the fact that when wild D. nigricornis females (uncaged) were captured and dissected numerous oocytes (eggs) which had not been laid were found in their ovaries.

Fecundity of D. nigricornis was closely related to repeated copulations. This relationship is common in many insect pests (Oh, 1979). Because of multiple mating, population increase must be affected by the presence of sexually active males. There may be two sets of circumstances largely affected by repeated copulation. Mates emerged from coffee plants within 12 or 18 months (this study). Therefore, most of the females had a chance of repeated copulation with males of different generations. Moreover, they lived for a relatively short time of 11.4-14.17 days. Thus population growth in an invading generation may become partly increased not only by the environmental factors (temperature) but also by the presence of repeated copulations resulting from adults of different broods.

The peripheral location of beetle eggs is therefore, related to properties of the tips of the host plant, excluding possibly the indirect and deleterious effects of the host on the pest, which were not studied. The gross reproductive, intrinsic and finite rates of increase in the current studies appeared justifiably accurate for the pest because the data from which they were derived was realistic. Additionally, in view of Birch's (1948) studies, the methods used to gather data involved negligible assumption.

From analysis of life table data all the stages of D. nigricornis were susceptible to a variety of mortality factors. There was no egg parasite or predator. Parasitism was prevalent on the larval stage while formicid ant predation was oligophagous on larval-adult stages. It was likely that the combined effects of parasitism, predation and brooding had significant impact on the incidence of occurrence of D. nigricornis in the field. In these studies on D. nigricornis the natural mortality was due to many factors. This is possibly the reason why the species has occurred throughout Central, Coastal, Rift Valley and Eastern parts of Kenya in most years, as single specimens or scattered, low density population; although higher than normal number of adults were caught over a limited area in some estates such as Matungulu in Machakos district in the current studies.

One species of parasitoid I. varipalpis accounted for no more than 10.72% of the mortality in nature. Under laboratory evaluation, this rose to 57.66%. Evidence in literature on I. eurygaster a relative of this parasitoid, shows that the parasite attained upto 21.0% level of parasitism on Aspen borers (Grimble and Knight, 1970). Higher parasitism on Aspen could be due to the sparse plant canopy and more borers which was easier for I. eurygaster to search. The borers on coffee were 1-6 per plant and concealed in the compact canopies and were

therefore more difficult to detect. Search was enhanced in the laboratory and thus accounted for increased parasitism.

Since the laboratory evaluation was confined on infested coffee shoots free of foliage, it can be argued that the starting D. nigricornis : I. varipalpis ratio that occur in nature were increased manyfold. Consequently, the proscribed numerical response of the parasites on the pest was generally quicker.

The current observations indicated that the braconids tend to remain on the same D. nigricornis infested shoots for rather too long. Therefore if the parasite is in the same area as the host; the chances of contact are increased; and more effective parasitism should result. Additionally, caging the braconid made it more efficient than otherwise as it possibly eliminated hyperparasitism (Hassel, 1966, 1968; Hassell and Varley, 1969). However, there is no report in literature to show that hyper-parasites of the braconids as parasites of cerambycids do occur. It was also possible and probable that there existed other unidentified agents whose role in the regulation of this pest appeared crucial.

Many studies on beetles are not in full agreement on how extensive damage occurs. Some researchers contend that economic damage caused by beetle borers on both crop and ornamental plants tends to be cosmetic rather than organic. They state that shortened internodes, malformed fruit, distorted leaves and galls do not harm the crop (Beal et al., 1952; Beaver, 1976). Damage by D. nigricornis is immensely destructive rather than cosmetic and affects most parameters that relate to coffee yield. However, the amount of the main stem damaged by the pest accounts for the losses incurred and should be used as a parameter for taking decisions to manage the beetle. Besides, the pertinent findings of this study (Appendix 6) can be practiced to control and regulate the pest without relying solely on insecticides. The new measures could include trapping to disrupt mating, physical removal of egg niches every season, modifying of coffee canopies to limit oviposition and to enhance levels of parasitism and predation.

These measures cause no hazards to the environment. The separation of the adult beetles by trapping would disrupt the sex ratio and probably enhance predation levels from formicid ants posed on the stems. The latter predators could still be encouraged to colonize beetle infested stems by eliminating the application of residual insecticides (Le Pelley, 1968) to control the ant species that attend to coccids.

It would be adequate for growers to maintain seasonal surveillance by removing all the shoots that desiccate

during the ovipositional period of the beetles. The egg stage would appear difficult to control with ovicides as it is concealed not only within canopies above ground but also among the different shoots of the plant where it occurs not only sparsely but at specific levels of the canopies.

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APPENDIX I. Ranking of within canopy height (cm) location of D. nigricornis egg niches relative to ground level estimated for two varieties, French Mission (FM) and SL34 during different years, 1982-1984.

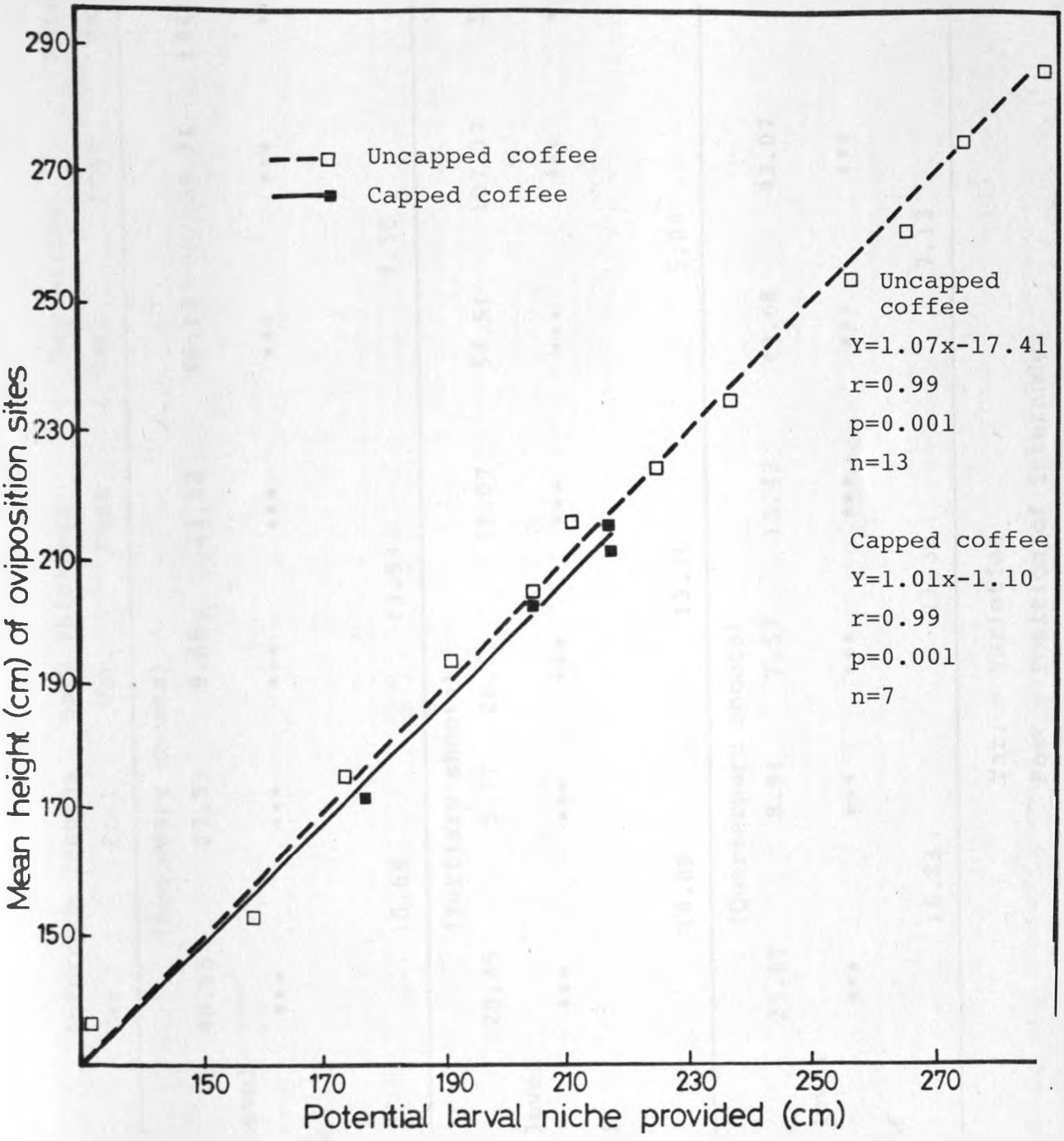
Category of shoot sampled	Long rains			
	FM		SL34	1982
	Range	Mean±s.e.	Range	Mean±s.e.
Primary	158.0-165.0	161.5±3.5	175.0-275.0	190.5±5.8
Secondary	105.0-217.0	161.1±5.9	106.0-179.0	142.4±9.6
Tertiary	50.0-220.0	168.6±1.7	126.0-170.0	148.5±2.5
Quarternary	153.0-208.0	169.0±17.0	NA	
Sucker	160.0-180.4	167.4±12.4	NA	
				1983
Primary	133.0-203.0	173.7±5.8	107.0-273.0	203.9±4.3
Secondary	104.0-217.0	164.8±2.9	108.0-270.0	181.2±4.8
Tertiary	83.0-217.0	168.4±1.9	121.0-225.0	177.4±3.6
Quarternary	NA		165.0-185.0	175.0±10.0
Sucker	143.0±0.0		NA	
				1984
Primary	NA		115.0-314.0	169.7±6.9
Secondary	135.0-220.0	182.6±2.3	110.0-300.0	179.3±5.1
Tertiary	125.0-225.0	183.9±1.4	130.0 210.0	145.6±3.4
Quarternary	160.0-192.0	180.4±3.5	NA	
Sucker	137.0-205.0	183.3±5.0	93.0-250.0	191.6±3.5

APPENDIX I CONTINUED

Category of shoot sampled	Short rains			
	FM		SL34	1982
	Range	Mean s.e.	Range	Mean s.e.
Primary	155.0-210.0	181.8±7.9	165.0-175.0	160.0±2.8
Secondary	130.0-224.0	179.6±5.6	140.0-175.0	167.6±13.7
Tertiary	90.0-226.0	175.4±1.5	103.0-220.0	177.9±6.9
Quarternary	170.0-180.0	175.9±6.9	145.0-185.0	177.5±3.2
Sucker	145.0-205.0	176.8±5.0	NA	
				1983
Primary	135.0-205.0	169.0±5.0	115.0-285.0	215.7±4.7
Secondary	125.0-230.0	163.70±8.4	115.0-240.0	180.7±7.2
Tertiary	95.0-235.0	171.92±2.7	215.0±0.0	
Quarternary	140.0-210.0	161.45±6.6	NA	
Sucker	106.0-270.0	175.4±2.4	230±0.0	

NA = Not infested

Appendix. 2. Relation between height of egg niche location by D. nigricornis and potential larval niche provided in two coffee culture systems.



Heights were determined perpendicularly while potential larval niches were measured as mean accumulated length (cm) measured from ground level to the site of initiation of infestation by D. nigricornis along the host plant stems and branches.

APPENDIX 3. Calculations on F Ratios on the internode length, bark thickness, dry matter and moisture content in secondary, tertiary and quarternary shoots of coffee.

	Internode lengths		Bark thickness		Dry matter		Moisture content	
	Var.	Post	Var.	Post	Var.	Post	Var	Post
	(Secondary shoots)							
F ratio	46.55	27.53	9.66	23.52	46.17	59.71	1444.81	275.24
Significance level (P = 0.001)	***	***	***	***	***	***	***	***
Coefficient of variability (11 d.f)	10.64		13.83		4.58		2.62	
	(Tertiary shoots)							
F ratio	20.45	5.77	26.60	21.07	54.51	107.77	56.0	110.70
Significance level (P = 0.001)	***	***	***	***	***	***	***	***
Coefficient of variability (11 d.f)	18.89		13.36		5.06		1.57	
	(Quarternary shoots)							
F ratio	25.67	8.91	7.57	15.43	49.68	43.07	49.12	42.83
Significance level (P = 0.001)	***	***	***	***	***	***	***	***
Coefficient of variability	16.83		11.39		7.13		4.40	

Var. = Varieties

Post = Position of internodes

APPENDIX 4: The internode length, dry matter, moisture content and bark thickness for tip internodes determined from tertiary branches of coffee.

Clone	Value at 1, 6 and 12 internode positions of the clones											
	Internode length (cm			Moisture Content (%)			Dry Matter (%)			Bark thickness (mm)		
	1	6	12	1	6	12	1	6	12	1	6	12
French Mission	2.1	4.0	3.6	73.0	65.0	55.0	27.0	35.0	44.2	1.2	1.5	1.8
Caturra	1.8	2.0	2.5	61.0	40.0	38.0	39.0	60.0	62.0	0.5	1.0	1.2
SL34	2.4	5.0	5.1	66.0	55.0	56.0	34.0	45.0	44.0	0.7	1.2	1.7
SL28	2.3	4.9	4.5	63.0	56.0	55.0	37.0	44.0	45.0	0.7	1.0	1.6
Purparescens	0.9	2.5	1.0	70.0	64.0	47.0	30.0	36.0	53.0	0.6	1.5	1.7
KS series A	1.0	5.0	2.5	71.0	65.0	55.0	29.0	35.0	45.0	0.8	1.2	1.5
Kit 37	2.0	3.5	3.0	80.0	63.0	55.0	20.0	37.0	45.0	0.7	1.4	10.
Gersha hybrid	2.5	4.0	3.5	78.0	67.0	55.0	22.0	33.0	45.0	0.8	1.3	1.2
Kit 83	1.5	2.5	3.0	73.0	70.0	55.0	27.0	30.0	45.0	0.6	1.2	1.8
M48	2.0	4.5	2.5	73.5	63.5	55.0	26.5	37.0	45.0	0.9	1.3	1.5
ES 65x												
Blue mountain	0.3	5.0	3.0	75.0	61.0	51.0	25.0	39.0	49.0	0.2	0.7	1.1
Egg niches	17	114	13	17	114	13	17	114	13	17	114	13
% occurrence	11.8	79.2	9.0	11.8	79.2	9.0	11.8	79.2	9.0	11.8	79.2	9.0

APPENDIX 5. The comparative duration (weeks) of boring and the amount of frass (mg) excreted by larvae of D. nigricornis which later emerged as female and male adult beetles.

Male beetles	Female beetles	Male beetles	Female beetles
Number of weeks of boring and excretion		Amount of frass excreted by larvae per period	
28	0	7876.0	0
29	0	7955.4	0
30	30	9101.1	6726.3
31	31	9730.5	12956.9
31	32	10049.8	13203.0
31	32	10184.0	13925.6
31	33	10614.8	14530.1
32	33	10856.4	14807.9
32	34	11037.5	16124.8
32	34	11296.1	17236.6
32	35	11348.0	17770.2
32	35	12362.6	18006.5
32	36	12437.9	18396.5
33	37	12558.7	18488.7
33	38	12856.1	10280.8
33	40	13170.9	24554.5
34	0	13230.6	0
34	0	13584.4	0
35	0	13676.7	0
35	0	13918.5	0
35	0	15789.2	0
36	0	15914.5	0
43	0	18011.7	0
Total 754	480	2770561.60	227008.8
n 23	14	23	14
Mean 32.78	34.29	12067.90	16214.91
s.e. 0.62	0.74	510.73	1105.61
C.v. 9.0	8.0	21.0	26.0

APPENDIX 6. List of manuscripts that have been accepted for publication in order to add to scientific knowledge from the thesis.

1. F.M.E. Wanjala and B.M. Khaemba. 1986 Parasites and predators of the yellow headed borer, Dirphya nigricornis Ol. in Kenya. Kenya Coffee. 249-252.

2. F.M.E. Wanjala and B.M. Khaemba. 1987. Oviposition behaviour and its relation to egg niche location in the Yellow headed borer Dirphya nigricornis Olivier (Coleoptera : Cerambycide). Phytoparasitica. 15(2): 97-107.

3. F.M.E. Wanjala and B.M. Khaemba. 1987. Seasonal distribution and abundance of immature stages of the yellow headed borer Dirphya nigricornis Olivier (Coleoptera: Cerambycidae) on coffee. 1987. Insect Science and its application. 8(2): 171-175.

4. F.M.E. Wanjala and B.M. Khaemba. 1987. The biology and behaviour of Iphiaulax varipalpis Cary (Hym. Braconidae) as a parasite of Dirphya nigricornis Olivier (Coleoptera: Cerambycidae). Entomophaga. 32(3): 281-289.

5. F.M.E. Wanjala and B.M. Khaemba. 1987. Some factors pertaining to coffee shoots and within canopies

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affecting the distribution of yellow headed borer Dirphya nigricornis Olivier (Coleoptera: cerambycidae) egg niches in Kenya. Insect Science and its application. 8(3): 331-336.

6. F.M.E. Wanjala and B.M. Khaemba. 1987. Regulation of Dirphya nigricornis Olivier (Coleoptera: Cerambycidae) oviposition and incubation by weather. Turrialba. 37(2): 161-164.

7. F.M.E. Wanjala and B.M. Khaemba. 1988. Reproductive characteristics that influence birth rates of Dirphya nigricornis Olivier (Coleoptera: Cerambycidae) in Kenya. Environmental entomology. 17 542-545.

8. F.M.E. Wanjala and B.M. Khaemba. Evaluation of coffee canopy damage by Dirphya nigricornis Olivier (Coleoptera: Cerambycidae). Insect Science and its application (In Press).

9. F.M.E. Wanjala. Potential for integrated control of yellow headed borer Dirphya nigricornis Olivier in Kenya. Proceedings of Symposium on integrated pest management in Tropical and subtropical cropping system. Bad Durkhem, Federal Republic of Germany (In Press).