Birth and the mother-infant relationship in the Camargue horse

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OBSERVATIONS ON THE DEVELOPMENT AND MORTALITY FACTORS IN THE LEAF MINING STAGE OF THE BEECH WEEVIL *RHYNCHAENUS FAGI* L.

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CONTENTS

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1.INTRODUCTION

The beech leaf mining weevil, *Rhynchaenus fagi* L. (Col. Curculionidae) is one member of a genus of approximately 50 species, many of which are leaf miners in habit. Most of these leaf miners are strictly monophagous in the larval stage, i.e. they only lay their eggs in one species of plant on which the larvae feed and mature. The host plant is usually a tree of wide distribution, there being for example *Rhynchaenus* species on oak *Quercus*, alder *Alnus*, willow *Salix*, poplar *Populus*, and beech *Fagus*, (HERING 1951). *R.fagi*, as its name suggests, is associated with the beech *Fagus sylvatica* L. to which it is monophagous in the larval stage. It does not, however, feed solely on this tree as an adult, as shown by BALE & LUFF (1978) and discussed later.

As one might expect the distribution of this weevil closely follows that of the host tree, being widespread throughout the moister areas of Northern and Central Europe (NIELSEN 1966). Further its distribution has been extended by the introduction of beech, by man, to areas such as Southern Ireland (BEIRNE 1946). *R.fagi* often reaches pest proportions, discolouring beech leaves as if they had been attacked by frost. LEATHERDALE (1962) records a case of heavy attack by this weevil on the Chiltern beechwoods in 1960.

The beech weevil is a well known insect in Britain and familiar to most entomologists. FOWLER (1891) gave an early description of the adult refering to it by its older alternative name of *Orchestes fagi* Ill. Such early works were largely descriptive and mention little of the organisms ecology. TRAGARDH (1910,1911) described the larval stages, pointing out the morphological changes they undergo during growth, and he concluded from such changes that there were 4 instars. Van EMDEN (1938) cleared up some problems concerning past misidentifications among the genus, as well as correcting Tragardh in recognising only 3 larval instar stages instead of 4. He pointed out that what Tragardh had regarded as a second instar was in fact a later form of the first instar stage. Several general descriptions of the larval stages have subsequently been published agreeing with Van Emden, (EIDMANN 1951, SCHERF 1964) and the most comprehensive description that by NIELSEN (1966). All the following information on the immature stages of *R.fagi* has been taken, except where additional references are given, from the latter reference.

More recent work by Bale in Northern England has concentrated on the behaviour and biology of the adult beech weevil, particularly its overwintering and feeding habits (BALE 1977,1979,1981, BALE & LUFF 1978). Relevant work on the immature stages of the beech weevil has, as previously mentioned, been done by NIELSEN (1966,1968) in Denmark, he followed this up by more diverse, but still relevant work on the activity of beech leaf-feeding guilds of insects in general, (NIELSEN 1974,1975,1978a,1978b,1978c, NIELSEN & EJLERSEN 1977).

The beech weevil has been found to be a predominant insect on beech, in areas where its abundance has been investigated, collections by NIELSEN (1975) have shown that in Denmark, together with the green leaf weevil, *Phyllobius argentatus* H., the beech weevil contributes 50-65% of all individual insects from beech trees, and 40% of the total beech canopy fauna. Annual population fluctuations of *R.fagi* have been noted (NIELSEN 1978b), but have not been recorded as being extreme in nature. However, as previously mentioned, there are reported cases of the beech weevil reaching very high densities in some beechwoods and causing considerable damage (LEATHERDALE 1962).

R.fagi is a univoltine species which overwinters as an adult (BALE 1977), egg laying occurs soon after beech bud burst in newly exposed young leaves. In Northern England bud burst on beech usually occurs in the last week in April according to BALE (1973), but in this study, in 1981, occured between the 29th April and the 20th May on different trees. The eggs are almost invariably laid in the mid vein of the leaf, but a very few are laid in a prominant lateral vein. The majority of eggs are positioned half-way along the mid vein towards the centre of the leaf (EIDMANN 1943). Previous work has shown that the number of eggs laid per leaf is most commonly 1, but is often more, and can be as high as 6 (EIDMANN 1943), further it is intuitively obvious that there is a correlation between the density of eggs laid and the average number of eggs per leaf. The behavioural aspect of oviposition is described by BALE (1973), and is apparently arranged so as to discourage the laying of more than one egg, by a female, in a given leaf. This led Bale to the conclusion that if a leaf contained more than one egg, each was probably laid by a separate female. The duration of the egg stage has been quoted as being anything from 3-10 days, and almost certainly depends to the greatest extent on temperature (EIDMANN 1951, SCHERF 1964).

The mine created by the subsequent hatching of the larva is usually refered to as a linear blotch mine, and the section of the mine created by each successive larval stage is quite characteristic. On hatching the 1st instar larvae eat their way up the mid vein of the leaf, always in the direction of the apex of that leaf, usually through the parenchymatous tissue of the lower side of the vascular bundle, although if the larva constructs the mine before the bundle sheath is sclerified the later may be consumed together with parts of the vascular bundle. After a short distance (4-5mm) the larva eats out into the leaf, parallel to the lateral veins, towards the edge of the leaf. This section of the mine is straight and narrow, some distance along which the larva enters the second instar stage. This is accompanied by an increase in body length and head capsule width. The discarded head capsule can quite easily be seen in the mine, with the use of a binocular microscope. The 2nd instar larva usually continues the mine to the edge of the leaf, and then begins the blotch phase of the mine. The succeeding 3rd instar stage then completes the blotch phase, the size of the blotch section varies a good deal, as does its position in the leaf. KLEINE (1925) stated that the area of the blotch section was larger in smaller leaves, because of the smaller depth of the leaf tissue. NIELSEN (1966) noted that the blotch area in shade leaves is approximately twice that of the blotch area in sun leaves. but correspondingly, sun leaves have approximately twice the depth of leaf mesophyll tissue, therefore the blotch phases of both types of leaf are constructed by the larvae eating the same volume of leaf tissue. Nielsen also noted a striking difference in shape of mines in sun and shade leaves, in the former the mines are regular and compact in shape, whilst the latter type of leaf has mines which spread irregularly through the tissue.

When two mines are constructed in the same leaf they often meet, but this does not appear to cause mortality, and the two larvae usually survive successfully together (EIDMANN 1943). All the larval instars mine the full depth of the leaf thickness. In the linear part of the mine the frass trail is straight, but in the blotch phase the frass is scattered in a random fashion.

The 3rd instar larva is responsible for spinning the pupal cocoon, which can clearly be seen as a dome within the blotch phase of the mine. The larva discards its head capsule in the cocoon and pupates. The pupa at first is very white in appearance, but gradually darkens to a creamy brown colour, the eyes are first to turn black, followed by the elytra, and then the rest of the body. The newly formed adult emerges from the cocoon by eating a small hole in either the upper or lower surface of the pupal casing and leaf. These new adults are not very mobile at first, and are lighter in appearance than the almost jet black adults of the previous generation. The entire developmental process from oviposition to adult emergence takes 30-35 days according to BALE & LUFF (1978), and 39-43 days according to NIELSEN (1978c). This variation may be due to the different climates in Northern England and Denmark, or to genetic differences in the populations, or to both factors.

From mid June onwards the newly hatched population of adult beech weevils becomes very mobile, and generally leaves the beech trees for alternative food sources. This movement was shown by an increase in density of *R. fagi* elsewhere in the beechwood studied by NIELSEN (1978c) at this time. BALE & LUFF (1978) found that out of 20 species of plant whose leaves were offered to beech weevils, 18 were fed upon, and these plants are listed in the paper refered to above. A second observation they made was that the leaves of the raspberry *Rubus idaeus* were significantly prefered to those of beech by newly emerged adults in June. This behaviour is probably due to the fact that as beech leaves age they become tougher in texture and probably also chemically or nutritionally unsuitable, rendering them relatively inedible (LEOPOLD & KRIEDEMANN 1975). A similar phenomenon has been studied by FEENY (1970) on oak leaves. He found that early spring feeding by the winter moth, *Cheimatobia brumata* L. on these leaves corresponded with the time of maximum leaf protein content. After this time the tanin content increases in the leaves, which inhibits the growth of the winter moth, thus rendering these leaves unsuitable for insect growth in general. It is reasonable to assume that this mechanism, or a similar one, is acting in beech leaves, causing *R.fagi* to seek alternative food.

As mentioned earlier *R.fagi* is a univoltine species, even though adults emerge by mid-June, and thus have ample time to mate and produce a second generation in a year. The ultimate cause of this behaviour is almost certainly due to the above mentioned unsuitable state of beech leaves late in the year. BALE (1979) has found that although males are sexually mature prior to overwintering, mating cannot take place due to delayed ovarian development in the corresponding females. It is further suggested by Bale that ovarian development is delayed by the occurence of a reproductive diapause in newly emerged adult females. This development is delayed until early spring, and the diapause is possibly controlled by photoperiod (BALE 1979) since the condition is terminated after 8-12 weeks of a short day followed by 4 weeks of long days.

It can easily be seen how the univoltine habit of the beech weevil is advantageous when it is considered that, even during the initial stages of the suceeding generation, many first instar larvae die due to their inability to penetrate the sclerified reticulate venation in the leaf because of late timing of oviposition (NIELSEN 1968). Therefore any attempted further generation, in the already highly sclerified beech leaf, would almost certainly lead to total mortality.

The first generation beech weevils move out of the beech canopy as soon as oviposition has ceased, usually moving to the herb layer (BALE 1981). Further GRIMM (1973) observed that this generation of adults die during the month of June, as shown by the marked decrease in the weevil population in the herb layer during this time. This gives *R.fagi* a lifespan, from the hatching of the larva to the death of the adult, of just over 12 months.

The method used by the beech weevil to move around was investigated by BALE (1981). He found that most weevils apparently fly to their host trees in late April, but these same weevils depart after oviposition largely by walking down the trunk. The new generation weevils emerging in mid June tend to fly from the beech trees to other sources of food. A high occurence of new generation weevils was discovered by Bale in the herb layer during late June and early July, which when dissected showed evidence of recent feeding.

After this period of feeding the new generation weevils move off to seek out hibernation sites which appear to be many and varied (BALE 1977). MORRIS (1968) mentions juniper, *Juniperus communis* L., ivy, *Hedera helix* L., and Scot's pine, *Pinus sylvestris* L. as possible overwintering sites in Britain. NIELSEN (1970) notes that spruce trees, planted within beechwoods, are important hibernation sites in Denmark, but he also records that large numbers of weevils overwinter in the herb layer, and in moss on the trunks of beech trees. An estimate for the density of weevils hibernating on the forest floor was put at 140,000/ha. A further favoured site was found to be on young beech trees which had retained their dead leaves. BALE (1981) found a significant preference for yew trees adjacent to beech, amongst hibernating adults, in the absence of other evergreen trees. Other incidental findings of overwintering beech weevils include STEIN (1970) who recovered them from meadows and red clover fields. According to NIELSEN (1970) it is probable that those individuals that hibernate in trees find such places as bark crevices in which to reside.

In spring the overwintering adults of *R.fagi* become increasingly active, BALE (1981) discovered this by finding increasing rates of capture in suction traps and from yew trees. Bale also found that as early as the 9th April beech weevils were captured on hawthorn, and these individuals were apparently feeding as green leaf material was found in the gut when they were dissected. The bud burst on hawthorn occurs some weeks before that on beech, and the former tree appears to be used by *R.fagi* as a source of food for egg development prior to beech bud burst (BALE & LUFF 1978). This phase precedes a peak of migration from other trees and ground vegetation on to beech at bud burst in early May, where they mate, and the females oviposit (NIELSEN 1974, BALE 1981).

The effect of the beech weevil on its host tree, in terms of reduction of leaf area and photosynthesis is uncertain. NIELSEN (1978a) calculated from 8 years of experimentation that between 3 and 9% of the leaf area index, of the average beech tree, was eaten by phyllophagous insects, of which *R.fagi* is a very major component, but he concluded however, that this had an insignificant effect in reducing photosynthesis. HERING (1951) however, stated that *R.fagi* was capable of having a devastating effect on beech forest trees, and may considerably reduce the yield of wood. BOAS (1921) noted that a premature fall of leaves, as early as June, may be caused by excessive numbers of beech weevils on rare occassions

The broad aim of this study was to investigate the causes of mortality of *R.fagi* during its leaf mining stage, and particularly mortality due to parasitisation. More precisely it was originally intended to locate trees, or parts of trees, with very different densities of the weevil mines in order to see if the parasitisation rate varied with this density. As will be seen the parasitisation rate, and other mortality factors, were not closely correlated with density, but appear to be related to other factors such as timing of bud burst and oviposition as well as degree of exposure of leaves to the sun, and overall position of the tree.

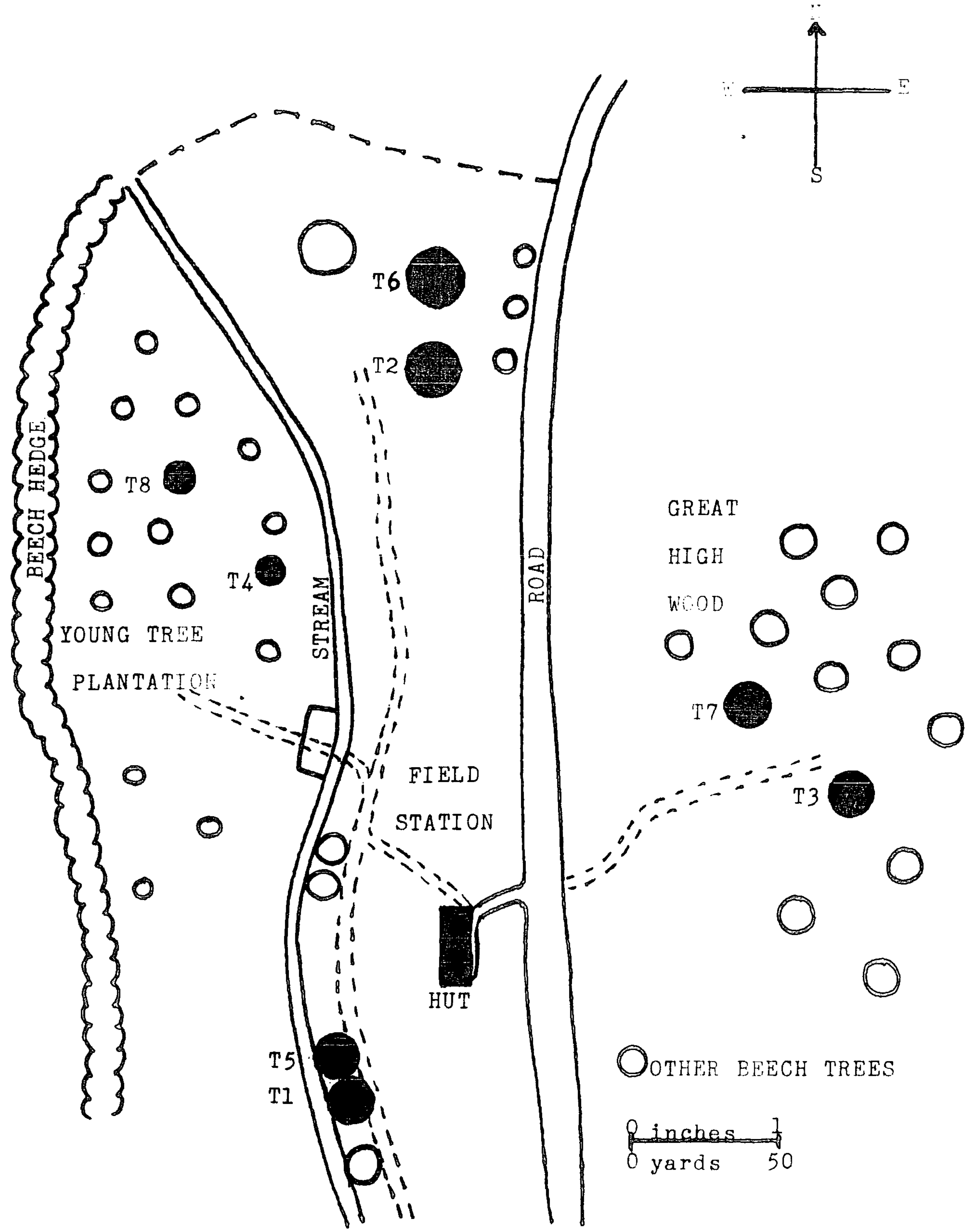
2.SITE DESCRIPTION

The majority of experiments necessary for this study were undertaken in the grounds of the Durham University Zoology Department field station and the surrounding woods, National Grid reference NZ 274406. For the purposes of the experiments, samples were taken from 8 separate trees and a beech hedge, all of these differing in terms of age, aspect, and surroundings. The situation of each of these is described later in this chapter.

In general the woodland refered to is a planted, mixed oak, *Quercus robur* L. and beech, *Fagus sylvatica* L. wood, with areas almost pure in each. The subdominant trees in the canopy are mostly sycamore, *Acer pseudoplatanus* L. which also contribute most of the tree seedlings in the shrub layer, with a small proportion of beech seedlings in some areas. Other major contributors to the shrub layer are honeysuckle, *Lonicera periclymenum* L. and wild raspberry *Rubus idaeus* L.. In the field station where the canopy is not so dense hawthorn, *Crataegus monogyna* Jacq. and birch *Betula pendula* Roth. are common up to a height of approximately 2 metres. The field layer is quite sparse with large areas covered with leaf litter, especially under stands of beech, the dominant grasses are *Deschampsia cespitosa* L. and *Holcus mollis* L. with patches of *Millium effusum* L., *Arrhenatherum elatius* (L.)J.& C.Presl. and *Poa trivialis* L. The only abundant ground layer species was the moss *Mnium hornum* H. On the west side of the field station there is a

FIGURE 1

SKETCH MAP OF THE FIELD STATION AND GREAT HIGH WOOD



young tree plantation which contained 2 of the experimental beech trees, and which is bounded by the beech hedge used in this study.

The following are individual descriptions of each of the beech trees used, plus the beech hedge, and a broad layout of all of these is shown in Fig.1.

TREE 1 - This tree is placed at the south end of the field station, and was the tree on which most work was undertaken. It is a mature specimen of approximately 30 metres in height and lies outside the main woodland in a fairly open position, adjacent to other mature beech and oak. The shrub layer is almost non-existent, but there is some nearby hawthorn and birch. Bud burst on this tree occured on the 5th May.

TREE 2 - This tree is sited at the north end of the field station, it is similar to tree 1 in that it is mature, and of approximately the same height. The canopy is slightly more closed however, and in this area the surrounding trees are other mature beech with a few subdominant birch. The ground under the tree was covered with leaf litter and the nearest shrub layer species are hawthorns some 10 metres away. Bud burst on this tree occured on the 3rd May.

TREE 3 - This was a tree sited in Great High Wood which is adjacent to the field station, on a steep easterly facing slope approximately 200 metres from the previously mentioned trees. It is again a mature tree, but in a closed canopy, where leaves in the lower canopy are in permanent shade. Surrounding trees are subdominant sycamores and mature beech, the understorey is sparse with wild raspberry being the only shrub and the majority of ground being covered by a thick layer of leaves. Bud burst was on 6th May.

TREE 4 - In contrast to the previous 3 trees, this is a young tree of approximately 5 metres in height and is located in the previously mentioned plantation on the west side of the field station. It lies in an open position, adjacent to similarly young Norway spruce, *Picea abies* (L.) Karst. and Scot's pine, *Pinus sylvestris* L., there are also some mature hawthorn close by. As would be expected there is no developed understorey, but there is a thick sward of grasses of mixed species, which has presumably been left from the time when this plantation was still a meadow. Bud burst occured on the 16th May.

TREES 5-8 - These trees were picked for their similarity to trees 1-4 respectively, and in each case were adjacent to the relevant tree (see Fig.1.). This enabled comparisons to be made between trees of almost identical position and status. Bud bursts occured on the 4th, 5th, 8th, and 12th May respectively.

BEECH HEDGE - The hedge used in this experiment was the one which surrounded the tree plantation separating it from a neighbouring meadow (see Fig.1.). The surrounding trees, therefore were the aforementioned spruce, pine, and beech, as well as some silver birch. The bud burst on the hedge was of varied date, i.e. of rather unsynchronised nature, as would be expected since it is effectively a group of small, separate trees, but the majority of these 'tree-lets' had a late bud burst, i.e. in the 3rd week in May.

One other tree was sampled, this being from nearby Little High Wood (approximately ½ a mile from the field station). This was done because the tree had the earliest noted bud burst in the surrounding area, this being on the 29th April. The tree is not mature and is subdominant in the canopy to mature beech and oak, the general surroundings are very similar to those in Great High Wood.

3. MATERIALS AND METHODS

QUALITATIVE SAMPLING FOR ADULTS;

Many different species of trees and shrubs in the area of the experimental site were sampled for adults for 3 weeks before the period of oviposition. The method of sampling used was the standard beating method (SOUTHWOOD 1966), using an iron rod and a beating tray of white cloth 64x64 cm. in size. The procedure used was to select a branch, place or hold the tray a few feet beneath, and beat the branch sharply, 3 times with the iron rod. The tray could then be examined for beech weevils, These organisms are quite mobile, being able both to jump and fly and therefore often escaped from the tray before being captured. For this reason, and because of the difficulty of applying this method quantitatively, it was a strictly qualitative investigation into whether adult beech weevils had any prefered tree, or shrub, on which to rest prior to beech bud burst and oviposition. The beating was carried out during the last 2 weeks in April and the first week in May.

ESTIMATION OF EGG LAYING CAPACITY;

Beech weevils captured by the above method were used to estimate the number of eggs laid by each female. This was done by placing each weevil in a separate Petri dish, containing a freshly picked beech leaf. The leaves were removed every day and examined for eggs under a binocular microscope. The leaves were then replaced by other freshly picked ones. Weevils which did not lay eggs were assumed to be, either males, or infertile females, and were therefore disregarded. This experiment was undertaken during the first 3 weeks in May and was discontinued when all captive weevils had ceased laying.

DENSITY OF EGG INFESTATION IN LEAVES;

Random samples of 100 or 200 leaves were removed from 5 different trees with differing times of bud burst (29th April - 16th May). Each leaf was examined under a binocular microscope for eggs laid in the mid or lateral veins in order that a quantitative estimate could be made of the density of eggs of *R.fagi* on each of the trees. Each leaf was also examined for feeding holes. The leaf samples were taken a week or more after bud burst, on any given tree, to allow time for oviposition

Leaves were selected at random at this stage, because it was not possible to tell by eye if a leaf contained a weevil egg or not. All samples were taken from the lower canopy, at this stage, because bud burst occured on the lower branches first, and because it provided the most direct comparison, with the younger tree, in terms of height above ground.

Later in the life cycle of *R.fagi*, when the mines were clearly visible in the leaf as brown blotch marks, sometimes covering as much as half of the surface area of the leaf, (last week in May onwards) it was possible to compare densities in different canopy levels of the larger trees simply by using a pair of binoculars. This study revealed that the densities were very similar at all levels (see appendix) and therefore all subsequent experiments were carried out on the lower canopy for obvious reasons of convenience.

A later set of samples were also taken in order to see if any change in density occured due to later egg laying. These samples were taken in the first 2 days in June when infested leaves were easily distinguishable, and therefore could not easily be picked at random by sight. It was then decided to pick leaves by a regular pattern from this point onwards to remedy the problem. The method used was to select a branch at random, but then to remove every third leaf or group of leaves along that branch, therefore bias caused by sight of infested leaves was eliminated.

MARKING LEAVES ON THE TREES;

A selection of leaves containing one or more eggs were marked with cardboard and string name tags on the tree. This enabled the developmental stages of *R.fagi* to be followed right up to the time of adult emergence. A total of 100 eggs were marked on each of trees 1-4, each was individually examined approximately every 3 days with the aid of a hand lens. The mines are transparent if held up to the light and the larvae can clearly be seen inside enabling the successive instar stages to be traced. This made it possible for the timing of development to be recorded, plus the action of mortality factors on the successive developmental stages. The different types of mortality factors and their recognition will be mentioned in the discussion section.

REMOVING LEAVES TO FOLLOW DEVELOPMENTAL STAGES;

As a partial comparison with the above method, samples of 100 or 200 leaves were removed by the regular sampling method, from tree 1 every 3-4 days. These leaves were then brought in to the laboratory and examined under a binocular microscope. Any leaves containing weevils at any stage of development (except eggs after the expected time of hatching) were recorded, further any signs of mortality were recorded, and as far as possible, the reasons for that mortality.

COMPARISON OF SUN AND SHADE LEAVES;

A comparison of infestation by *R.fagi* on sun and shade leaves was undertaken by removing samples of 100 leaves by the regular sampling method, from well defined areas of sun-exposed, and, shaded leaves which were in such a position in the canopy that they received no direct sunlight. This procedure was only practically possible on tree 1, because this was the only tree that possesed well defined sun and shade leaves in the lower canopy. Two sets of samples were taken, in late May, and early June.

SAMPLING FOR LEVELS OF PARASITISATION;

Samples of up to 250 leaves were removed, each containing one or more 3rd instar larvae or pupae, from all eight trees and the beech hedge. Leaves were removed as five separate samples of 50 (or less in some cases), the method of removal being simply to pick every leaf found containing the appropriate stage of *R. fagi* until the sample number was reached. The casual glance needed to distinguish these stages was not sufficient to differentiate parasitised individuals from healthy ones, so no bias was possible. Some samples, particularly those taken from the younger trees were necessarily less than 250 leaves in size because of the low density of infestation. Only 3rd instar larvae and pupae were selected, since from past work (NIELSEN 1968) these are the only stages that are apparently parasitised to any extent. All larvae and pupae were examined under a binocular microscope, and any which was found to be the host of a parasite was recorded. The characteristics of each parasite was recorded, and where possible (i.e. when it was possible to keep it alive) each was placed in a separate petri dish, retaining it within the leaf, with its host, on top of dampened filter paper. Each parasite that successfully emerged was preserved, and a representative sample was sent to the Commonwealth Institute of Entomology for comfirmation of identity.

4.RESULTS

Adults were difficult to find during the first beating operations in mid April which concentrated on the hawthorn hedges, and trees around the site. The first adults were found on some young European larch trees in Great High Wood on the 23rd April. During later beating operations in late April virtually all types of local vegetation was sampled, but very few yielded any beech weevils (see Table 1). No adults were found on beech trees prior to bud burst, nor were any found on broad leaved trees, of other species with an earlier bud burst, except hawthorn which yielded only 2 weevils. By far the largest number of adults were collected from evergreen trees and shrubs. The most fruitful tree in these terms was the Norway spruce which yielded 40 weevils, approximately 50% of adult weevils captured. As mentioned in the site description these trees were grouped together in a young stand with other tree species, including young beech (see Fig.1). Also growing in this stand were a number of Scots pine which yielded less than half the number of Norway spruce for the same amount of beating effort. The only other plant species on which *R.fagi* was commonly found at this time was the gorse bush, individuals of which were thinly scattered near the field station. Six weevils were recovered from such bushes in half an hours beating. As previously mentioned, no adults were found on beech trees prior to bud burst. However at the time of bud burst, at the end of April, adult beech weevils became increasingly common on these trees.

The number of eggs laid by each captive female is shown in Table II. Of the 24 females used in the experiment, two died in the early stages of egg laying, and are discounted in the calculation of the average egg laying capacity, since their death may have been due to the conditions of captivity. These two weevils are represented in the table by the number of eggs laid followed by the letter D.

Table III shows the density of egg infestation in sampled beech leaves. This table is arranged with the trees in order of date of bud burst, and the number of leaves with feeding holes is included as a measure of adult feeding activity. The density of later infestation is shown in Table IV, all figures are expressed as in the previous table, except infestation refers to immature weevils, and not eggs. Also this table does not include the Little High Wood tree as this was not sampled at this time. Table V shows a comparison of the distribution of infestation in early and later samples, on trees 1-4. Infestation levels are expressed as percentages and no statistical analysis is carried out on this table because the period of time between the two sampling dates varies between 19 days for tree 2, and 10 days for tree 4, and this may not have allowed sufficient time for infestation to reach a peak level on the later tree.

The average time period of each successive developmental stage, together with their ranges, of *R.fagi* on trees 1-4 is shown on Table VI. These figures were calculated

TABLE II

EGG LAYING CAPACITY OF ADULT FEMALES IN CAPTIVITY.

FEMALE	NO. EGGS LAID	DURATION OF EGG LAYING	FEMALE	NO. EGGS LAID	DURATION OF EGG LAYING
1	21	6 DAYS	13	23	7
2	30	11	14	20	7
3	2D	2	15	14	5
4	15	6	16	23	8
5	24	8	17	25	9
6	21	8	18	6D	3
7	19	9	19	17	7
8	22	7	20	13	6
9	26	9	21	18	6
10	16	5	22	21	8
11	19	6	23	15	6
12	24	9	24	19	6

AVERAGE NUMBER OF EGGS LAID = 22.2

TABLE III

DENSITY OF EGG INFESTATION IN SAMPLES OF 100 BEECH LEAVES.

TREE	DATE OF BUD BURST	DATE OF SAMPLE	NO.LEAVES WITH EGGS	TOTAL NO. OF EGGS	NO.LEAVES WITH FEEDING HOLES
LHW*	APR 29	MAY 12	9	9	66
2	MAY 3	MAY 13	30	42	100
1	MAY 5	MAY 15	37	67	86
3	MAY 6	MAY 14	27	35	74
4	MAY 16	MAY 23	20	21	42

*Tree in Little High Wood mentioned in the site description.

TABLE IV

DENSITY OF LATER INFESTATION IN SAMPLES OF 100 BEECH LEAVES. (SOME SAMPLES WERE OF 200 LEAVES AND FIGURES FROM THESE HAVE BEEN HALVED).

TREE	DATE OF BUD BURST	DATE OF SAMPLE	NO.OF INFESTED LEAVES	TOTAL NO. OF IMMATURE WEEVILS
2	MAY 3	JUN 1	48.5	65.5
1	MAY 5	JUN 1	53	77.5
3	MAY 6	JUN 1	39.5	54.5
4	MAY 16	JUN 2	25	31

TABLE V

COMPARISON OF EARLIER AND LATER INFESTATION

NO. LEAVES INFESTED %			TOTAL NO. EGGS OR IMMATURES PER 100 LEAVES	
EARLY	LATER	TREE	EARLY	LATER
30	48.5	2	42	65.5
37	53	1	67	77.5
27	39.5	3	35	54.5
20	25	4	21	31

TABLE VI

AVERAGE DURATION (AND RANGE) IN DAYS, OF DEVELOPMENTAL STAGES OF *R.FAGI* ON DIFFERENT TREES

TREE	DEVELOPMENTAL STAGE			
	1st INSTAR	2nd INSTAR	3rd INSTAR	PUPAE
1	3.6 (3-4)	4.6 (4-5)	7.0 (6-9)	14.2 (13-15)
2	3.8 (3-5)	4.5 (3-6)	6.5 (5-12)	14.0 (10-16)
3	3.7 (2-5)	4.2 (3-6)	6.4 (6-8)	13.1 (13-14)
4	3.7 (3-5)	3.7 (3-5)	5.0 (3-8)	15.4 (12-19)

from the marked leaf data on the four trees. The pupal stage was assumed to have begun when the cocoon was complete and may therefore be an overestimate and the duration of the 3rd instar stage correspondingly an underestimate.

The marked leaf data was also used to construct Table VII which shows the relative effects of mortality factors on each of trees 1-4. Each of the mortality factors listed in the table, and in Table VIII, will be explained in turn below.

Egg mortality is grouped together since the causes were largely unknown and difficult to identify. It is possible that much of this apparent mortality, may not be mortality at all, but egg infertility or empty egg cradles being mistakenly counted as containing an egg. However when egg mortality was attributable to another factor it was listed under that factor.

Abiotic mortality has several components, the most important of these, in this study, was unfavourable weather conditions. The combination of wind and rain weakens and breaks open the mines, whereupon the larvae fall out and perish. The only other type of abiotic mortality noted in this study was the breaking off of branches containing mined leaves, again of course caused by wind.

Predators were of two types, invertebrates and birds, the former pierce and suck the larvae in the mine (NIELSEN 1968) leaving a characteristic empty larval skin. Birds rip open the mine and consume the contents, and this was directly observed.

TABLE VII

RELATIVE EFFECTS OF MORTALITY FACTORS IDENTIFIED BY OBSERVATIONS ON 100 MARKED, INFESTED LEAVES, ON EACH OF 4 TREES. DETAILS OF INDIVIDUAL SOURCES OF MORTALITY, LABELLED IN COLUMN 1, ARE GIVEN IN THE TEXT.

CAUSE OF MORTALITY	FATES OF 100 INDIVIDUALS			
	TREE 1	TREE 2	TREE 3	TREE 4
EGG MORTALITY*	26	13	18	54
ABIOTIC	6	6	6	1
PREDATION	4	4	9	2
COINCIDENCE	6	6	6	8
INTERSPECIFIC COMPETITION	3	3	10	2
PATHOGENS	3	6	6	7
PARASITES	3	5	1	10
UNKNOWN	1	0	4	2
ADULTS EMERGING	48	57	40	14

* See text

The coincidence factor was explained by NIELSEN (1968) as the degree of synchronisation of the life cycle of the beech weevil with that of its host tree. This synchronisation becomes most important in spring, at the time of oviposition. As explained in the introduction, the palatability of beech leaves deteriorates markedly as they age, and if oviposition does not take place directly after bud burst, considerable mortality may occur during the early stages of larval development. This mortality is caused by the sclerification of the leaf veins, which are seen as a reticulate pattern on the surface of beech leaves. This toughening of the veins renders them inedible to early stage larvae of *R. fagi* and prevents their passage through the leaf, thus such larvae die of starvation. The shape of such mines is characteristic, and as described by Nielsen, the mines are irregularly shaped instead of the normal linear shape of the 1st instar stage and often contains the dead larvae. Although the larvae may eat their way out of the leaf leaving an exit hole.

Interspecific competition was largely caused by other leaf-eating herbivores, especially caterpillars, eating through, or otherwise interfering with the mine. This type of mortality was easily recognised, large portions of the leaves usually having been eaten, thus opening the mine and causing the larvae to fall out.

Pathogenic mortality was only recognised in its advanced stage in this study, when the fungal growth on the larva or pupa was clearly visible. There is therefore no certain proof that this was the actual cause of death.

Parasites were recognised by examining larvae and pupae under a binocular microscope. External parasites could easily be seen in this way, but internal parasites were easily missed in their early stages. In the case of the marked leaves most parasites were not discovered until the leaves were picked and taken in to the laboratory at which time they had usually themselves pupated and could easily be seen.

In the cases where the mortality was unaccounted for the cause was listed as unknown

The stages of development of the beech weevil at which the different types of mortality factors acted are shown in Table VIII. As in the previous table, when a mortality factor could not be identified, it is listed as unknown. This applies particularly, in this table, to mortality in the egg stage. The same data is used as in the previous table, the results from the 4 trees being pooled.

A simple type of life table is shown as Table IX constructed, again, from the marked leaf data. This shows the percentage effect of the mortality factors in each developmental stage, the qx figures being unaffected by the proportion of weevils dying in earlier stages. The table is not complete however, since adult mortality was not investigated.

Results of removing leaves periodically from tree 1, to follow development and the action of mortality factors is shown in Table X. The numbers of weevils in each stage

TABLE VIII

RELATIVE ACTION OF MORTALITY FACTORS AT SUCCESSIVE STAGES OF DEVELOPMENT, IDENTIFIED BY OBSERVATIONS ON 100 MARKED, INFESTED LEAVES ON EACH OF 4 TREES (SAME DATA AS TABLE VII).

CAUSE OF MORTALITY	STAGE AT WHICH MORTALITY OCCURED EGG	1st INSTAR	2nd INSTAR	3rd INSTAR	PUPAE
ABIOTIC	0	5	5	8	1
PREDATION	2	3	3	0	11
COINCIDENCE	0	25	1	0	0
INTERSPECIFIC COMPETITION	5	6	3	4	0
PATHOGENS	0	0	1	11	10
PARASITES	0	0	0	17	2
UNKNOWN	110	0	2	4	1
TOTAL	117	39	15	45	25

TABLE IX

SIMPLE LIFE TABLE BASED ON MARKED LEAF DATA OF PREVIOUS 2 TABLES.

DEVELOPMENTAL	TREE 1			TREE 2			TREE 3			TREE 4		
STAGE	dx	lx	qx	dx	lx	qx	dx	lx	qx	dx	lx	qx
EGG	26	100	.26	13	100	.13	21	100	.21	58	100	.58
1st INSTAR	10	74	.14	7	87	.08	16	79	.20	8	42	.19
2nd INSTAR	4	64	.06	2	80	.03	4	63	.06	3	34	.09
3rd INSTAR	8	60	.13	16	78	.21	7	59	.12	14	31	.45
PUPAE	4	52	.07	5	62	.08	12	52	.23	3	17	.18
ADULT		48			57			40			14	

TABLE X

NUMBERS OF *R.FAGI* FOUND IN SUCCESSIVE DEVELOPMENTAL STAGES, AND NUMBERS SUCCUMBING TO MORTALITY FACTORS (TYPES EXPLAINED IN TEXT) IN SUCCESSIVE SAMPLES OF 200 LEAVES FROM TREE 1.

DATE OF SAMPLE	NO.LEAVES INFESTED	NO.OF EGGS	NO.1st* LARVAE	NO.2nd* LARVAE	NO.3rd* LARVAE	NO.OF* PUPAE	NO.ADULTS EMERGED	MORTALITY FACTORS					
								ABIOT	PRED	COIN	INTER	PATH	PARAS
MAY 11	37	50	-	-	-	-	-	-	-	-	-	-	-
MAY 15	54	114	-	-	-	-	-	-	-	-	-	-	-
MAY 19	47	16	38	12	-	-	-	2	-	-	-	-	-
MAY 21	62	-	29	45	-	-	-	4	-	3	-	-	-
MAY 26	108	-	5	33	86	-	-	-	7	14	1	-	2
MAY 28	114	-	-	6	134	2	-	4	6	16	6	4	2
JUN 1	106	-	-	6	138	11	-	3	11	3	4	4	2
JUN 4	121	-	-	2	35	104	2	6	8	10	3	11	1
JUN 7	115	-	-	1	17	87	18	8	3	9	2	-	12

* Refers only to live individuals.

refers only to live individuals and therefore the numbers of eggs were not counted after the 19th May. Also therefore figures in the mortality section are not a proportion of those in the developmental section.

A comparison of infestation and mortality in sun and shade leaves on 2 seperate dates from tree 1 is shown in Table XI. Leaves that were exposed to direct sunlight for a good part of the day when the sun was shining were regarded as sun leaves. Shade leaves were those which received virtually no direct sunlight on any day. The same factors apply as in Table X except a percentage mortality column has been added.

Table XIIa shows a comparison of the aggregate parasitisation of *R.fagi* **within and between trees.** All parasites of the larvae and pupae are included, and a species list can be found in Table XV . The figures are absolute levels of parasitisation, except in the cases of tree 4, tree 8, and the beech hedge, where the sample sizes were less than 50 because of the scarcity of 3rd instar larvae and pupae, the figures in these cases have been multiplied up. An analysis of variance was carried out on this table, and the calculations for this analysis are completed on Table XIIb. The results of this analysis show that there is a significant variation between trees, but not between samples taken from different areas of the same tree. This result allows the parasitisation level on each tree to be regarded as a whole, and therefore allows the correlations shown on Tables XIII and XIV to be calculated. The former is a

TABLE XI

COMPARISON OF DISTRIBUTION AND MORTALITY IN SUN AND SHADE LEAVES IN SAMPLES OF 100 LEAVES FROM TREE 1.

TYPE OF LEAF	DATE OF SAMPLE	NO.LEAVES INFESTED	NO.2nd* LARVAE	NO.3rd* LARVAE	NO.OF* PUPAE	NO.ADULTS EMERGED	MORTALITY FACTORS						%MORTALITY
							ABIO	PRED	COIN	INTER	PATH	PARA	
SUN	MAY 28	57	3	67	1	-	2	3	8	3	2	1	21.1
SHADE	MAY 28	10	4	4	-	-	-	-	5	-	-	-	38.5
SUN	JUN 4	60	1	18	52	1	3	4	5	3	6	1	23.4
SHADE	JUN 4	19	-	4	4	-	-	5	5	-	5	-	65.2

*Refers only to live individuals.

TABLE XIIa

COMPARISON OF PARASITISATION WITHIN AND BETWEEN TREES WITH 10 SAMPLES OF 50*INFESTED LEAVES FROM EACH OF 8 TREES AND A BEECH HEDGE USING ANALYSIS OF VARIANCE (CONTINUED ON TABLE XIIb OVERLEAF).

		NUMBERS OF LARVAE PARASITISED					
TREE	DATE SAMPLE NO.:	-1	2	3	4	5	TOTAL
1	10-6	3	5	3	7	4	22
1	25-6	4	3	5	5	3	20
2	10-6	3	3	2	2	2	12
2	25-6	5	0	0	2	3	10
3	10-6	6	0	0	6	0	12
3	25-6	2	4	2	0	2	10
4	12-6	12.5	12.5	10	10	15	60
4	1-7	6	6	6	10	10	38
5	12-6	2	3	3	2	1	11
5	1-7	4	2	0	2	0	8
6	12-6	3	2	2	2	0	9
6	1-7	4	6	0	2	0	12
7	12-6	0	0	2	2	0	4
7	1-7	4	0	2	2	0	8
8	12-6	7.5	5	2.5	2.5	7.5	25
8	1-7	2	2	6	0	0	10
BH	12-6	15	12.5	10	15	5	57.5
BH	1-7	4	4	6	12	22	48
TOT		87	70	61.5	83.5	74.5	376.5

* Some samples were less than 50, see text.

TABLE XIIb

ANALYSIS OF VARIANCE ON DATA IN TABLE XIIa.

SOURCES OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	VARIANCE RATIO
TREES	1,082.85	17	63.7	8.6
SAMPLES	23.54	4	5.9	0.79
RESIDUAL	505.36	68	7.43	-
TOTAL	1,611.75	89	-	-

VARIATION BETWEEN TREES IS SIGNIFICANT TO 1% LEVEL.

VARIATION BETWEEN SAMPLES WITHIN TREES IS NOT SIGNIFICANT.

TABLE XIII

CORRELATION BETWEEN MINE DENSITY AND LEVEL OF PARASITISATION

TREE	DENSITY OF 3rd INSTAR & PUPAE %	LEVEL OF PARASIT%	$(X-\bar{X})(Y-\bar{Y})$	$(X-\bar{X})^2$	$(Y-\bar{Y})^2$
1	47	8.4	0.38	160.53	0.001
2	51	4.4	-66.18	277.89	15.76
3	32	4.4	9.25	5.43	15.76
4	10	19.6	-273.26	591.95	126.11
5	52	3.8	-80.75	312.23	20.88
6	55	4.2	-86.19	427.25	17.39
7	35	2.4	-4.0	0.45	35.64
8	14	7.0	27.85	413.31	1.88
BH	13	21.1	-271.53	454.97	162.05
TOTAL	310	75.3	-744.43	2644.01	395.47
MEAN	34.33	8.37	-	-	-

$r = -0.728$

TABLE XIV

CORRELATION BETWEEN DATE OF BUD BURST AND LEVEL OF PARASITISATION

TREE	BUD BURST NO. DAYS AFTER MAY 1	LEVEL OF PARASIT%	$(X-\bar{X})(Y-\bar{Y})$	$(X-\bar{X})^2$	$(Y-\bar{Y})^2$
1	5	8.4	-0.1	11.09	0.001
2	3	4.4	21.16	28.41	15.76
3	6	4.4	9.25	5.43	15.76
4	16	19.6	86.13	58.83	126.11
5	4	3.8	19.79	18.75	20.88
6	5	4.2	13.89	11.09	17.39
7	8	2.4	1.97	0.11	35.64
8	10	7.0	-2.29	2.79	1.88
BH	18	21.1	123.10	93.51	162.05
TOTAL	75	75.3	272.90	230.01	395.47
MEAN	8.33	8.37	-	-	-

$r = 0.90$

calculation of the correlation between the density of beech weevil mines and the level of parasitisation. The result of this is a significant negative correlation, indicating that the lower the density of mines the higher the level of parasitisation. The later shows the correlation between the time of bud burst and the level of parasitisation. For the purposes of this calculation a mean time of bud burst was used for the beech hedge. The result shows a highly significant positive correlation suggesting that the later the bud burst on a given tree the higher the level of parasitisation of beech weevils on that tree.

Table XV shows the frequencies of the adult parasites of *R. fagi*, seperated into species were possible, successfully from the two samples taken of 3rd instar larvae and pupae from the 8 trees and the beech hedge. Not all parasites found were put aside for rearing to the adult stage because of the numbers involved, and therefore these figures may contain a bias, especially against the commoner species. Of those parasites put aside for rearing 75% were successfully reared to the adult stage.

TABLE XV

FREQUENCIES OF THE SPECIES OF PARASITES IN THOSE CASES WHERE THE ADULTS WERE SUCCESSFULLY REARED.

SAMPLE NO.	SPECIES OF PARASITES SUCCESSFULLY REARED				
	COLASTES BRACONIUS	*CHRYSOCHARIS NEPHEREUS*	*PNIGALIO* LONGULUS*	*CIRROSPILUS DIALLUS*	*PTEROMALUS* sp.
1	15	7	2	0	0
2	16	18	11	5	1

*Includes *Pnigalio pectinicornis*.

FULL LIST OF PARASITE SPECIES REARED

Colastes braconius HALIDAY. Braconidae.

Chrysocharis nephereus WALKER. Eulophidae.

Pnigalio longulus ZETTERSTEDT. Eulophidae.

Pnigalio pectinicornis LINNAEUS Eulophidae.

Cirrospilus diallus **WALKER** Eulophidae.

Pteromalus sp. Pteromalidae.

5.DISCUSSION

From the results of the tree beating experiments, it is clear that there is a preference amongst individuals of *R.fagi* for residing in evergreen trees and shrubs as opposed to deciduous ones, in the period just prior to beech bud burst. This is shown in Table I by the fact that the 2 trees on which *R.fagi* was most commonly found at this time are evergreen; the third, gorse is a dense shrub and would provide similar cover, and the fourth is another conifer with an early bud burst. In contrast, all those trees and shrubs on which *R.fagi* was not found are deciduous. This finding is in general agreement with previous literature (MORRIS 1965, 1968, NIELSEN 1970, GRIMM 1973). In particular the finding that the most popular tree of refuge was the Norway spruce is in direct agreement with NIELSEN (1970) who estimated that 35,000 individuals per hectare were overwintering in a spruce stand within a beech forest. GRIMM (1973) also mentions spruce as a favourite site for overwintering adults. Previous work also suggests however, that leaf litter and ground vegetation are more highly favoured than trees and shrubs as overwintering sites. NIELSEN (1970) found four times as many beech weevils (140,000) in the ground layer of a beech forest than in spruce stands, and BALE (1981) found a greater density of beech weevils in the ground layer than in yew trees, which was the most highly favoured tall vegetation in his sampling area.

The reasons for this apparent dichotomy in choice of overwintering site is a matter for speculation, but it can easily be understood, that in the absence of organised planting by man, beech woodlands would not normally contain evergreen trees in which beech weevils could take refuge overwinter. It is possibly the case that the natural overwintering site of *R.fagi* is the normally deep leaf litter of pure beech forest, and that the recent practice of planting spruce and other evergreens in beech forest, particularly on the continent, has provided the beech weevil with an alternative refuge. Further this may have enabled a higher density of beech weevils to be sustained in a given area of beech forest, thus possibly leading to heavier attacks on beech trees.

As mentioned in the introduction, BALE (1981) noted that *R.fagi* could commonly be found feeding on hawthorn in a period of 2-3 weeks prior to beech bud burst. This phenomenon was not observed in this study despite the abundance of hawthorn in the area, and the close proximity of this study to the site of Bale's study near Newcastle. The only explanation I can offer for this difference is the spell of cold weather experienced in the North-East of England during late April 1981, including a moderately heavy snowfall on the 27th of that month. This may have delayed the emergence of adults from their overwintering sites preventing feeding right up until near the time of beech bud burst in the first few days in May.

At the time of bud burst on beech, *R.fagi* became very common on this tree, much more common than would be anticipated from the numbers found in the beating experiments. This suggests that the major site of refuge for adult beech weevils prior to beech bud burst was not sampled in this work, and this was most probably the ground layer vegetation.

The egglaying capacity of adult females, defined in this study as the number of eggs laid in beech leaves in tests carried out as given in the methods section, appears from the results to be rather variable. Table II shows that the minimum number of eggs laid by a female (excluding those that died) to be 13, and the maximum 30, with an average approximately halfway between these at 22.2 . Previous estimates of egg laying capacity have varied somewhat, SCHERF (1964) estimated it at 30-35 eggs and EIDMANN (1951) quoted the egg laying capacity of one female as 57. NIELSEN (1966) made his estimates by dissection of female ovaries and arrived at the figure of 22.2 as the mean, with a minimum of 12, and a maximum of 30. These later figures are almost identical to those arrived at by the method used in this study. This is obviously due to chance rather than consistency of egg laying capacity since the distribution of results is so wide. Nielsen does suggest that the figure of 57 quoted by Eidmann was probably the combined produce of 2 Or 3 females, and this of course is supported by the results in this study. Further, Nielsen considers that the observed mean is an underestimate because of the inclusion of immature females. This is probably the case in that the difference in maximum and minimum egg laying capacity is so wide, but there is no clear polarisation of results to either extreme to make this obvious. Further since there is no evidence that eggs laid by females with a small capacity are infertile, it remains valid to include these in the calculation of the mean.

The density of egg infestation on different trees, shown in Table III, and the density of later infestation, shown in Table IV, exhibit a wide range of infestation levels. The lowest infestation level of 9 eggs in 100 leaves was found on the Little High Wood tree with the earliest bud burst. The peak of infestation is reached on tree 1 with a bud burst on the 5th May, after this the level of infestation decreases to tree 4 with the latest bud burst on the 16th May, which has the second lowest infestation. A comparison of earlier and later infestation is shown on Table V as percentages. It is clear that the proportional distributions are approximately the same, but since the sampling dates are not directly comparable no statistical analysis will be made. Also the table shows that the majority of eggs are laid in the first 10 days after bud burst. The distribution of infestation suggests that this may be the result of timing, that is to say the tree with bud burst most synchronous with mating and oviposition in *R.fagi* is likely to have the highest infestation. Consequently those trees most asynchronous in their bud burst, in relation to mating and oviposition, will have the lowest infestation. This phenomenon probably depends heavily on the position of the tree in relation to other beech trees and the mobility of adult beech weevils. Since

BALE (1981) found that the beech weevil does not move far from its overwintering site to its host tree, it is probable that an isolated beech tree would have an infestation that depended, to a greater extent, on the nearby overwintering density of *R.fagi* than its time of bud burst. However all the beech trees in this study are in close proximity to other beech trees, and time of bud burst may therefore be the main controlling factor determining infestation levels.

The average duration, in days, of the developmental stages of *R.fagi*, shown on Table VI, was constructed from observations on the leaves marked on trees 1-4. Consequently the duration of the egg stage could not be estimated so accurately as each leaf was marked when the egg had already been deposited in the leaf, therefore the time of oviposition was unknown. However from all general observations the duration appeared to be from 4-6 days. This duration is undoubtedly very dependent on temperature, EIDMANN (1951) is of the opinion that the duration can vary from 3-9 days, being 3 days at 21°C and 9 days at 7°C. SCHERF (1964) estimates the duration as 6-10 days and NIELSEN (1966) found average durations in successive years of 8 and 10 days. All of these of course are continental European studies, where the temperatures tend to be lower in early spring, which may account for the slightly higher estimates than in this study.

Table VII shows the relative effects of mortality factors on the immature stages of *R.fagi*, in terms of absolute numbers in samples of 100 beech leaves from each of tree 1-4. The characteristics of these mortality factors are described in the results section, their action however, is further discussed below.

NIELSEN (1968) comments on the problem of identifying the cause of egg mortality and mentions that in the cases where the mortality is genuine there can be several causes. It is possible that predation accounts for a proportion of the mortality, but the identity of the predators is unknown. Abiotic mortality can be a cause because the laying of an egg in the mid vein weakens this structure and high winds may cause the leaf to bend at this point of weakness thus destroying the egg. Since this study took place I have been informed that a parasite of the egg stage exists which may also have contributed to the mortality (CLARIDGE pers comm). Since the data on this type of mortality is so uninformative it will not be further discussed.

Besides the types of abiotic mortality noted in this study, and described in the results section, NIELSEN (1968) mentions that late frosts can apparently kill larvae in the mine. In such cases when the ecological conditions in the mine become unfavourable to the larvae Nielsen also notes that the larvae may leave their mines by eating a small exit hole on the top side of the leaf.

Abiotic factors caused identical mortality on trees 1, 2, and 3 which was not expected since tree 3 is sheltered in the middle of Great High Wood, and therefore would be expected to incur a lower mortality of this type than the more exposed trees 1 and 2. Tree 4 incured only one death amongst the marked leaves by this cause, possibly due to the development of the beech weevil on this tree being approximately one week behind that on the previous 3 trees. This means that some of the worst wind and rain may have been experienced by weevils on tree 4 that were in an earlier stage of development (eggs and 1st instar larvae) than those on the other trees (2nd and 3rd instar larvae). This may have rendered the mines less prone to damage by this cause, but may have also led to the higher egg mortality which was observed on tree 4.

As mentioned in the results section there appears to be 2 main types of predators of the immature stages of *R. fagi*, invertebrates and birds. NIELSEN (1968) has noted *Anthocoris* sp. (Hemiptera) which pierce and suck the larvae in the mine, whilst the larvae of other invertebrates, namely the Neuropterans *Chrysopa* and *Hemerolius*, have been named as predators (BUKOVSKIJ 1936). Small insectivorous birds are common predators of leaf miners (GIBB & BETTS 1963) and both blue tits, *Parus caeruleus* and great tits, *Parus major* were positively observed in this study feeding on beech weevils; further other titmice, *Paridae* and warblers, *Sylviidae* were seen feeding in the same manner. Tree 3 appears, from the results, to have incured the highest level of mortality due to predation, being over twice the level incured by trees 1 and 2, this may be due to Great High Wood containing higher populations of predators, but this is not proven and requires further study.

The distribution of larvae dying from the coincidence factor between the four trees was almost even, this suggests that each of the trees' populations of beech weevils timed their oviposition equally well to their respective trees' bud burst. There appears to be a small but constant population of beech weevils which are sufficiently asynchronised with their host tree so as to lead to the death of their offspring or at least a fraction of it. This in evolutionary terms would tend to bring the local population of *R.fagi* into greater synchrony with the time of bud burst on local beech trees. However due to the wide variation in time of bud burst between the different beech trees in this study, it is difficult to see how this synchronisation is advantageous to the beech weevil unless individuals remain very restricted in their range i.e. to those trees bursting buds over a short period of the total time shown for beech bud burst. Evidence from past literature suggests that *R.fagi* has a restricted range when overwintering (NIELSEN 1970, BALE 1981), and it is possible that the majority of females return to the same tree from which they emerged the previous year.

Before discussing interspecific competition it must be mentioned that throughout this study no mortality was noted that could be attributed to intraspecific competition. This is perhaps suprising since the density of mines was so high on many trees, and as mentioned in the introduction no direct competition appears to take place between two or more larvae mining in the same leaf; rather a type of coexistence often takes place, with the two larvae together in converged mines. The adults also appear to avoid competition with the larvae by only feeding on beech leaves during oviposition, after which they move off to feed on other food plants (BALE 1981).

Interspecific competition comes mainly from Lepidoptera larvae. NIELSEN (1968) notes that caterpillars of *Cheimatobia* SP. have been observed to eat into the mines of beech weevils in order to moult. This deliberate destruction of the mines may account for some of the mortality in this study, as mines were observed in the blotch phase that had clearly been chewed open. The greatest level of mortality due to this factor can be seen from Table VII to be on tree 3, this suggests a higher population of other herbivores, especially caterpillars, in Great High Wood than in the field station, and indeed a greater number of caterpillars was noticeable on tree 3 than on the other trees.

Information on the mortality of larvae and pupae of *R. fagi* due to the action of pathogens is very sparse. BEIRNE (1946) reported mortality in larvae due to a species of yeast, but no identification of pathogens was attempted in this study. The distribution of this mortality factor between the four trees is approximately even, and as the action of these pathogens is unknown I shall discuss them no further.

Mortality due to parasitisation will be discussed only briefly here since it is discussed in more detail later in this section. Table VII shows that the highest level of parasitisation occurs on tree 4, being twice that of the second highest on tree 2. This difference could be due to several factors, two of which, timing of bud burst and oviposition and density of mines were investigated and are discussed later.

Table VIII showing the distribution of the individual mortality factors between the successive developmental stages, and Table IX showing a simple life table, are most conveniently discussed together. The life table has the advantage of showing mortality as a percentage of those remaining alive at the beginning of each age interval. This enables it to be recognised that there was a higher percentage mortality on tree 4 in the egg, 2nd instar, and 3rd instar stages, than on the other three trees, and had the second highest percentage mortality in the remaining two stages after tree 3. The lowest overall mortality clearly occured in the 2nd instar stage, when only between 3 and 9% of larvae died. The highest mortality however does not occur in any particular stage. The reasons for these observations can to some extent be explained by reference to Table VIII. The column refering to the second instar stage in this table clearly contains no peak of any action of any of the mortality factors, which accounts for the low percentage mortality observed at this stage in the life table. All other stages contain a peak of at least one mortality factor.

Mortality due to abiotic factors shows a wide distribution over the developmental stages, as one might expect since it is obviously not specific in its action. However the peak does occur at the 3rd instar stage, when the mine is at its largest expanse and is therefore more vulnerable to damage from wind and rain. Pupae do not succumb to such mortality easily, because even if the mine is riped open by unfavourable weather the pupa remains safe within the self constructed cocoon. Mortality due to predation appears to have two separate periods of action, the first is shown as a broad peak covering the egg to the 2nd instar stage, and the other shown as a sharp peak at the pupal stage (see Table VIII). This I tentatively suggest both from observation and from past literature is due to the action of the previously mentioned two types of predator. The first acting on the early stages, are invertebrates (mainly insects), and the second predating the pupae being insectivorous birds, particularly the titmice, *Paridae*.

As would be expected from previous discussion (page 7) mortality due to the coincidence factor was almost entirely confined to the 1st instar stage. This factor was also by far the most important in this developmental stage, causing the death of more 1st instar larvae than all the other mortality factors put together. Interspecific competition had no significant peak of action, being approximately equal in effect from the egg to the 3rd instar stage, however this mortality factor did not affect the pupal stage. This is probably again because of the protection afforded by the cocoon. These observations suggest that the action of other herbivores is non-specific in nature, and that the majority of this mortality is incidental.

Pathogenically induced mortality has a peak of action at the 3rd instar and pupal stages and contributes important amounts to the mortality in these stages. The reasons for this observed distribution of action are apparently unknown, but could possibly be the result of delayed action of the pathogens, involving an incubation period.

The action of parasites is seen to be quite specific to the 3rd instar stage with just 2 being discovered on pupae. These findings agree with past literature (NIELSEN 1968) in that parasites only attack the above mentioned developmental stages.* Since there is a time lag in the development of parasite larvae however, it is possible that the parasite egg is actually introduced to the host larvae during the hosts' 2nd instar stage. However parasites were the greatest cause of mortality in the 3rd instar stage accounting for over a third of deaths in this stage.

The life table clearly shows that tree 4 suffered by far the highest mortality of weevils, 86% dying before reaching the adult stage. This appears mainly to be due to the greater mortality both in the egg stage and due to parasites on this tree. The reasons for the former are unknown and require further investigation, but the reasons for the latter will be discussed later in this section.

Table X shows the results of the examination of successive samples of 200 leaves taken from tree 1. The number of leaves infested continues to rise until the last week in

* This is excepting the previously mentioned egg parasite.

May despite the fact that the peak number of eggs occured around the 15th May. This is possibly because some eggs may have been overlooked in early examinations, or a second wave of egg laying may have taken place. The peak of 1st instar larvae was quite sharp and occured in the third week in May, the 2nd instar stage reached a peak very soon afterwards (4 days) as would be expected from the estimated development times. The peak of 3rd instar larvae came 5-6 days later, approximately as would be expected, but the figures show a considerably higher number of this stage larvae at its peak than previous stage larvae. This is a puzzling observation and I can only suggest that this is a result of some heterogeniety in the distribution of infestation which the sampling method has failed to eliminate. Pupal numbers rise to a sharp peak 5-6 days after the previous peak which is slightly shorter than would be estimated.

The distribution of mortality factors is of limited use in this table, because few of them could be said to be dynamic in their action, i.e. they do not progress in their intensity over time. Parasitic and pathogenic [illegible] could be said to be dynamic in nature however, and both show an increase to a peak in the first week in June. This is as would be expected, being somewhat after the peak in 3rd instar larvae, because of the delay in the appearance of both the parasite larvae and pathogenic activity.

A comparison of development and mortality of beech weevils in sun-exposed and shaded leaves is shown in Table

XI. The samples were taken in late May and early June when the majority of beech weevils were in the 3rd instar and pupal stages of development. The table clearly shows a significantly greater level of weevil infestation on sun leaves (prob. that they are the same < 0.01 by χ^2). Also the progression of the developmental stages in shaded leaves appears to be behind that of sun leaves. It is possible that eggs laid in shade leaves are those of immature or asynchronised adults which lay their eggs on these leaves because of the already high density on sun leaves. The percentage mortality of *R.fagi* is clearly higher in shade leaves, and this may possibly be linked to physiological differences in the two types of leaf, but may also be the poor timing of *R.fagi* in shade leaves causing high mortality due to the coincidence factor, which is shown in Table XI to be the most important cause of mortality in shade leaves.

A comparison of parasitisation, within, and between trees using analysis of variance is shown in Table XIIa and XIIb. 10 samples were taken from each of the 8 trees and the beech hedge, 5 samples were taken in early June, and the remaining 5, 2-3 weeks later in late June, and early July. The majority of samples were 50 leaves in size, but those from the small trees and the beech hedge were a little less so as not to deplete infested leaves on these trees during sampling. Considerable variation can be seen in the levels of parasitisation, many of the samples having none, whilst one sample from the beech hedge yielded 22 parasites from 50 3rd instar larvae or pupae of *R.fagi*.

This table was subjected to an analysis of variance test in order to see if there was any statistically significant variation, either within, or between trees. Table XIIb shows the results of this analysis, namely that there is a significant difference in the level of parasitisation between trees, but not within individual trees. These facts suggest that there are characteristics which differ between the trees used in this study, which renders beech leaf miners, on different trees, differentially susceptible to attack by parasites. Within the same tree however, these leaf miners appear, largely, to be equally susceptible to attack, i.e. there is little patchiness in the distribution of action of the parasites, at least within the sampled canopy layer of single trees.

One characteristic that could cause variation in the level of parasitisation is the density of mines on the tree. This possibility is investigated in Table XIII. This table compares the density of mines, measured for each individual tree, with the observed average level of parasitisation. A calculation of the correlation coefficient is shown, the result being $r = -0.728$, this with 8 degrees of freedom is a significant negative correlation to the $P > 0.98$ level. This is a suprising result, and effectively means that the lower the density of mines on a given tree the higher the level of parasitisation. This phenomenon may however, be due to a greater extent to the timing element discussed above. Table XIV shows a comparison between the date of bud burst on each tree, expressed as the number of days from the 1st May, an arbitrary date near the date of the earliest bud burst, with the percentage parasitisation on each tree. The correlation coefficient of these two mesurements $r = 0.90$, which with 8 degrees of freedom, is a significant positive correlation to the $P > 0.999$ level.

This correlation suggests that the timing of attack by the parasites, of the immature stages of *R. fagi*, is such that the major proportion of beech weevil larvae, on the trees of earlier bud burst, which contain the highest densities of beech weevils, are suitably advanced in their development so as to escape the worst of this attack. Larvae on trees of later bud burst however, are at a suitable stage of development (3rd instar stage) when the majority of adult female parasites are ready to oviposit. These larvae therefore suffer a higher level of parasitisation even though they exist in lower densities.

The above observations are however complicated by the fact that, in this study, the larvae of *R. fagi* were parasitised by six identified species of Hymenoptera which are named in Table XV. This table shows the difference in the numbers of each species of parasite, successfully reared, from collections in the early and late samples. This table is not directly related to the timing element in the level of parasitisation previously discussed, because firstly, in comparison with the number of parasites recorded few were reared successfully. This was particularly the case with internal parasites, many of which were destroyed during the dissection of *R. fagi* larvae in order to ascertain whether that larvae contained such a parasite. Secondly, as previously mentioned, not all samples taken for this experiment were of the same size, those trees having a late bud burst being represented by smaller samples (because of lower mine density on these trees), therefore the relative numbers of parasite species are biased towards those species predominantly parasitising *R, fagi* larvae in trees of early bud burst. These problems aside , general observations can be made on the timing of action of each species parasite.

The most commonly reared parasite was *Colastes braconius* Hal. (Ichneumonoidea, Braconidae) which was found to be an external parasite of *R, fagi* larvae. This observation is in disagreement with BEIRNE (1946), and BALE (1973), both of whom consider this species to be an endoparasite. However SHAW & ASKEW (1976), after extensive studies on this species (named by them as *Exothecus braconius*) on many different hosts, including *R. fagi*, regarded it as an ectoparasite, and state that Beirnes' illustrations of the 1st instar larvae of this species suggests that he may have confused the parasite larvae with that of another species. This parasite is very polyphagous in habit, parasitising leaf miners of Lepidoptera, Coleoptera, and Diptera, and normally has several generations in one year (BOUCEK & ASKEW 1968). The larvae spins a silken white cocoon in the mine, turning pale blue on pupating, and the adult is of typical Braconid shape with a dark brown-black body and pale yellow legs. *C. braconius* occurs almost equally in samples 1 and 2, suggesting a broad period of oviposition, although it was noticeable that those found in sample 2 were predominantly in an advanced stage of development.

Chrysocharis nephereus Walk. (Chalcidoidea, Eulophidae) is a solitary endoparasite which however leaves its host to feed externally on it before pupating, hence many individuals of this species were recorded as external parasites in this study. The species is polyphagous, attacking larvae of both Lepidoptera and Coleoptera. Once the larva has finished feeding it changes to a shiny black pupa clearly visible in the mine. The adult is an attractive metallic green-blue colour with pale cream legs. The table shows that the majority of this species was found in sample 2 suggesting a late period of oviposition, more suited to the timing of those larvae on trees of late bud burst

***Pnigalio** longulus* and *P.pectinicornis* (Chalcidoidea, Eulophidae) are closely related species and will therefore be considered together. They are both solitary ectoparasites of a wide range of Lepidopterous and Coleopterous larvae. The adults are dark green in colour with dark grey legs. As with *C.nephereus* the majority were collected in sample 2 suggesting a timing most suited to attack of larvae on trees with a late bud burst.

Cirrospilus diallus Walk. (Chalcidoidea, Eulophidae) are also polyphagous ectoparasites of leaf-mining larvae and occasionally of gall makers. The adults are light yellow-brown with darker legs. All individuals of this species were reared from sample 2 collections again suggesting timing in synchrony with larvae on trees of late bud burst.

One individual of a *Pteromalus* sp. (Pteromalidae) was reared from a sample 2 collection on tree 1 of early bud burst. The majority of species of this genus are external, gregarious parasites of Lepidopterous and Coleopterous larvae and pupae. However internal parasitism is known within the genus (CLAUSEN 1940) and this individual was recorded as such in this study.

In general the majority of parasites were reared from sample 2 collections, particularly those of the Chalcidoidea, and this suggests a relatively late period of action, although the data is such that it cannot be linked with the timing of development of *R.fagi*. Such a link could only be made by more detailed sampling and extensive rearing of parasites which was not foreseen in this study but would be advised in any future experiments.

As all six species of parasites are non-specific to *R.fagi* it may not be necessary for them to synchronise their oviposition with the larval occurence of *R.fagi*. It may however be the case that the majority of the population of *R.fagi* may escape parasitisation by timing their 3rd instar and pupal stages to be earlier than the main occurence of these parasite adults. The timing of those beech weevils on trees with a late bud burst however is suitable for parasite attack and therefore would explain the higher incidence of parasitisation in these populations.

6. SUMMARY

A detailed study was made of the ecology of the leaf mining stages of the beech weevil *Rhynchaenus fagi* L. in Durham during the spring of 1981. This was from the time prior to oviposition, through the entire developmental stage, up to the time of adult emergence in mid-June.

The major experiments involved removing samples of 100-200 leaves on each of 4 trees with differing times of bud burst to measure the distribution of infestation, and successive samples of this size from a single tree to follow rates of development. The level of infestation on sun and shade leaves was compared by removing samples of 100 of each type of leaf, on two occasions, from a single tree. 100 leaves were marked on each of 4 trees to further record rates of development, plus the action of mortality factors and their relative effect on the population during the same period. Later experiments involved removal of samples of 250 3rd instar larvae or pupae to measure levels of parasitisation during mid-June and again during late June-early July.

The results of these experiments show the distribution of infestation on trees of different times of bud burst to be uneven, and the rate of development of successive stages of *R. fagi* is shown. The relative action of seven recognised mortality factors, namely egg mortality (various agents) abiotic (weather), predators (invertebrates and birds), coincidence factor (death of larvae from leaf sclerificati-

on), interspecific competition (caterpillars eating mine), pathogens and parasites, plus their mode and time of action are discussed. The results of the comparison of sun and shade leaves show a higher level of infestation on sun leaves and a higher percentage mortality on shade leaves. The study of parasites showed a significant variation in the level of parasitisation between trees, but not within the same tree. A significant negative correlation is shown between density of mines and level of parasitisation, but this is partly explained by the positive correlation between time of bud burst and level of parasitisation, i.e. the later the bud burst on a tree the higher the parasitisation of *R.fagi* on that tree.

From the rearing of parasites, six types were identified to species level and one to genus level, all of which had previously been recorded for this host.

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APPENDIX I

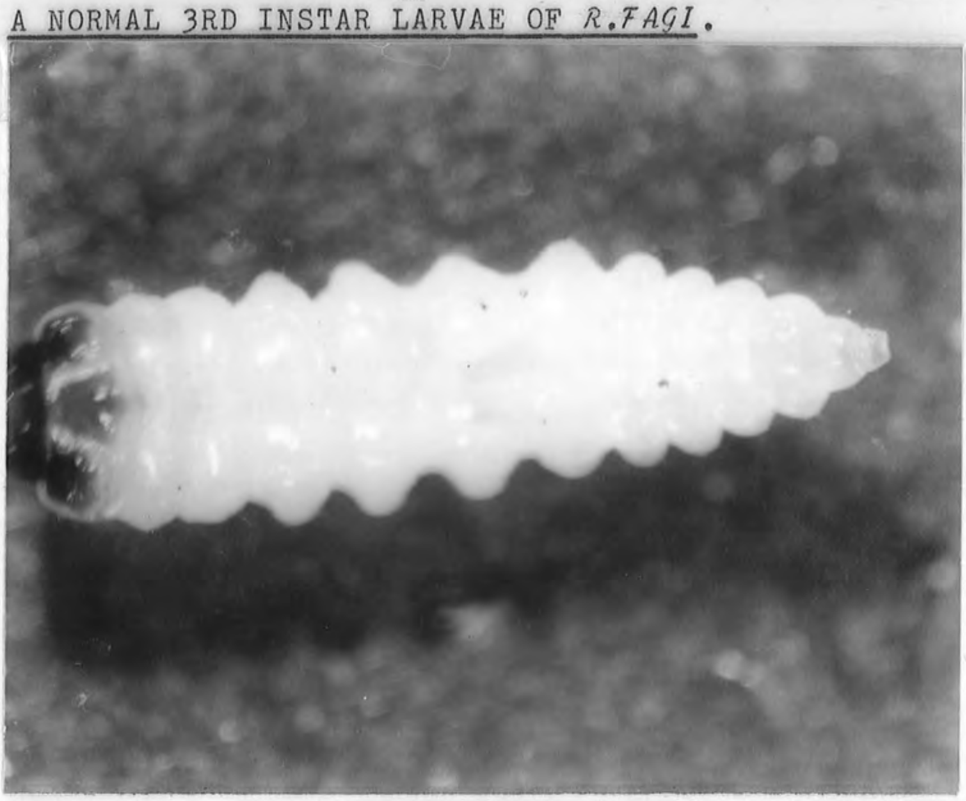
DENSITY OF *R.FAGI* MINES AT DIFFERENT CANOPY LEVELS FROM COUNTS MADE WITH BINOCULARS (8 X 10) IN THE FIELD, SAMPLE SIZE = 500

TREE	PERCENTAGE INFESTATION IN LEAVES		
	LOWER CANOPY	MIDDLE CANOPY	TOP CANOPY
1	52	49	59
2	54	48	57

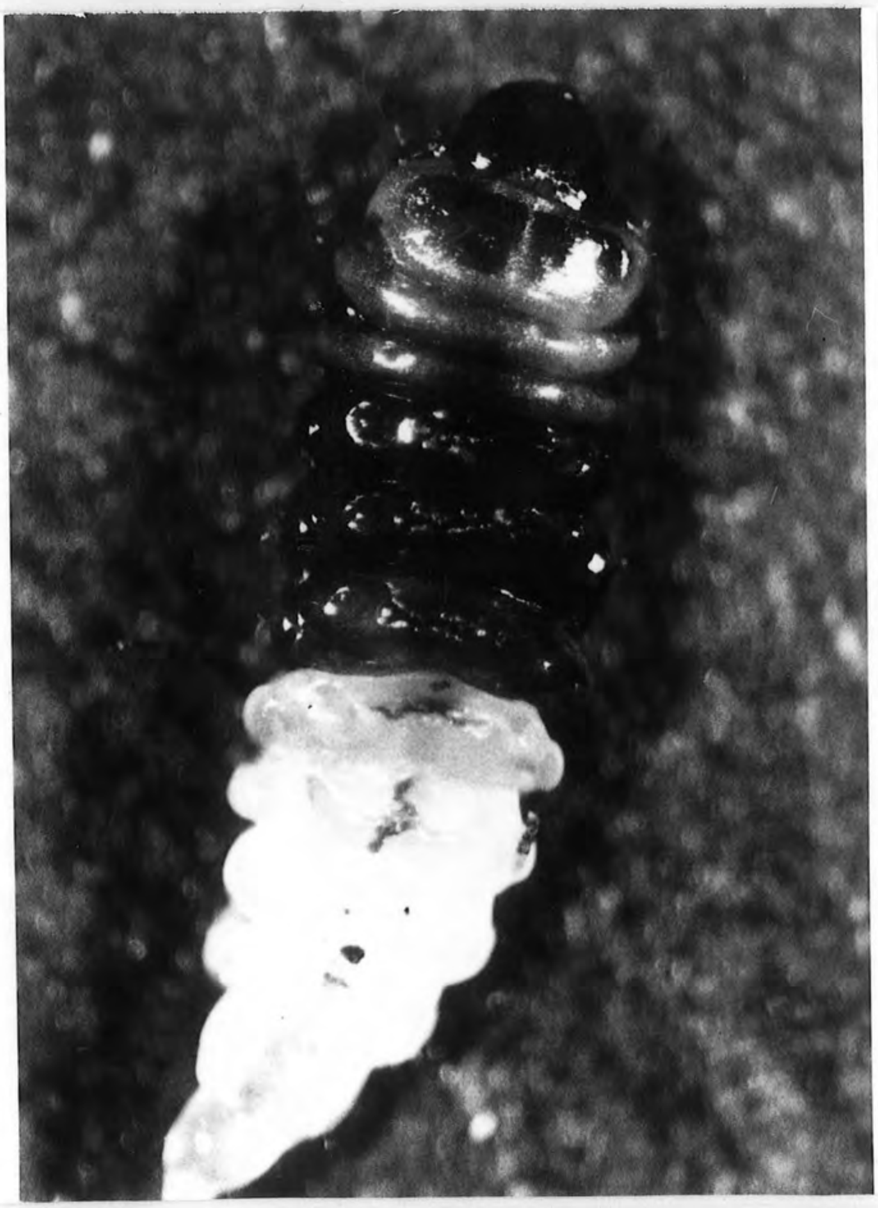
APPENDIX 2

1. AN EGG OF *R.FAGI* THAT HAS BEEN TEASED FROM ITS CRADLE IN THE MID VEIN OF A LEAF.

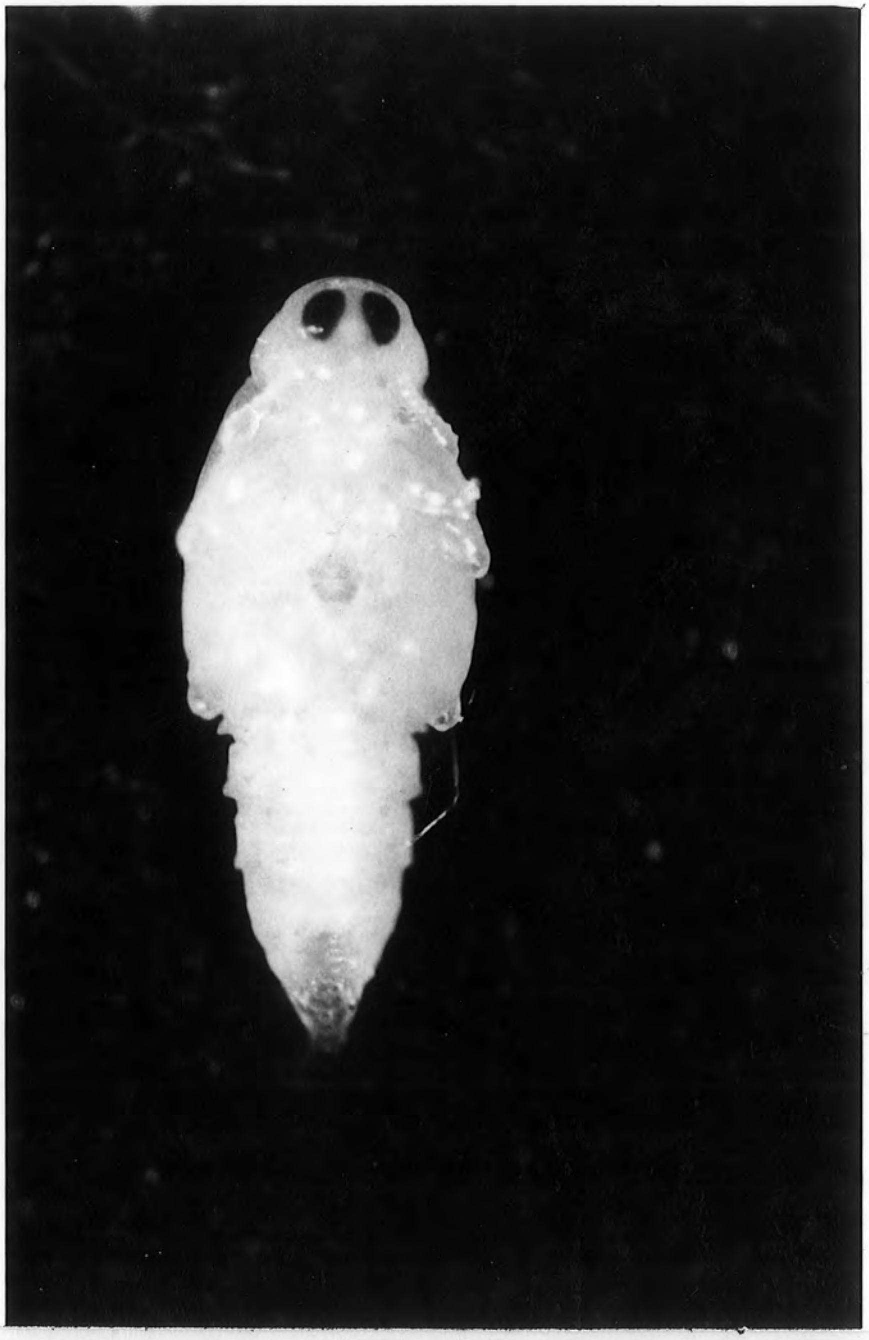
2. A NORMAL 3RD INSTAR LARVAE OF *R.FAGI*.



3. A 3RD INSTAR LARVAE OF *R.FAGI* THAT HAS BEEN PARASITISED BY THE INTERNAL PARASITE *CHRYSOCHARIS NEPHEREUS*.



4. A PUPAE OF *R.FAGI* THAT HAS ALREADY DEVELOPED BLACK EYES.



5. THE PUPAL COCOON CONTAINING THE EXTERNAL PARASITE *COLASTES BRACONIUS*.