STUDIES ON THE BIOLOGY AND ECOLOGY OF THE CABBAGE MOTH, *MAMESTRA BRASSICAE* L. (LEPIDOPTERA : NOCTUIDAE)

by

AQUILES MONTAGNE

Ingeniero Agronomo

(Venezuela)

A thesis submitted for the degree of Doctor of Philosophy of the University of London and the Diploma of Imperial College

Department of Zoology and Applied Entomology,
Imperial College Field Station,
Silwood Park,
Ascot
Berkshire

September 1977

TABLE OF CONTENT

Table of Contents (Continued)

Table of Contents (Continued)

ABSTRACT

Mamestra brassicae L. (Lepidoptera: Noctuidae) is mainly a pest of brassicas. Experiments with this species were conducted both in constant temperature rooms and in the field.

In the laboratory, the effects of different constant temperatures on the rate of development and mortalities of eggs, larvae and pupae were investigated; at 20°C, fecundity, fertility and longevity of adults were also measured.

The effects of larval rearing density on the behaviour of larvae and morphological and morphometrics characteristics of larvae and pupae were examined. A comparison was made of the abilities of individually-reared larvae and larvae reared in groups to survive starvation and dessication, and treatment with the insecticide DDT.

Both the synchrony of eggs within an egg mass and the effects of grouping during the first instar larvae were studied.

Using artificial infestations, the mortality factors acting on the egg and larval stages were studied in the field. The study of larval mortality factors was aided by caging to exclude ground predator, parasite, birds and rainfall; additional observations were made using the natural uncaged population. Observations were made on the distribution of egg masses and different larval instars on the host plant, and the egg masses distribution over the leaf surface. The dispersal and mortality of the sixth instar larvae and their pupation sites were studied using radioactive tags (Ir^{192}).

GENERAL INTRODUCTION

The cabbage moth, Mamestra brassicae L. is mainly a pest on cabbages and although it has been recorded from a number of different plant species belonging to several families, it prefers cabbage and it is consistently reported as a serious pest on it more than on any other.

M. brassicae is distributed almost completely throughout the Paleartic Region, except in the far north, from Western Europe to the coasts of the Pacific ocean reaching Japan. In the south it reaches the coasts and islands of the Mediterranean sea, the subtropical zone of Asia Minor, and the mountain districts of north-western India and southern China.

The adaptability of M. brassicae to different climatic conditions and its recognised status as a major pest in many temperate and subtropical regions makes the study of M. brassicae important from the economic as well as from the biological point of view. Therefore, it is not surprising to find that in a survey of the literature many papers deal with this insect. However, most of them are concerned with brief accounts of observations on the bionomics including biology, life history, seasonal variation, geographical distribution, host-plants or just its occurrence. A few deal with some aspects of its ecology and population dynamics, and in this respect Japanese workers have contributed the most. Many of the published papers on Mamestra are total or partially devouted to its control, either chemical or by other means e.g., parasite, disease, cultural measures. This seems to be justified because of the relatively high value of the crops which it attacks.

Along with a number of other species, the larvae of M. brassicae progressively change colour from pale to dark with increasing population density, and at the same time, other changes occur in its behaviour and physiology. This type of continuous polymorphism has been called "Phase variation" because it is very similar in many respects to that in locusts (Iwao, 1968). This and the frequent reports of mass outbreaks cited in the literature make "Phase variation" an important aspect in the study of the biology of this insect.

Although M. brassicae is considered a major pest in eastern Europe, U.S.S.R., Japan and other places, in England it is a minor pest. Attacks are most common in gardens and allotments occurring occasionally on field scale; which perhaps accounts for the relatively little attention given to it by British entomologists. In this respect, it is then, interesting to obtain information on the mortality factors that operate under field conditions in this country as the findings may be relevant to other situations.

The aims of the present study were to investigate some aspects of the biology and ecology of the cabbage moth and can be summarised as follows:

a) To give a general description of the life history and habits of M. brassicae; to study in some detail the effect of temperature on the pre-imaginal stages; and the fecundity and longevity of the adults.

b) To examine some aspects of the effect of larval density on its physiology, morphology and behaviour.

c) To study the causes and rates of mortality of M. brassicae in

field conditions.

It was hoped that the study would have importance in the approach to control strategies by means of a better understanding of the insect.

SECTION 1

THE BIOLOGY OF *Mamestra brassicae*

1.1 Introduction

As already emphasised, there is a great deal of literature dealing with the bionomics of *Mamestra brassicae*. However, most of it consists of brief accounts of the biology, life history, seasonal variation, host-plants etc., many being only either records of uncommon plants or of its simple inclusion on annual reports stating its occurrence along with other pests.

Among the papers which give some detail regarding the general bionomics of this species are: Masaitis (1925), Nikolova (1945), Way *et al.* (1951), Dolidze (1957), Ishikura *et al.* (1958), Stepanova (1962), Noll (1963), Peiu (1963), Dusaussoy (1966), Ionescu (1964), Afonskaya (1966), Petrukha *et al.* (1967), Karadzhov (1970), Dochkova (1971), Maleki-Milani (1971), Rygg *et al.* (1975).

There are some papers dealing in detail with specific aspects of the biology of this species. The main factors affecting the fecundity and fertility have been studied by Bonnemaison (1960b; 1961 a, b, c; 1962 a, b) in France. The factors involved in the pupal diapause have been thoroughly investigated by Matsumoto *et al.*, (1953), Otuka *et al.* (1955), Uchida *et al.* (1953, 1954), Santa (1955), Masaki (1956 a, b), Masaki *et al.* (1965), Masaki (1958), and Bonnemaison (1959, 1960a, 1961 b, c, d).

In Japan, Hirata (from 1954 to 1967) has researched in several

aspects on the biology, habits and ecology of Mamestra and other Lepidoptera on cruciferous crops. He has also produced papers on phase variation in Mamestra which will be dealt with in the next Section.

This Section gives a general description of the life cycle of Mamestra and incorporates data and comments on its habits on the brussels plant. The effect of temperature on the immature stages, and the study of fecundity and longevity of the adults is also investigated and discussed in the context of the published information.

1.2 General Description of the Stages

EGG

The eggs (Fig. 1.1) are semi-spherical, circular in outline when viewed perpendicular to the substrate. They have between 17-18 ridges running vertically from the micropyle to the base, in between those there are a series of ridges that do not extend as far upwards as the others. The grooves between ridges bear minute transverse ribs. When first deposited the eggs are cream coloured, but after 24 hours embryonated eggs develop a pattern of reddish brown spots around the micropyle and also near the equator; as incubation proceeds they darken; shortly before hatching and on magnification, the larva can be seen coiled with the head in the middle, just beneath the micropyle, and explains why the exit hole is normally in the upper half of the egg. The average diameter is 0.67 mm.

LARVA

A general description of the larvae, particularly the last instar

has been given by many authors e.g., Balachowsky and Masnil (1936), Balachowsky (1972), Cameron (1939), Smith (1931), South (1946), Jones & Jones (1974). A very detailed description with emphasis on the morphology is that of Melis (1936). The description of the fully-grown larvae to be given is based mainly on those authors.

There are six larval instars.

Just after hatching the larva is about 2.2 mm in length. It has a head and prothoracic shield black. The body is white coloured but the thorax and first part of the abdomen are reddish brown due to the amniotic fluid swallowed before hatching. The 1st and 2nd pairs of prolegs are subnormal in size which makes it loop while crawling. This becomes less noticeable as the larva develops and is barely perceptible by the 4th instar. After the first meals they take a green colour due to the pigment of the host plant.

The second instar has a cream coloured head with each setal base black. Body green with three, just deliniated, white lines running dorsally and one laterally. From the third instar the head is only cream and the lines on the body are somewhat more conspicuous. In addition during the 4th instar and also 5th instar the dorsum and lateral sides are flecked with yellowish white.

The 6th instar (Fig. 1.2) is rather cylindrical in shape and hairless. Its colour varies greatly, sometimes light green, dark green, brown and even black on the upper surface. Sometimes this coloration is observable during the two preceding instars (details on the coloration are given in Chapter two). There are three light lines on the back with

oblique black dashes on each segment. The subspiracular line is yellowish or orange flecked. The fully-grown larve is about 4 cm in length.

PUPA

The pupa (Fig. 1.3) is typical of Noctuidae, shiny and brown in colour. It measures an average of 2.2 cm in length.

ADULT

The moth (Fig. 1.4) has been described by many authors. Smith (1931) gives the following: General colour ashy grey, varying to darker or almost black, often with an ochreous tint; the remiform mark is distinct with a white outline and white sub-marginal line; orbicular mark with a black margin; claviform mark often indistinct. There is a white transverse zigzag line across the fore wing near the basal margin; hind wings brown with a central spot. Wing expanse 42 mm.

1.3 Life History and Habits

The female lays a single layer mass of eggs that can exceed 500 eggs.

The distribution of egg masses on the Brussels sprouts plant was investigated in 1976. The plant was divided into three parts: the head which comprised those leaves on top and some slightly open encircling them; the lower part comprising the basal leaves, some of which usually touch the ground. Between these two the intermediate part which was sub-divided into upper and lower parts. According to this, the distribution

Figure 1.1. *Mamestra brassicae* egg mass.

Figure 1.2. *Mamestra brassicae* sixth instar larvae. Characteristic C-shaped curled position after disturbance.

Larval colour types (see section 2 for details)

V II I IV III

X4.3

X1.4

Figure 1.3. *Mamestra brassicae* pupa. Ventral (right) and lateral (left) aspects.

Figure 1.4. *Mamestra brassicae* adult. Resting position.

X3.3

X4.0

of egg masses and mainly hatching places, which were more easily found, were recorded.

The majority of the masses were located in the intermediate part of the plant, especially in the lower part which accounted for 54.1% of the total (Table 1.1).

TABLE 1.1 Distribution of Egg Masses and Hatching Places on Brussels Sprouts Plant

Plant part	Number of egg masses found	%
Head	1	1.6
Intermediate / Upper	18	29.5
Intermediate \ Lower	33	54.1
Lower	9	14.8
TOTAL	61	100.0

On the cabbage Hirata (1962b) observed that the females deposited the egg batches on the leaves of the middle and upper parts of aged plants.

In general the eggs are deposited on the underside of leaves (Hirata 1962b) and in only one case, in our observations was an egg mass found on the upper surface. This preference for the underside was also observed in oviposition cages under laboratory conditions using towel paper as substrate. (Fig. 1.5).

In an attempt to study the distribution of egg masses over the

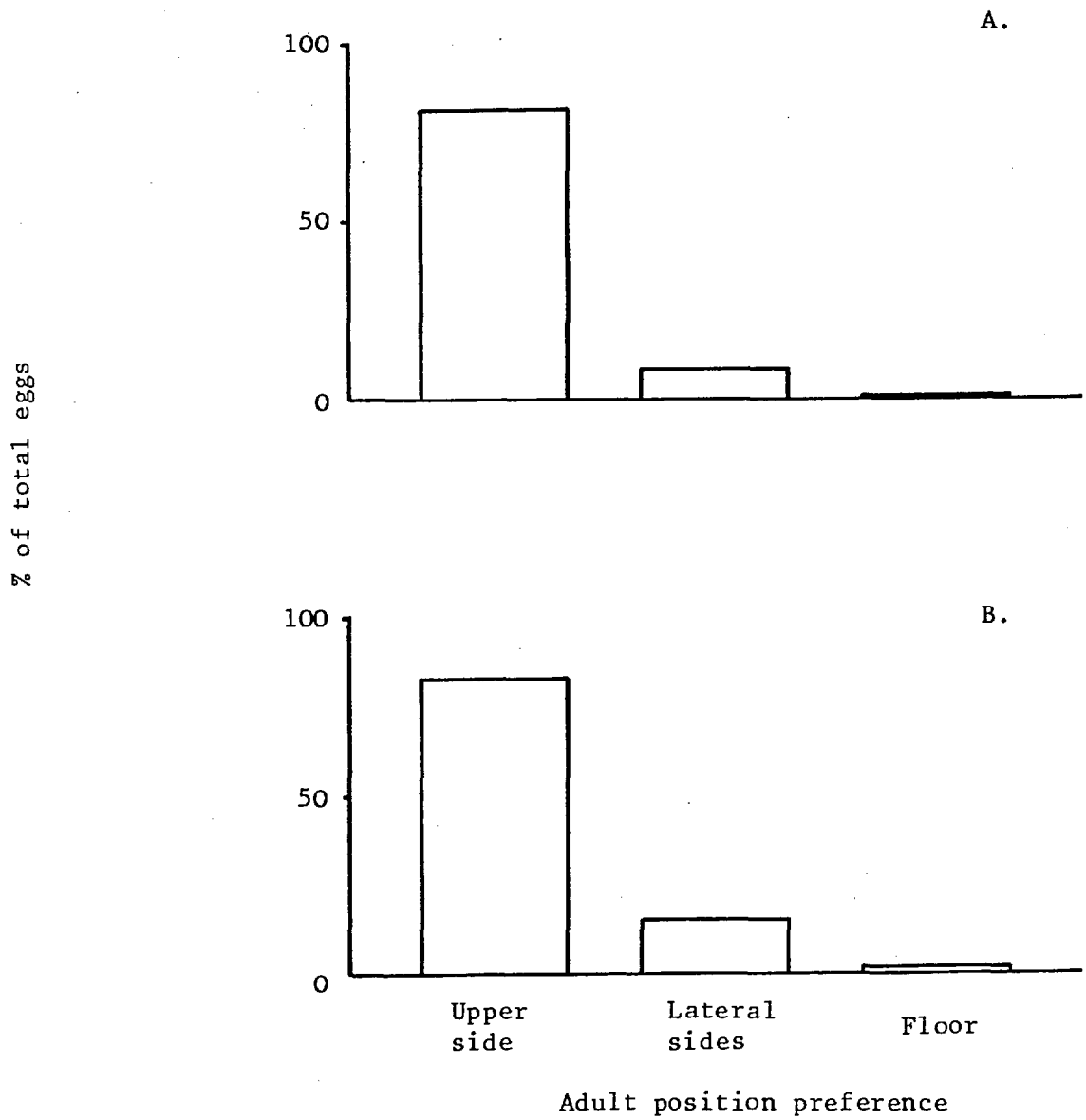


Figure 1.5. Adult position preference for oviposition under laboratory conditions.

A. Adults from larvae reared on Brussels sprouts.

B. Adults from larvae reared on artificial diet.

surface of the leaf, in 1976 leaves known to have borne Mamestra egg masses were brought to the laboratory and photocopied. From these copies, measurements were taken from the egg mass position to the nearest edge of the leaf. This method was found to be the most suitable as there was considerable variation in size and shape of the leaves. From the frequency distributions (Fig. 1.6) it can be seen that the highest frequency was located in the 2nd class from the edge. This may be a consequence of the position of the female while ovipositing. The position of this 2nd class would correspond to the maximum reach of the female abdomen when clinging to the edge of the leaf. The bimodality observed is probable because the females also use the main rib to get support while laying. Observation of the behaviour of females searching for a place to lay, especially while landing or moving about the leaves is necessary to ascertain the mechanisms involved. Harcourt (1963b) noted that generally Trichoplusia ni (Hbn) females deposit their eggs near the leaf margin.

Oviposition on the underside of the leaves may be an adaptation to reduce egg mortality resulting from rain or direct sunlight exposure. High solar radiation has been shown by Dolidze (1957) to be lethal to the egg stage.

When ready to hatch the larva eats the chorion until a roughly circular area, similar in diameter to its head has been devoured, then it thrusts it head through the emergence hole helped by muscular contractions (peristaltic waves) passing forward over the body from tail to head. On completing hatching the larva usually is extended full length upon the neighbouring eggs, with its head farthest from the egg. After swaying from side to side several times, the larva reverses its position, bringing its head into contact with the egg shell, and this shell, on which the

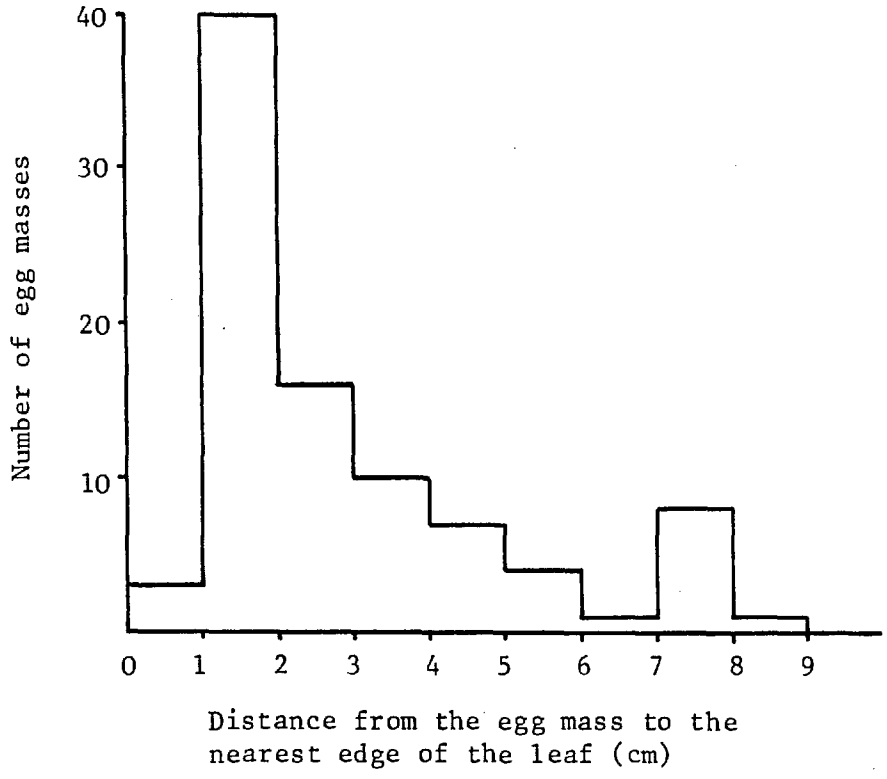


Figure 1.6. The distribution of *Mamestra* egg masses over the surface of the leaf.

larva has already fed during hatching usually is its first food. During the process of hatching, it is possible to see larvae moving about on the egg mass while others are eating or making swaying movements. Although first instar larvae are photopositive (Omino et al., 1973) during hatching and before eating, they remain grouped on the egg mass seemingly unaffected by light during that period.

The hatchlings remain on the egg mass, usually eating all the egg shells. They move within or about, the area where they hatched and spin silk threads. These threads may serve as guides or support for the legs and prolegs when crawling and also may help the larvae to stay together. When one or more larvae begin a feeding place the rest of the larvae soon join them, enlarging the holes, thus, almost all the individuals from the egg mass get their first meal in a short period of time.

The larval aggregation may be maintained up to the second instar, thereafter, the larvae disperse to other leaves of the same plant. Hirata (1966b) has noted that the direction of their dispersion is always towards the upper leaves of cabbage plants.

The distribution of the different larval instars on the brussels sprouts was recorded during July and August 1975. The plant was divided in three parts namely, head, intermediate and lower part. Later the ground beneath the plants was taken into account. Moulting stages were also included.

The results, expressed as % of total number of a given instar within the different divisions (Fig. 1.7) showed that the first instar was mainly found in the intermediate part of the plant, entirely influenced by egg

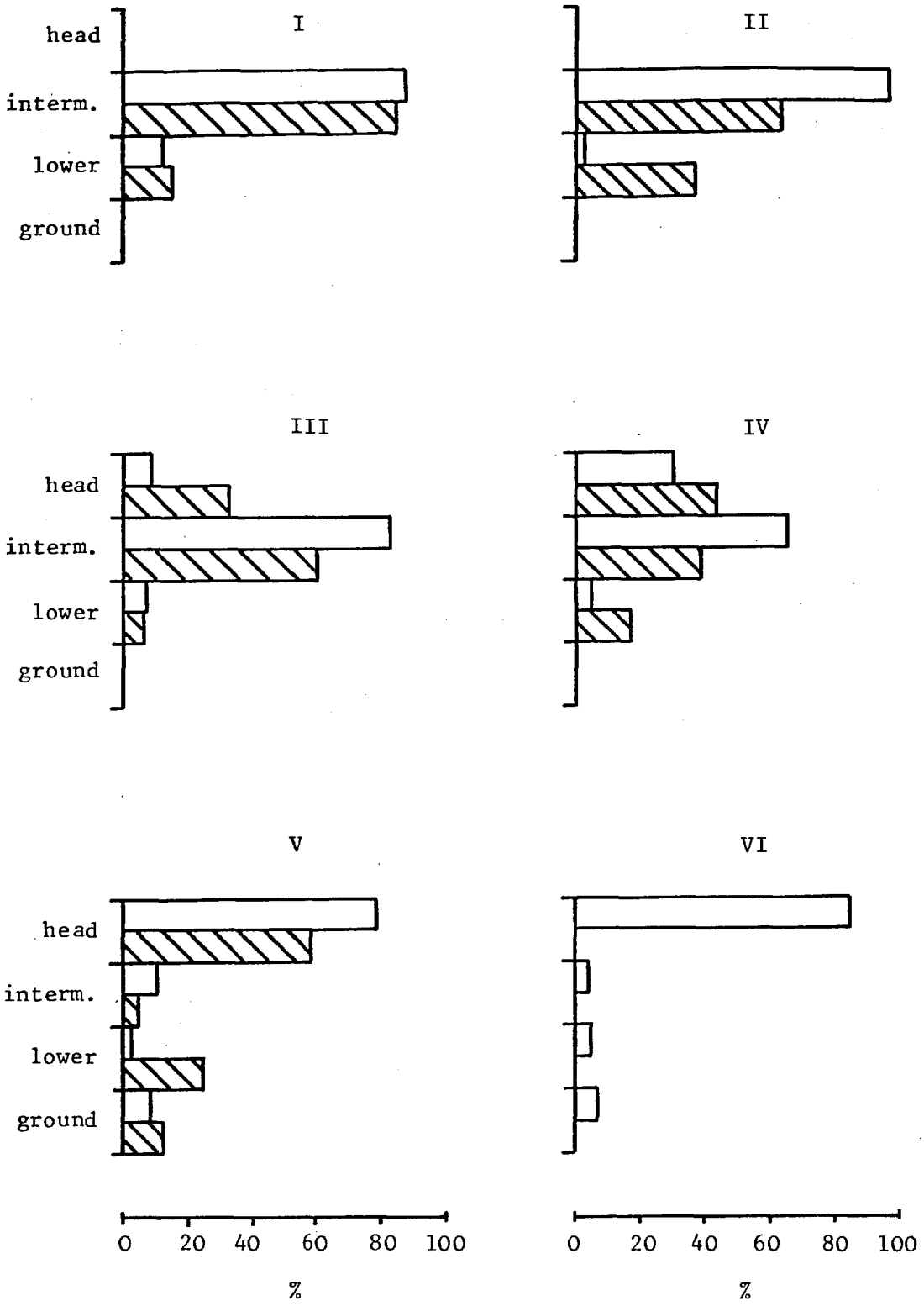


Figure 1.7. Distribution of *Mamestra brassicae* larvae on the host plant.
(open bar: active period; shaded bar: moulting period)
(Roman numerals indicate larval instar)

laying. The second instar followed a similar pattern. Thereafter there was an increased tendency to migrate towards the upper part of the plant; the 5th and 6th instars were located mainly in the head of the plants. Some individuals of the last two instars were found on the ground beneath the plants, hidden under fallen leaves or partially buried in the ground. This pattern of distribution agrees with that found by Hirata (1967) on cabbage. The difference in habits of growth between these two brassicas suggests that other factor(s) is(are) involved. The negative phototaxis observed during the last two instars (Omino et al. 1973) might explain the tendency of the older larvae to hide either in the head or beneath the plant. It should be said that the distribution observed was on plants with relatively low number and although the pattern is clear it requires additional studies on issues like size, growing conditions of the plants, weather and especially larval density. Although Hirata (1966 found that high density accelerated the movement of larvae to the upper part and Yokai et al. (1975), under experimental conditions he observed that Mamestra larvae at densities of 5 or 10 individuals per leaf remained on the leaves of chinese cabbage (Brassica chinensis) or chinese mustard (B. juncea) with no tendency to migrate. However, during outbreaks mass migration is reported which might indicate then changes in behaviour.

While in routine counts, it was observed that the larvae seemed to rest more frequently on the veins than on the leaf lamina. Some observations were made of 3rd, 4th and 5th instar larvae by counting the number of larvae that were resting on the veins, leaf lamina or in the leaf folds. The result shows (Table 1.2) that there was a clear tendency for the larvae to occupy the veins. Additional information was sought under laboratory conditions, where the different instars including moulting stages, except the first instar, were tested.

TABLE 1.2 Larval Position Preference for Resting, on the Underside of Brussels Sprout Leaves Under Field Conditions

Stage	Number of larvae obs.	% of larvae resting on:		
		vein	lamina	folds
3rd instar	59	67.8 (40)	32.2 (19)	0.0 (0)
3rd moult	29	72.4 (21)	27.6 (8)	0.0 (0)
4th instar	144	77.8 (112)	22.2 (32)	0.0 (0)
4th mou	73	46.6 (34)	21.9 (16)	31.5 (23)
5th instar	20	55.5 (11)	10.0 (2)	35.0 (7)

A fresh cut Brussels sprout leaf measuring approximately 14 x 20 cm was placed inside a plastic box (28.0 x 15.9 x 9.0 cm), and its petiole passed through a hole made in one side. Groups of larvae of the instar to be tested were placed on the underside of the leaf, and after allowing a few minutes for the larvae to settle down on the leaf, the lid was fitted and secured with a rubber band. The box had three windows (2 on the sides and one on the side opposite to the petiole) which were covered with nylon mesh. The box was stood on a wide necked bottle filled with water in which the petiole was immersed.

The tests were set up at 11.00pm., and the next morning at 8.00am. observations were taken of the number of larvae that were: (a) on veins or at least with their prolegs on them, (b) on the lamina, or (c) when on places like the inner surface of the box, upper side of the leaf, petiol etc., were all considered under the common heading "other places". The first instar was not tested because the larvae generally are aggregated

on one part of the underside of the leaf. Larvae of 2nd instar although often still on the same leaf are more loosely aggregated and were chosen as the starting instar for the experiments.

The results (Table 1.3) showed that there was a strong tendency for the larvae to stay on the veins, especially from the 2nd instar until the 4th instar. Larvae moulting into the 5th instar seemed to have a tendency to move to "other places" of the experimental arena. The 5th and 6th instars gave a different response because being photonegative in reaction they tried to move away from the light source, resulting in a concentration of larvae to one side of the box. However, when tested in constant darkness they followed the same pattern as in previous instars. The response of the larvae moulting to 6th instar was not affected when they were tested in constant darkness.

This behaviour is also apparent when examining leaf area eaten by Mamestra larvae, especially middle instars. In general the feeding holes are limited by some extension with the vein and larvae may be seen to start feeding while standing on a vein. This suggests that they need some ridge to hold while feeding; in order to continue enlarging a feeding place they may then move from the vein to the edges of the hole. While moulting the larvae change from a dark to a paler green which matches very well with that of the veins which may have survival value against predators that hunt by sight. On the other hand, being on the vein may render them easier to catch by predators that crawl over the plant since some of them use the veins during hunting (Evans, 1976). Evidence is needed to substantiate this argument.

The last instar larvae feeds mainly on the upper parts of the plant

TABLE 1.3 Larval Preference for Resting Position on the Underside of Brussels Sprout Leaves Under Laboratory Conditions

Stage	Number per replicate	Number of replicates	% of larvae resting on:		
			Veins	Lamina	Other places
2nd instar	20	6	69.2 (83)*	13.3 (16)	17.5 (21)
2nd moult	20	4	80.0 (64)	16.3 (13)	3.7 (3)
3rd instar	20	6	82.5 (99)	11.7 (14)	5.8 (7)
3rd moult	20	4	68.8 (55)	16.3 (13)	15.0 (12)
4th instar	15	6	66.7 (60)	17.8 (16)	15.6 (14)
4th moult	15	3	37.8 (17)	17.8 (8)	44.4 (10)
5th instar (light)	10	6	26.7 (16)	5.0 (3)	68.3 (41)
5th instar (dark)	10	6	76.7 (46)	3.3 (2)	20.0 (12)
5th moult (light)	10	4	7.5 (3)	0.0 (0)	92.5 (37)
5th moult (dark)	10	4	12.5 (5)	0.0 (0)	87.5 (35)
6th instar (light)	5	6	3.3 (1)	0.0 (0)	96.7 (29)
6th instar (dark)	5	6	80.0 (24)	0.0 (0)	20.0 (6)

* Number of larvae

and also bores into the heads of cabbages and brussels sprouts. When fully fed the larvae leave the host plant and may remain on the ground for some time before burying into the soil to construct the pupal cell.

The depth of pupation varies with soil type, being greatest in sandy soil, but also varies with moisture content (Dolidze, 1957). In an experiment described in Section three, larvae with radioactive tags were allowed to pupate and the depths of pupation measured as the distance from the soil surface to the head of the pupa. It was found that the average depth was 4.0 cm (pooled data) (Table 1.4).

TABLE 1.4 Depth of Pupation of Mamestra brassicae Larvae Tagged with Radioactive Wires

	Number of pupae recovered	Depth of pupation $\bar{x}$ ± S.e (cm)	Range (cm)
Release 1	17	3.9 ± 0.34	(2.5 - 6.5)
Release 2	11	4.0 ± 0.26	(3.0 - 6.2)

It is interesting that all recovered pupae were invariably underneath Brussels sprouts plants, mainly in the area where senescent leaves touched the ground or fallen leaves were present. This might have been due to the fact that the plot was relatively weed free so the shelter was provided mainly by the Brussels plants. Also the soil beneath the plants was softer as the frequent walking in and between rows had made it more compact elsewhere.

The pupae may undergo diapause remaining in the soil until the next season or according to the geographical region may emerge or pass

through an aestival diapause. The seasonal variation of M. brassicae throughout its entire range has been well documented.

It produces one to three generations depending on the latitude. Thus, the northern U.S.S.R. (Danilevskii, 1965) and southern Norway (Rygg et al., 1975) there is one generation. In England there is usually one generation but a partial second may be produced, which is responsible for the caterpillars occurring late in October (Smith, 1931; Cameron, 1939; South, 1946; Jones & Jones, 1974). In places like Italy (Zangheri, 1952), Rumania (Ionescu, 1966) there are two generations while in Bulgaria a partial third may be observed (Dochkova, 1971). Three complete generations are observed in Azerbaijan, southern U.S.S.R. (Abdinbekova, et al. 1976). Danilevskii (1965) has worked out that this species forms a photoperiodic cline between 40°N and 60°N in eastern Europe, through which the onset of winter diapause is adjusted to the seasonal changes at different latitudes. In Japan there are two generations in the north, moving south in spite of the increase in temperature the number of generations does not increase, and even in south Japan where the development of six or seven generations might be expected, only two are actually observed. This was explained in terms of a summer diapause (Masaki, 1956; Masaki et al., 1965; Masaki, 1968) with its incidence and duration influenced by extrinsic as well as intrinsic factors. In Europe a summer diapause is present in the population of the Caucasian region (Danilevskii, 1965) and more recently has been observed in France (Poitout et al., 1973)

Changes in the photoperiodic threshold of the winter diapause and evolution of a different type of diapause (summer diapause) seems to have enabled this species to occupy a wide range in geographical distribution with many differences in climatic conditions (Masaki et al., 1965;

Danilevskii, 1965). The local variability in the diapause pattern is so remarkable that northerly and southerly populations behave as if they were distinct species (Masaki, 1956). In such circumstances a larval genotype may fail to survive when it is transferred to a different climatic area, which Masaki (1968) suggested could be used as a method of autocidal control.

1.4 Laboratory Studies on the Effect of Temperature on the Development and Survival of the Immature Stages

1.4.1 Materials and methods

The insects used were obtained from the stock culture. Egg, larval, and pupal development times and survival rates were determined in constant temperature rooms of 15, 20, 25 and 29 ±1°C, and at 16:8 hours light: dark cycle; the duration of the prepupal stage was not considered separately, therefore the larval data includes this stage.

Humidity was not controlled but it seemed to be higher than 65% most of the time, and probably higher inside the rearing containers during the larval development due to the transpiration of the leaves given as food.

For egg development, 8 egg masses laid within a 4 hours period were cut into 4 sections and each one placed in a 76.2 x 24.4 mm sample tube which was then plugged with cotton wool. Each tube was assigned to one of the above-mentioned temperatures. The mean hatching time was taken when half of the eggs in an egg mass had hatched, with observations being made every three hours once hatching commenced.

Development times and survival values for larvae and pupae at the

different temperatures were determined using newly-hatched larvae from eggs incubated at 20°C. The larvae were confined, in groups of 20, in cylindrical plastic cages each 105 mm diameter and 43 mm high with a 30 mm circular terylene covered ventilation in the lid (approx. 300 cc capacity) (designated as container A). Brussels sprouts leaves from late summer plants were provided as food. Five replicates were used at each temperature. Once the larvae reached the third instar they were transferred to 220 x 114 x 80 mm plastic boxes with two, 30 mm circular terylene covered, ventilation holes in the lid (container B). When in the prepupal stage the insects were transferred to containers A and provided with peat for pupation. When pupae were three days old they were sexed and put individually into sample tubes which were plugged with cotton wool.

Observation on mortality, pupation, and adult emergence were made.

1.4.2 Results and discussion

Egg survival was 90% or greater within the range of temperature used (Table 1.5). The time required for completion of embryogenesis and hatching of eggs decreased as the temperature increased from 11.60 days at 15°C to 3.46 days at 29°C (Table 1.6).

Larval survival was high, 88% on average, ranging from 86% to 91.0% (Table 1.5). Larval duration varied from 48.0 and 50.5 days at 15°C to 19.4 and 20.4 days at 29°C for males and females respectively (Table 1.7); as expected it decreased as temperature increased. Males developed significantly faster than females during the larval period at the different temperatures tested, except at 25°C when significance was just outside the 5% level. The ratio of males/females duration was relatively consistent at

about 0.95.

Survival of pupae was also high, averaging 95.4% (Table 1.5). The duration of this stage decreased from 48.6 days at 15°C to 12.8 days at 29°C (Table 1.8).

When the durations (Y) of eggs, larvae, and pupae were plotted against temperature, the curves followed a general hyperbola (Figs. 1.8, 1.9 and 1.10). The observed rates of development for egg, larval and pupal stages (Tables 1.6, 1.7 and 1.8), showed a linear relationship with temperature (Table 1.9; Figs. 1.8, 1.9 and 1.10). The large coefficients of determination (r^2) indicate that the linear function is an adequate description of the data.

In general, the curve of rate of development is a shallow sigmoid (Howe, 1967), rising slowly at first, then steeply, then more slowly to a maximum and falls again to end abruptly at lethal temperatures (Wigglesworth, 1972). The curve is almost straight over a range of some 10-15°C (Howe, 1967), and has been applied to the development of many different species although the actual range of temperatures varies.

In the case of M. brassicae the assumption of a linear model adequately describes the data, within the temperature range studies here, 15 to 29°C. In other Lepidoptera linearity has been demonstrated, for example, between 14°C and 26°C for Hyphantria cunea Drury (Ito et al., 1968). 10°C to 27.5°C for Acrolepia assectella Zeller from hatching to adult emergence (Noyes, 1974). From 11.5°C to 28°C, for the immature stages of Epiphyas postvittana (Walker) (Danthanarayana, 1975a). Miyashita (1971) found 16°C to 31°C for for Spodoptera litura F. In Pseudaletia unipuncta (Waworth) the range was

TABLE 1.5 Survival of Immature Stages of M. brassicae at Constant Temperatures. The Numbers of Eggs, Larvae and Pupae Observed are in Parenthesis

Stage	Temperature in °C			
	15	20	25	29
Egg	95.7 (398)	92.1 (647)	90.0 (380)	95.1 (473)
Larvae	87.0 (100)	86.0 (100)	91.0 (100)	88.0 (100)
Pupae	97.7 (87)	89.5 (86)	96.7 (91)	97.7 (88)

TABLE 1.6 The Effect of Constant Temperatures on the Duration and Rate of Development of the Egg Stage of M. brassicae

Temperature in °C	Egg duration (days)	Rate of development
15	11.60 ± 0.14*	0.0862
20	6.14 ± 0.04	0.1629
25	4.03 ± 0.05	0.2481
29	3.46 ± 0.02	0.2890

* Mean ± Standard error

TABLE 1.7 The Effect of Constant Temperatures on Duration and Rate of Development of the Larval Stage of M. brassicae

Temperature in °C	Sex	Larval duration (days)	Rate of development
15	♂♂	48.0 ± 0.40*	0.0208
	♀♀	50.5 ± 0.34	0.0198
20	♂♂	28.2 ± 0.29	0.0355
	♀♀	30.0 ± 0.27	0.0333
25	♂♂	21.8 ± 0.34	0.0459
	♀♀	22.7 ± 0.31	0.0441
29	♂♂	19.4 ± 0.17	0.0515
	♀♀	20.4 ± 0.20	0.0490

* Mean ± Standard error

TABLE 1.8 The Effect of Constant Temperatures on the Duration and Rate of Development of the Pupal Stage of M. brassicae

Temperature in °C	Pupal duration (days)	Rate of development
15	48.6 ± 0.24*	0.0206
20	22.5 ± 0.11	0.0444
25	15.6 ± 0.14	0.0641
29	12.8 ± 0.07	0.0784

* Mean ± Standard error

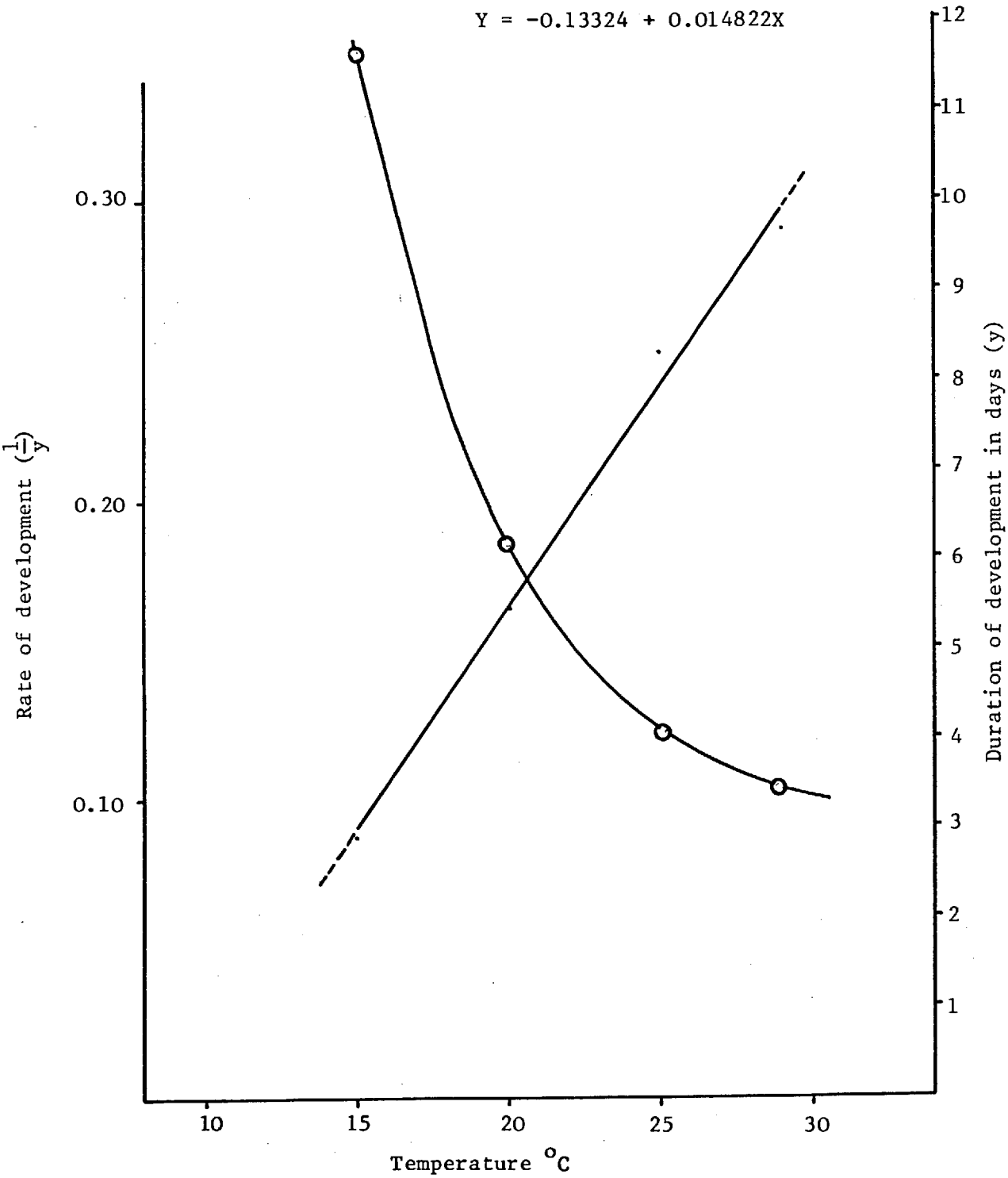


Figure 1.8. Effect of different constant temperatures on the duration and rate of development of the egg stage of *M. brassicae*.

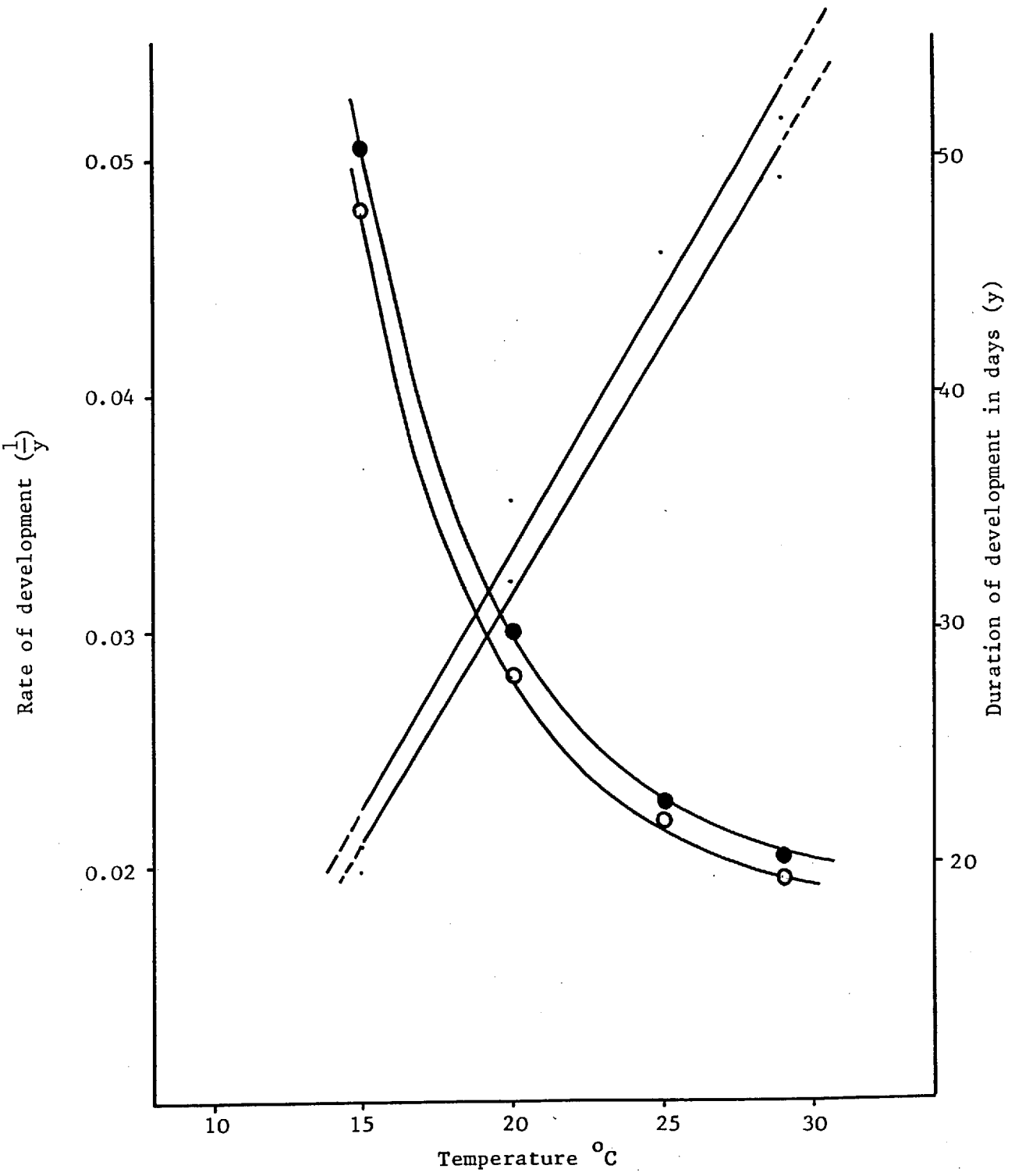


Figure 1.9. Effect of different constant temperatures on the duration and rate of development of the larval stage of *M. brassicae* (o-o : males; •-• : females).

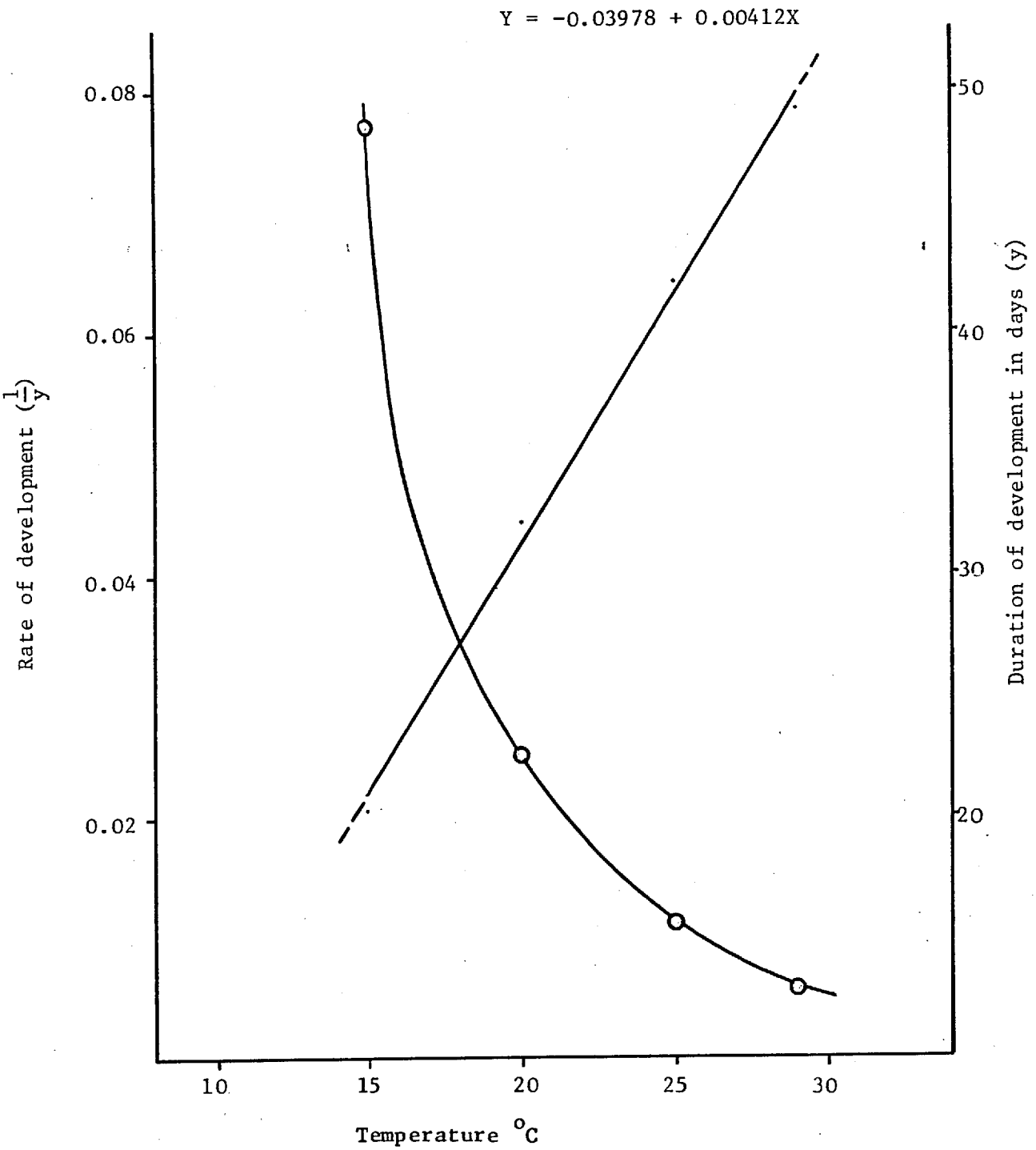


Figure 1.10. Effect of different constant temperatures on the duration and rate of development of the pupal stage of *M. brassicae*.

TABLE 1.9 Regression Equations, r^2, and Levels of Significance Expressing Rate of Development (Y) of Eggs, Larvae, and Pupae of M. brassicae at Constant Temperatures (X = days).

Stage	Regression equation	r^2	Significance
Egg	Y = -0.13324 + 0.01482 X	0.99	F = 266.5, $1/2^1$ P<0.005
Larva			
male	Y = -0.01020 + 0.00218 X*	0.97	F = 664.0, 1/18 P<0.001
female	Y = -0.00996 + 0.00208 X*	0.97	F = 614.0, 1/18 P<0.001
Pupae	Y = -0.03978 + 0.00412 X**	0.99	F = 491.4, 1/2 P<0.005

* Equation calculated by using the replicated means at each temperature

** Equation calculated by pooling the duration for both males and females

1 Degrees of freedom in Analysis of variance

13°C to 29°C (Guppy, 1969).

The range, 15-29°C, in which the rate of development is proportional to temperature is in agreement with that of 15-30°C and 15.4-30°C found by Stepanova (1962) and Dochkova (1972) respectively.

There are few data published on the effect of different temperatures on the development of M. brassicae. While this work was in progress more information became available particularly for the larval stages (Dochkova, 1972; Oku et al., 1973a) which with the data of Stepanova (1962) and Dousaussoy (1964) are compared with our in terms of threshold of development. This was calculated for the two later authors from their tables on average duration of the larval stage under the different temperatures. In the case of Stepanova it was recalculated as there was some discrepancy between the raw data and his graphical representation.

The results (Table 1.10) indicates differences in threshold of development. Different results are to be expected as the result of differences in strains, methods of rearing, host-plants, and different method of analysis. In our case the differences seem to follow the climatic gradient, at least along the European continent, which suggests differences among strains. However, the final proof can only be provided by using material collected from different geographic regions and rearing them simultaneously under the same conditions. Differences in threshold of development have been observed among different geographic population in many species e.g., Agrotis ypsilon Rott (Druzhelyubora, 1976), and Plutella xyllostella L. (Umeya et al., 1973).

TABLE 1.10 The Variation in Threshold of Development in M. brassicae Larval Stage

Place and Country	Author and Year	Latitude	Range temperature used to calculate threshold of development	Threshold of development
Leningrad, USSR	Stepanova (1962)	59 55N	(14.7 - 30.3)	3.1
London, England	Montagne (1977)	51 30N	(15.0 - 29.0)	♂♂ 4.7 ♀♀ 4.8
Versailles, France	Dusaussoy (1964)	48 48N	(14.0 - 25.0)	7.5
Pleben, Bulgaria	Dochkova (1972)	43 25N	(15.4 - 30.0)	8.1
Morioka, Japan	Oku et al. (1973)	39 43N	(17.0 - 23.5)	7.9

1.5 Laboratory Studies on Longevity and Fecundity

1.5.1 Materials and methods

Longevity and fecundity were studied in a constant temperature room at 20°C with a 16:8 hours light:dark cycle. Adults used in this experiment were obtained from a preliminary experiment in which larvae reared either on Brussels sprouts or an artificial diet (David and Gardiner, 1966) were compared.

Newly-emerged adults (6-8 hours old) were paired, one male to each female, by placing them in a container B lined with Kimwipe as the oviposition substrate. A small lid with a cotton wool plug wetted with 10% honey solution was placed in the bottom of each cage to provide adult food; this was renewed daily.

The boxes were examined every morning and when eggs were found the pair was moved to a new box and the eggs cut from the paper and stored at the same temperature for subsequent counting. A total of 12 pairs was set up for each treatment.

Data on longevity were obtained by following the survival of each adult from the day of emergency to death. Fecundity was recorded as the number of eggs laid daily and the total number of eggs, and fertility as the total number of fertile eggs produced. Females that died were dissected to count the number of eggs left in the ovaries, and to record the number of spermatophores in the bursa copulatrix. Additionally, records were taken on the distribution of the eggs inside the oviposition box.

The term fecundity and fertility are often used as synonymous, but a clear distinction between them is essential. Fecundity, as used in this study, is a measure of the total egg production by a female. Fertility, however, is the total number of viable eggs laid by a female.

1.5.2 Result and discussion

1.5.2.1 Longevity

On both diets, there was a high adult survival rate during the first ¾ of the average life span, declining thereafter sharply (Table 1.11). The distinction made between females will be discussed later under fecundity and longevity heading.

Some appreciable differences between treatments, and also between sexes were observed. Males from larvae reared on brussels sprouts lived longer than did those reared on the artificial diet (t test, $P<0.05$).

TABLE 1.11 The Longevity of Adult M. brassicae from Larvae Reared on Brussels Sprouts Compared with Those Reared on Artificial Diets

Food	Male	Female	
		High fertility	Low fertility
Brussels sprouts	(12)* 19.08 ± 0.36**	(7) 17.14 ± 0.70	(5) 22.00 ± 1.08
Artificial diet	(12) 17.83 ± 0.37	(6) 15.83 ± 1.05	(6) 19.83 ± 0.60

* The number of adults observed

** mean ± Standard error

Among the females, in both diets, those laying a higher percentage of fertile eggs had a significantly shorter adult life (t test, $P<0.01$) than the low fertility type moths. No differences were found between diets for high fertility type moths nor for low fertility type moths.

In the brussels sprout treatment, males had a longer life span (t test, $P<0.05$) than high fertility females, but a shorter one (t test, $P<0.01$) than the low fertility type. The same trend was observed in the artificial diet treatment.

The fact that high fertility type moths, in both treatments, were shorter-lived than their counterparts seems to be associated with a higher rate of egg-laying (Fig. 1.13), which probably accelerates the aging of females. This has also been observed in Drosophila subobscura (Smith, 1958).

1.5.2.2 Fecundity and fertility

It was observed that about half of the pairings in each treatment produced either no fertile eggs or a very low percentage of fertile ones, this in spite of normal matings. The reason is unknown, but since the paired-adults were reared from a single egg mass inbreeding might have been important. This heterogeneity was taken into account in the analysis by dividing the females within each treatment into two groups on the basis of the proportion of infertile eggs laid. Thus, those females laying over 50% of fertile eggs were considered as "high fertility" type moths whereas those with less than 50% of fertile eggs as "low fertility" type moths. As it will be seen both groups exhibited different characteristics.

On both diets, high fertility type moths laid significantly more

eggs than their counterparts (t test, $P<0.05$) (Table 1.12). Diets did not have a significant effect on the fecundity of high and low fertility moths.

The maximum number of eggs laid in a day by any one moth was 816. The highest individual fecundity was observed in the brussels treatment when a female oviposited 3482 eggs over a 16 days period, in a total life span of 19 days. This female also had the highest recorded fertility of 95.2%.

The oviposition curves of the high and low fertility types followed different patterns (Figs. 1.11 and 1.12). The high fertility moths laid most of their eggs during the first 5-6 days of oviposition, thereafter, showed a moderate decline in the daily oviposition rate. A definite peak was shown only by the females reared as larvae on the artificial diet. The low fertility moths produced many less eggs and without definite peaks in daily production. High fertility moths had a higher rate of egg production and laid more eggs than their counterparts (Fig. 1.13). Larval food had no effect on the rate of oviposition, both high and low fertility types moths having similar curves.

The mean fertility (Table 1.12) for high fertility moths for the brussels diet was 86.5 (range 63.9-95.2%) and 80.6 (range 52.8-96.0%) for the artificial diet. The low fertility types averaged 7.7 (range 0.0-21.4%) and 4.4 (range 0.0-15.5%) for the brussels and artificial diets respectively.

High fertility moths tended to have somewhat shorter, although not significant, preoviposition, oviposition and postoviposition periods (Table 1.13). The differences might have been masked by the greater variation exhibited by the low fertility types.

TABLE 1.12 Fecundity and Fertility of High and Low Fertility type Moths of M. brassicae Reared as Larvae on Brussels Sprouts Compared with those Reared on an Artificial Diet.

	Larval food			
	Brussels sprouts		Artificial diet	
	High fertility	Low fertility	High fertility	Low fertility
Fecundity	2981.9 ± 168.4*	1907.6 ± 458.2	2717.0 ± 190.7	1903.5 ± 316
Mean fertility (%)	86.5	7.7	80.6	4.4
Fertility range (%)	(63.9 - 95.2)	(0.0 - 21.4)	(52.8 - 96.0)	(0.0 - 15.5)

* Mean ± Standard error

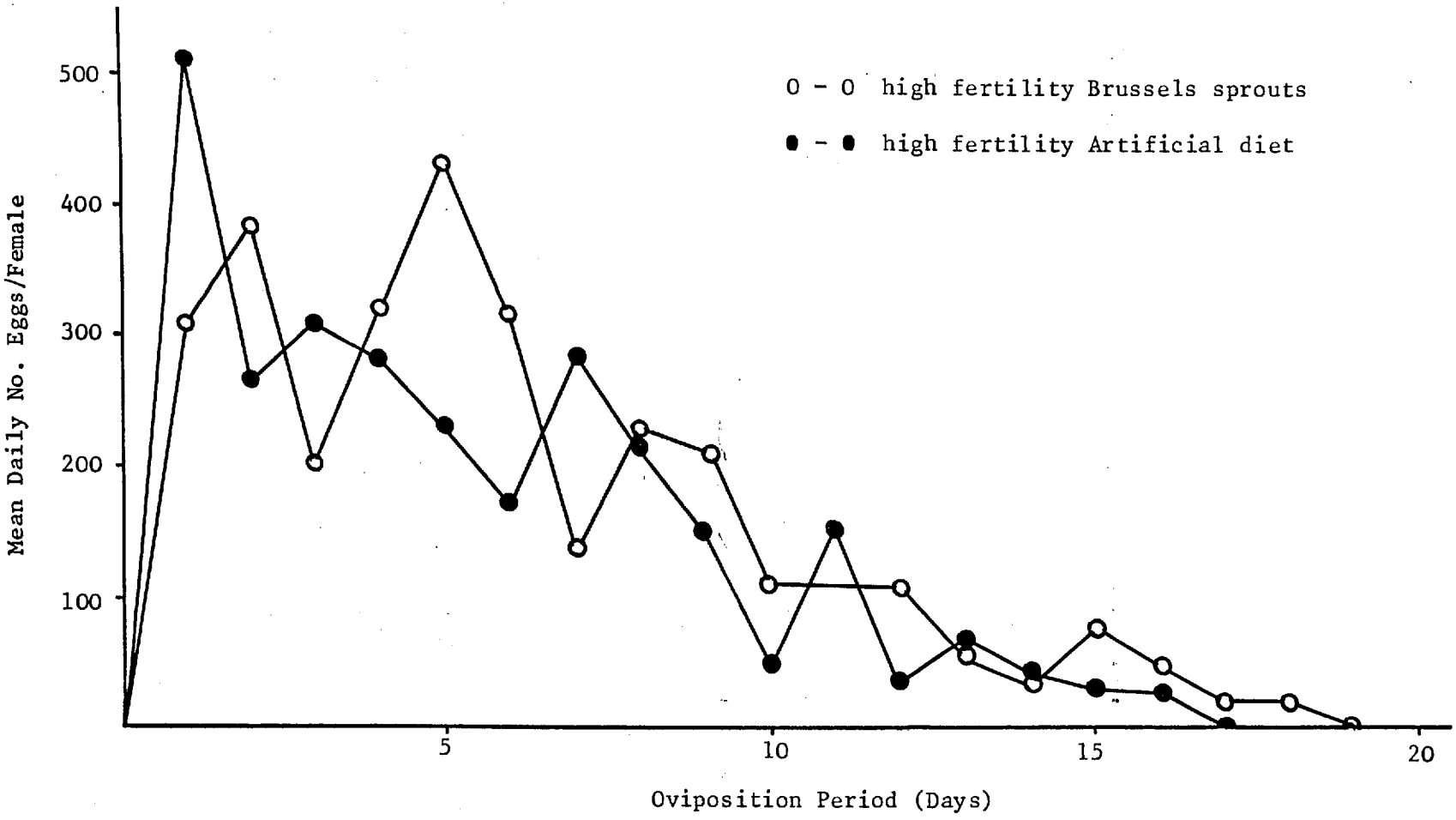


Figure 1.11. Oviposition curves of high fertility type moths of *M. brassicae* from larvae reared on Brussels sprouts and on Artificial diet.

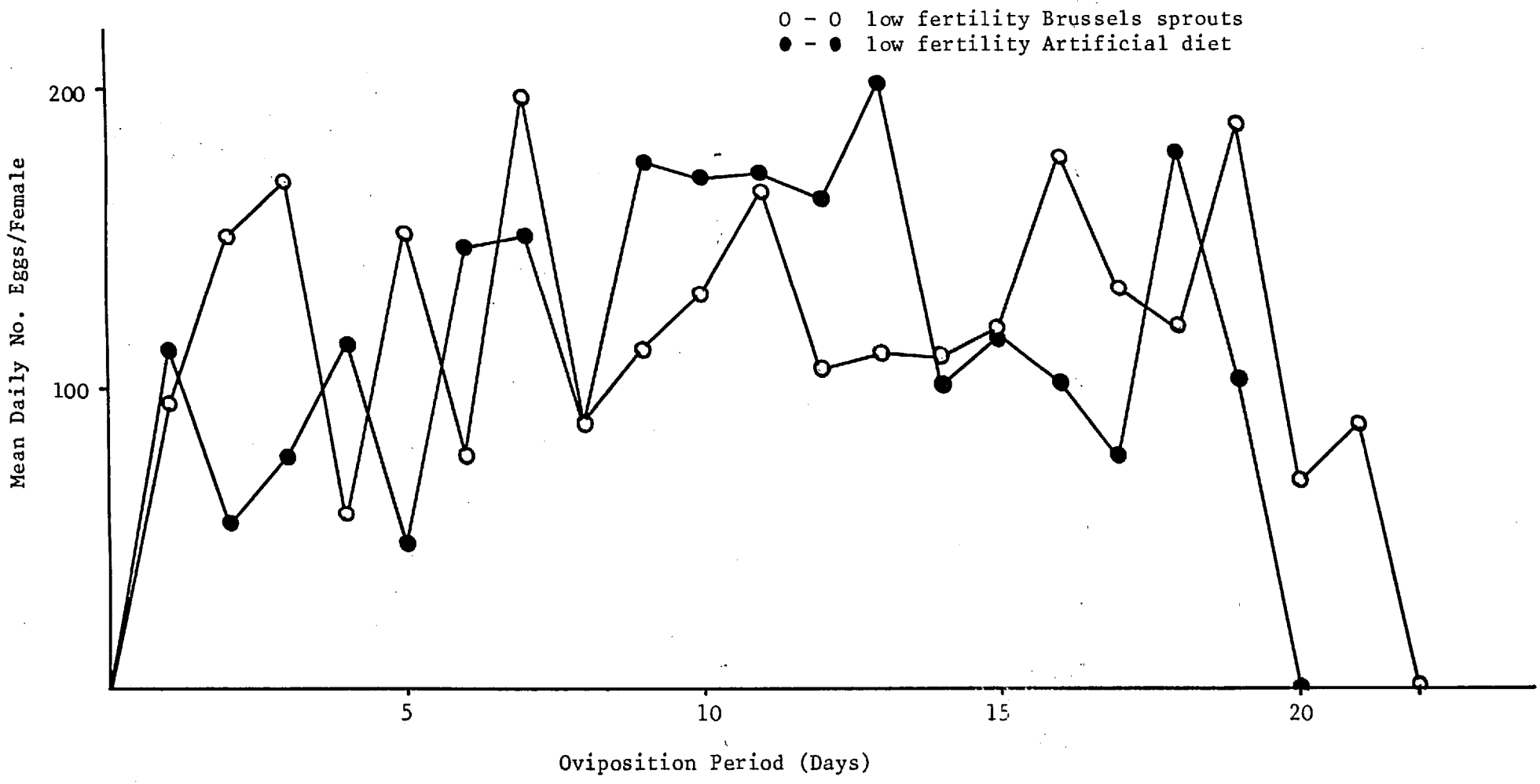


Figure 1.12. Oviposition curves of low fertility type moth of *M. brassicae* from larvae reared on Brussels sprouts and on Artificial diet.

Figure 1.13. Oviposition rate of high fertility and low fertility type moths of *M. brassicae* from larvae reared on Brussels sprouts and on Artificial diet.

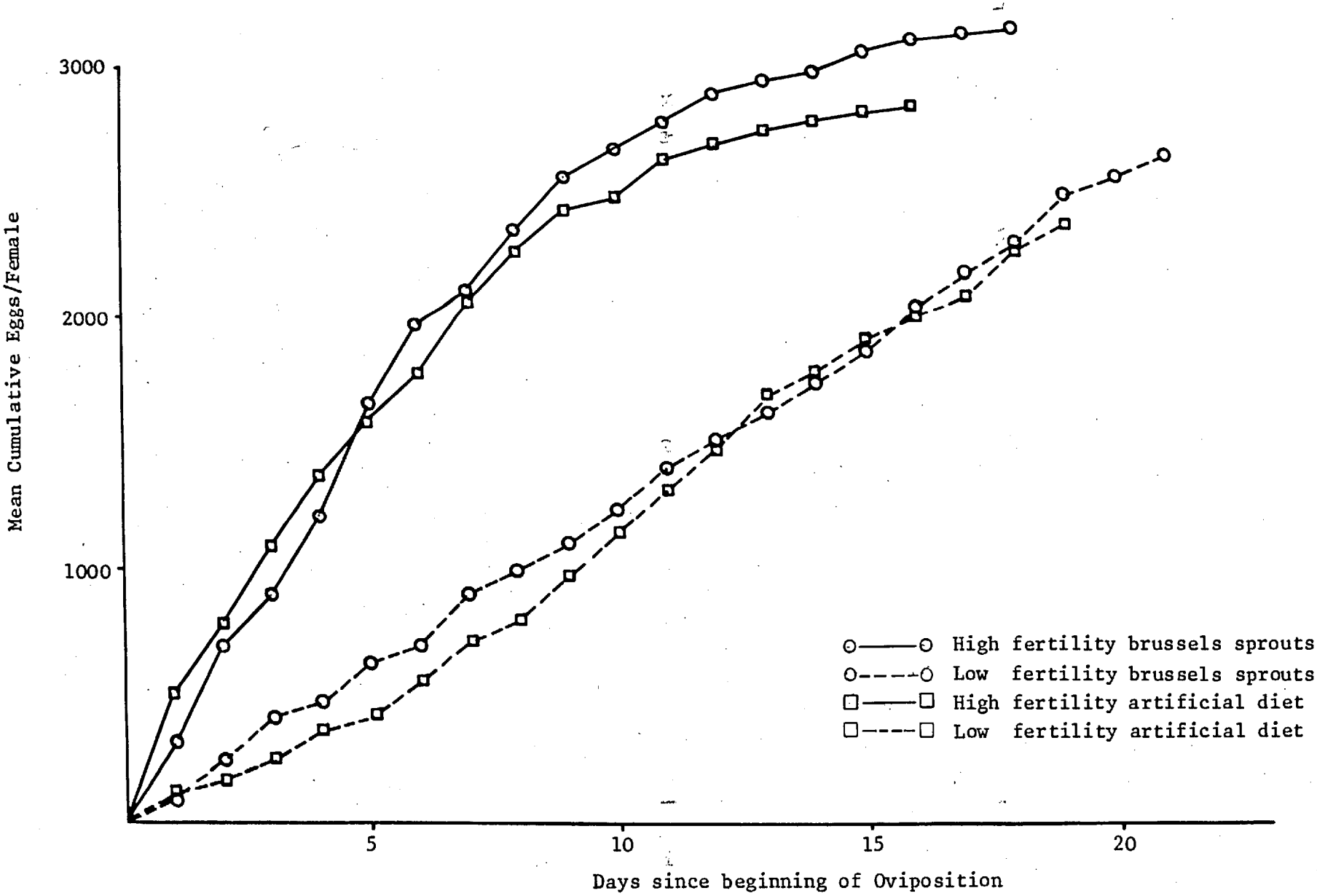

3000
2000
1000
Mean Cumulative Eggs/Female
5
10
15
20
Days since beginning of Oviposition
High fertility brussels sprouts
Low fertility brussels sprouts
High fertility artificial diet
Low fertility artificial diet

TABLE 1.13 The Duration of the Reproductive Performances of High Fertility and Low Fertility type Moth of M. brassicae from Larvae Reared on Brussels Sprouts Compared with those Reared on an Artificial Diet

Larval food	Preoviposition (days)	
	High fertility	Low fertility
Brussels sprouts	(7)* 2.71 ± 0.42**	(5) 4.00 ± 1.05
Artificial diet	(6) 2.17 ± 0.17	(6) 3.33 ± 0.61
	Oviposition (days)	
	High fertility	Low fertility
Brussels sprouts	(7) 14.00 ± 0.79	(5) 14.20 ± 2.24
Artificial diet	(6) 13.00 ± 1.10	(6) 14.50 ± 1.30
	Postoviposition (days)	
	High fertility	Low fertility
Brussels sprouts	(7) 0.43 ± 0.20	(5) 1.60 ± 1.12
Artificial diet	(6) 0.67 ± 0.21	(6) 2.00 ± 1.18

* Number of adults

** Mean ± Standard error

Dissection of females after they died showed that multiple mating occurred in all except one female. The single-mated female, from the brussels treatment, laid 2710 eggs with 91.0% fertility which clearly indicates that one mating is sufficient to ensure the fertility of a female and confirms Dusaussoy's observation (1964). On the basis of the number of spermatophores, the average number of matings was significantly lower (t test, $P<0.01$) in the high fertility types (Pooled data), 4.69 ± 0.56 compared with 7.55 ± 0.56 in the low fertility group (pooled data). The most spermatophores found in one female was 10 (Table 1.14).

TABLE 1.14 Spermatophores and Unlaid Egg Counts in High and Low Fertility Type Moths (Pooled data)

	High fertility	Low fertility
Mean number spermatophores	4.69 ± 0.56*	7.55 ± 0.56
Range	1 - 8	4 - 10
Mean number eggs in ovaries at death	20.4 ± 4.5	184.4 ± 59.63

* Mean ± Standard error

Post mortem egg counts from ovaries showed that the number of unlaid eggs by the high fertility group (pooled data) was very low, on average 20.4 eggs; while in the low fertility type (pooled data) the average number of eggs was 184.0. The fat bodies were depleted in almost all females.

The relevance of multiple mating is not clear as the single mating provided sufficient sperm to fertilise all the eggs which the female produced. It is not known to what extent laboratory conditions affect behaviour. The fact that both types of moths had multiple matings and that their number was

significantly higher in the low fertility type seems to indicate that extra mating may play an additional role, perhaps by enhancing oviposition rather than egg production since moths showing low fertility had a lower and rather steady rate of egg production. This point needs further studies.

The high number of matings recorded here is apparently not unusual; similar findings have been reported by Jacobson (1970) for Euxoa ochrogaster (Guenee); Gehring et al. (1963) for the codling moth, Carpocapsa pomenella (L.). Finally, although multiple mating has been reported from most Lepidoptera studied, the factors responsible for this behaviour have not been detailed and consequently its adaptive significance is not understood (Taylor, 1967).

1.6 Section General Discussion

Laboratory and field investigations on some aspects of the biology and habits of Mamestra brassicae have been described.

On brussels sprouts, M. brassicae lays its eggs mainly in the intermediate region of the plant, generally on the underside of the leaves and most of the egg masses observed were deposited near the edges. The first instar larvae are found mainly in the intermediate part of the plants, influenced by the female laying habit, as they pass through the different instars they tend to migrate to the head of the plants, with the result that the majority of the 5th and 6th instars inhabiting the head with some moving to the ground underneath the plant and some may reach neighbouring plants. On the leaf the larvae tend to rest and move using the veins, perhaps because they get a better grip; this could also have some survival value especially during moults, when the colour of the larvae matches that of the veins.

The habit of inhabiting the 'head' of cruciferous plants like cabbages and brussels sprouts, and the increase in relative resistance to insecticides as the larvae grow (Ichinose, 1955; Ishikura and Ozaki, 1958) may in part explain the difficulty of getting effective control of the older larvae, especially when dusts are applied. However, reports (Butovskii, 1965) of use of up to 3 times the normal rate of application suggests that resistance to insecticides may also have been present in the target populations.

The rate of development of the caterpillars, in agreement with previous authors, was linearly related to temperature in the range 15-29°C, which is the range of temperatures usually observed during the summer. Survival of the immature stages was very high. The life span of the adult was about 20 days. The females generally have a high fecundity, but large variations in fertility are usually observed (Bonnemaison, 1960b ; Noll, 1963; and Dussaussoy, 1964). It was found that groups of females with high or low fertilities differed in their reproductive characteristics. Nevertheless, in field conditions fertility seems to be less important since no infertile eggs were seen during field observations, and no references have been found in the literature mentioning this aspect.

A comparison of the general biology data obtained by previous authors with ours shows some differences that may be attributable to various factors such as rearing conditions, host-plant, strain, etc., (Table 1.15).

Summing up, we may say, taking into account that biological values obtained in the laboratory are not necessarily directly applicable to field populations of M. brassicae, that its potential for increase is very high. The usually low number recorded in England suggests that limiting factors in nature keep its populations very low.

TABLE 1.15 A Comparison of H. brassicae Biological Information from Several Authors

Authors and Country	Masaitis (1925) Russia	Way et al. (1951) England	Maleki-Milani(1971) France	Nikolova (1945) Bulgaria	Dusaussoy (1964) France	Karadzhov (1970) Bulgaria	Bonnemaison (1961d) France	Stepanova (1962) Russia	Noll (1963) Germany	Ionescu (1966) Rumania	Montagne (1977) England
Rearing Conditions	Lab.	24°C	20°C	Lab.	20°C		20°C	20°C	Glasshouse	Field	20°C
Duration (days)											
Egg		6.0	7.0	6-9	5.5		7.5	6.5		2-7	6.1
Larva		27.0	22.5	(25-30)	26.5		30.0	26.3		(19-36)	28.2
Prepupa			3.5		3.0						30.0
Pupa		approx. 20	21.0	(13-36)	(21-23)		18.0	20.0			22.5
Longevity											
males	15.9 (6-24)		9.4	- (8-25)	15.6 (12-24)		- -		(5.2-11.3)		19.1
females	16.6 (8-21)		8.4	- (9-27)	16.6 (10-27)		11.8 (1-26)		(5.9-12.8)		17.1
Preoviposition					4 (2-10)		3-3.5		0.8-4.4		2.7
Oviposition				3-7		3.8 (1-8)	1-15		2.4-14.7		14.0
Fecundity (No. eggs)	1494		1378		950				507		2982
Range	476-2003			(438-2725)		up to 2700	(0-2455)		(108-1346)		

SECTION 2

STUDIES ON THE EFFECTS OF LARVAL DENSITY ON M. brassicae

2.1 Introduction

Some studies on the effect of density during the larval stage have been carried out with M. brassicae (Hirata from 1954 to 1966a; Bonnemaison, 1962 a, b; Ishikura et al., 1958; Burov et al., 1970). However, some aspects such as the effects on growth, activity, resistance to stresses like starvation, desiccation, chemical agent: DDT; also the effects of larval density during hatching and during the first instar, have not been studied and some experiment on the effects of density on M. brassicae were done to aid understanding the mechanism and effects involved. Other experiments were carried out to clarify seemingly contradictory results obtained by the above-mentioned authors.

In the text, the terms "isolated", "solitary", "singly" are used interchangeably in connection with larva, individual, group, to indicate that the larvae in question were reared singly in separate containers. Similarly, the adjectives "crowded", "grouped", mean that four or more larvae were reared together in one container, throughout their larval life unless otherwise stated. Only the effects of larval grouping were studies; hence, "density", as used in the term density effect, refers to conditions during the larval stage.

2.2 Review of Literature

The literature concerning the effect of population density in the animal kingdom is vast. This review will be confined to lepidopterous insects

with special reference to phase variation.

The effects of density in Lepidoptera have been studied in many species, and principally in Noctuidae, and in stored product pests.

The main characteristics affected by density have been tabulated in Appendix 1, Table 1 and 2, by using information from previous reviews (Uvarov, 1961; Brown, 1962; Iwao, 1968, and mainly Gruys, 1970) and other sources.

Although a few cases of direct competition for food are included, for example : Laspereysa pomonella (L.) (Ferro et al., 1973); Ephestia kuehniella (Zeller) (Ulleytt et al., 1947; Smith, 1969); E. cautella wlk (Takahashi, 1961); Plodia interpunctella Hubner (Snyman, 1949), and also in some of the higher densities used in experiments with species like Diacracia obliqua Walker (Islam et al., 1971), Persectania ewingi (Doull, 1953), the examples quoted have been suggested to be the result of "group effect", that is, the effect produced by proximity of individuals in population of low density (Chauvin, 1967).

As suggested by Long (1959) and critically reviewed by Iwao (1968), the response to density of a given species is probably related to its mode of life in nature. In spite of the interspecific variation observed, sometimes even with discrepancies among authors dealing with the same species (see App. 1, Table 1 and 2), some general characteristics seem to be equally affected: Species showing density-related colour changes tend to have their rate of development increased by increased density while the converse is observed in those showing no colour changes. Consistent reduction in larvae, pupal and adult weight with reduced fecundity and increased overall mortality.

Different sorts of functional-adaptation to changing environments are found in Lepidoptera e.g., additional moults to compensate for reduced growth rates in some gregarious species when undercrowded (Mizuta, 1960); reduction in size to maintain a higher surviving proportion (Ullyett et al., 1947); density-related incidence of diapause (Tsuji, 1959; Iwao, 1962); phase variation (Long, 1953; Iwao, 1962). Phase variation will be dealt with in some detail because M. brassicae shows a strong density related variation (polymorphism).

Phase variation

It has long been known that caterpillars of a number of moths exhibit colour differences associated with fluctuation in their population densities (for examples references: Long, 1953; Uvarov, 1961; Brown, 1962; Iwao, 1968). They have been observed in Noctuidae, Notodontidae, Sphingidae, Geometridae, Saturniidae, Arctiidae and Hesperiidae.

Individual larvae from dense populations became much darker in colour in their later instars, and at the same time other changes are observed to occur in their physiology and behaviour. This type of density dependent polymorphism has been called "Phase variation" because in many respects it resembles that in locusts (Iwao, 1968).

The term was first referred to Lepidoptera by Faure (1943 a, b), who observed that the occurrence of dark caterpillars in the field was often associated with the presence of a high population density, and he experimentally showed that the effect could be reproduced in laboratory by crowding Spodoptera exigua (Hubner) and S. exempta (Walker).

The parallel between the phase of locust and the effect of crowding in caterpillars has been considered by Long (1953).

In general, species showing phase variation respond to density by increasing the rate of development sometimes with a reduction in the number of larval instars. Larval weight is affected which in turn affects pupal and adult weight. The reduction in adult weight usually, but not necessarily results in a decrease in fecundity.

Activity of larvae is frequently reported to be affected by density, thus, crowding produces active individuals while solitary individuals are usually sluggish. In adults, the wing loading has been noted to decrease. (For details about a particular species consult Appendix 1, Table 2.)

Biochemical differences have been found between crowded and solitary-reared individuals. Fat content is higher in crowded populations of Spodoptera exempta and Spodoptera abyssinia (Guenee) (Mathhee, 1945), Plusia gamma L. (Long, 1953). In Spodoptera exigua (Hanna et al., 1973) crowded and solitary larvae contained, equal amounts of fat in their summer generation but the crowded larvae less in the autumn generation. Fat content decreased in crowded cultures of Spodoptera littoralis (Boisduval) (Zaher and Moussa, 1961) and Agrotis ypsilon (Zaher and Moussa, 1962). Water content is usually lower in crowded larvae (Mathhee, 1945; Long, 1953; Zaher and Moussa, 1961, 1962; Hanna et al., 1973). In S. exempta and S. abyssinia crowded larvae have more lactic acid but less uric acid (Mathhee, 1945).

Few data are available to demonstrate physiological differences. Oxygen consumption increased with density in Leucania separata Walker and S. litura (F.) (Okauchi, cited by Iwao, 1968), and M. brassicae (Burov, et al., 1970).

The expression of phase variation may be affected by other factors. At low temperatures (20°-22°C) the percentage of dark individuals of M. brassicae increase while high temperatures (25°-28°C) induce more rapid development (Hirata, 1962a). In P. gamma (Cayrol, 1957) the effect of density was influenced by photoperiod and temperature. Light and relative humidity did not influence the degree of darkening of larvae of Leucania separata (Iwao, 1962); while Faure (1943a, b) found that in S. exigua and S. exempta, solitary larvae reared in darkness or semi-darkness become blackish as in crowded individuals.

In M. brassicae the effect of crowding on acceleration of development is influenced by the food plant (Hirata, 1960). Solitary larvae show diverse colouration which is possibly, related to the quality of food. However, in crowded cultures the influence of food quality is overshadowed by the density effect (Hirata, 1960). In contrast food quality had no effect on the darkening of Alabama argillacea Hubner (Calcagnolo et al., 1955).

The inheritance of phase variation, especially larval colouration, has been superficially studied by some authors. Mathhee (1946, 1947) attempted to intensify phase characters through three generations in S. exempta and S. abyssinia. He obtained some degree of intensification of solitaria characters (colouration) in "Solitary lines", but evidence of intensification of gregaria characters in the converse direction was not clear. His conclusion differs from that of Faure (1943), who reported no intensification of phase characteristics whatsoever with S. exempta. Long (1953) observed in P. gamma that crowded cultures from "light" colour-type parents were somewhat less dark than those of "dark" colour-type parents. No effect was seen in the colour composition in the F_1 generation in solitary individuals of either light or dark lines. Calcagnolo et al., (1955) could not

show that the density of the previous generation had any effect. In L. separata, the progeny of high-density type (dark) parents seemed to be somewhat darker than those of the low density type (pale) parents, in both crowded and isolated cultures; the speed of development was also slightly faster in the former (Iwao, 1962). Similar observations were obtained in Diacrisia obliqua (Islam and Sardar, 1971).

The evidence suggests that density effects may be modified by other influences, but that the differences induced by density alone are the most important and probably dominant.

The problem of the mechanisms underlying phase variation has been given some attention, especially in its relation with larval colouration.

Olfactory stimulation was not a causative factor in Drooz (1966b), Iwao (1962) and Calcagnolo et al., (1955) experiments. In M. brassicae, Bonnemaison (1962b) observed a slight effect caused by odour. Visual stimulation, at least in caterpillar, should not be a cause because of their poor sense of sight, and was confirmed by Long (1955) and Bonnemaison (1962b), however it was considered the main factor in the darkening of Alabama argillacea (Calcagnolo et al., 1955). Contamination of food with excreta had no effect in L. separata (Iwao, 1962). CO_2 accumulation was thought to be a possible factor but experimental work did not yield positive results (Long, 1955; Bonnemaison, 1962b; Iwao, 1962; Schneider, 1973). The contact stimuli are not (Sharov, 1953) or not always completely specific (Iwao, 1962; Drooz, 1966) but Long (1955) demonstrated specificity in P. gamma. The nature of the contact stimulus seems to differ with the species; thus, artificial continuous direct contact causes darkening in Cephonodes hylas L. (Sasakawa, 1973) while mechanical irritation with a brush failed

to produce coloured individuals in Erynnis ello L., even when accompanied with the juice from regurgitation of other caterpillars (Schneider, 1973). Periodic rotation or shaking of the larval container increased the proportion of dark coloured caterpillars in M. brassicae (Burov et al., 1970).

The black pigment deposited in the larval cuticle of crowded larvae is melanin (Ikemoto, 1970; Reay-Jones, 1971).

The development of the phase variation characteristics in locust is controlled hormonally (Joly, 1972) with Juvenile Hormone playing an important role (Joly and Meyer, 1970; Joly and Joly, 1974). Recent studies showed that the hormonal mechanism involved in the "phase" of caterpillars is analogous to that in locust (Reay-Jones, 1971; Yagi, 1976; Sehnal, 1976; Sehnal et al., 1976).

Juvenile Hormone (JH) has been shown to lengthen the last instar, to reduce subsequent blackening considerably, and to make the cuticle of formerly black caterpillars appear very like those of solitary ones in S. littoralis (Reay-Jones, 1971; Sehnal et al., 1976; Sehnal, 1976), and S. litura (Yagi and Kuramochi, 1976). However, complexity in the mechanism is seen in P. gamma, where although JH lengthened the instar duration, its action on the blackening was uncertain; and in L. separata (Ogura, 1975) JH did not inhibit the formation of melanin in the crowded larvae even when a high dose was injected. Ogura suggested that in this species JH may act as a melanization inhibitor if present throughout the whole of the larval development, and was confirmed later by Kuramochi (cited by Yagi and Kuramochi, 1976).

The blackening hormone in S. littoralis is suggested to be bursicon

which has its main source in the abdominal ganglia (Reay-Jones, 1971). In contrast, the suboesophageal ganglia release the hormone(s) that promote(s) the black pigmentation in L. separata (Ogura, 1976) and M. brassicae (Ogura et al., 1971 cited by Mochizuki and Agui, 1976).

Phase variation in Lepidoptera can be considered as adaptation either to the biological or to the physical environment.

An example of density related adaptation to the biological environment is provided by Exaereta ulmi Schiff. (Sharov cited by Gruys, 1970), in which the larvae are procryptically coloured at low density and match the elm tree colours; the larvae feed at night and cling to the substrate when touched. However, at high population density colour and behaviour change, thus the caterpillars develop a contrasting colouration with melanized patches, become day feeders and drop to the ground when disturbed. Sharov argues the survival value of this density-induced change as a defence against predation by birds. Key's theory of facultative aposematism (Key, 1957) may be applicable to this situation. In S. littoralis the evidence from laboratory experiments does not support the idea that the black colouration of crowded caterpillars constitutes a serious deterrent to bird predators (Reay-Jones, 1971).

S. exempta provides an example where the density effect carries over to the progeny of the succeeding generation which migrate (Brown, 1962; Brown and Swaine, 1966), following high density outbreaks, which seldom last for more than one generation. It has been suggested (Whellam, 1954) that migration after an outbreak may be important in avoiding a build up of natural enemies in a localised area. Migration can equally be important to avoidance of food shortage, or indeed any other requirements, in the crowded

or succeeding generation.

As pointed out by Iwao (1968) phase variation in Lepidoptera may primarily have evolved as an adaptation to conditions of larval life. Thus, he emphasised the important of migration of caterpillars, greater resistance to starvation, wider tolerance of unpalatable food plants, observed in the high density type larvae of L. separata. Greater activity and marching behaviour observed in S. exempta (Faure, 1943; Mathhee, 1946) could enable the caterpillars to reach new food sources after depletion of their own.

Migration of the adults of L. separata is observed when they develop from larvae or pupae which have been subjected to unfavourable conditions and thus increasing the chances of finding a habitat more favourable to their offspring (Quo et al. cited by Gruys, 1970).

Beside being a possible anti-predators device, the blackening response of caterpillars in dense populations may serve two other possible functions (Reay-Jones, 1971). Reay-Jones pointed out that under outbreak conditions black caterpillars experience a very different environment to that of pale individuals from sparse populations, for example, they are likely to be exposed to conditions of heat, desiccation and ultraviolet radiation. A layer of black pigment in the cuticle could absorb ultraviolet light thus protecting internal organs from damage. It could also cause an increase in internal temperature, which might have the effect of increasing activity and marching, and increased body temperature might result in more rapid development. Rose (1975) attributed the increase in the rate of development he observed in S. exempta in field populations to this rise in temperature.

Along with the blackening, Reay-Jones (1971) has suggested that the cuticle of black S. littoralis larvae is more sclerotized than that of pale ones, being bulkier and less easily torn, this he considered could help the caterpillars to withstand better the abrasion to which they are subjected while crawling in marching hordes.

2.3 Materials and Methods

All larvae used in these experiments were obtained from egg masses laid by moths from the stock culture.

The insects were reared at a constant temperature of 25 ± 1°C, with 16:8 hours light:dark cycle. Relative humidity was not controlled but was probably high because of transpiration of the leaves given as food.

Larvae were reared in isolation or in groups of 4, 8, 16 and 32 in container type A.

To prevent food shortage, plenty of brussels sprouts or spring greens leaves were provided as food. They were changed once or twice daily during the last two instars in the higher density treatments. With every change of food the containers were cleaned to keep contamination as low as possible.

The hatchlings were assigned to the different densities while in the first moult because in natural conditions, the first instar, and sometimes the second remain aggregated. Once the larvae entered prepupal stage they were transferred to a similar container with peat for pupation. Pupae three days old were weighed and sexed, and observed until emergence.

Observations were made of larval colouration; larval, prepupal and pupal periods; pupal weight; mortality and diapause.

At a later date, two experiments using similar conditions to those mentioned above were set up to study the changes in larval development within the different instars and the rate of increase in weight.

More detailed descriptions of the experiments are given within each subsection.

2.4 Results and Discussion

2.4.1 Colour variation in larval stage

2.4.1.1 Larval colour types

Two days-old sixth instar larvae were classified into five colour types (Fig. 1.2).

Type I Head pale beige. General colour varying from pale to yellowish green, dorsum sometimes slightly darker, and with or without three narrow broken whitish lines along the body, a central one and the other two on each side subdorsally. Subspiracular band whitish yellow, frequently not well defined. Area around the spiracles not pigmented. Latero ventral zone speckled with whitish yellow. Prolegs bearing no marks.

Type II Head pale brown with areas mottled with beige. Dorsum pale pinkish brown to pale greenish brown with or without

the whitish dorsal lines. Subspiracular band greenish yellow slightly flecked with orange, below the spiracles. Sometimes a little black pigment around the spiracles. Latero-ventral zone and prolegs as in Type I.

Type III Head as in Type II. Dorsum greenish brown to pale blackish brown. Subspiracular band greenish yellow to light yellow, more flecked with orange than Type II, sometimes extending further along the band. Black area round the spiracles more noticeable and somewhat extended above the upper limit of the subspiracular band. Latero-ventral zone and prolegs as in Type I.

Type IV Head dark brown with areas mottled pale brown. Dorsum blackish brown. Subspiracular band light yellow, flecked with orange sometimes quite heavily. The black area around each spiracle well defined and extending above the subspiracular band so that they are interconnected. Latero-ventral zone flecked with pale brown and yellowish white. Prolegs with pale brown to dark brown patches.

Type V Head as in Type IV. Dorsum black. Subspiracular band yellow to almost completely orange. Dorsal lines normally present. Black area round each spiracle as in Type IV. Latero-ventral zone flecked with brown intermingled with beige. Dark brown patches on the prolegs.

It is clear that the colouration of the larvae is very variable, and that the types merge one another but generally it is possible to place a given

individual in one of the above-mentioned types.

2.4.1.2 The colour of larvae reared at various densities

No detailed information of the colour changes throughout the larval period was collected, nevertheless it was noted that the higher the degree of crowding the earlier the colour changes began to appear. At high densities (16-32) some individuals showed darkening during the 4th instar; many during the 5th instar and all the 6th instar larvae. Isolated individuals, however, were always pale green throughout until the 6th instar when some of them showed colour changes, and were mainly classified between Types I and III.

For the present experiment as well as for those set up to study the rates of development (see Fig. 2.5) and growth (see Table 2.3), the colour types of two days old sixth instar larvae were classified using the classification above described (Figs. 2.1, 2.2 and 2.3).

Individuals reared in isolation were included within the first four types, mainly in Type II and a very small percentage in Type IV. With increasing density the degree of darkening of the caterpillars increased, and is already apparent at a density of 4 larvae per container.

This density related darkening observed on M. brassicae larvae agrees with Hirata (1954, 1956), Bonnemaison (1962a), and Burov et al., (1970) findings.

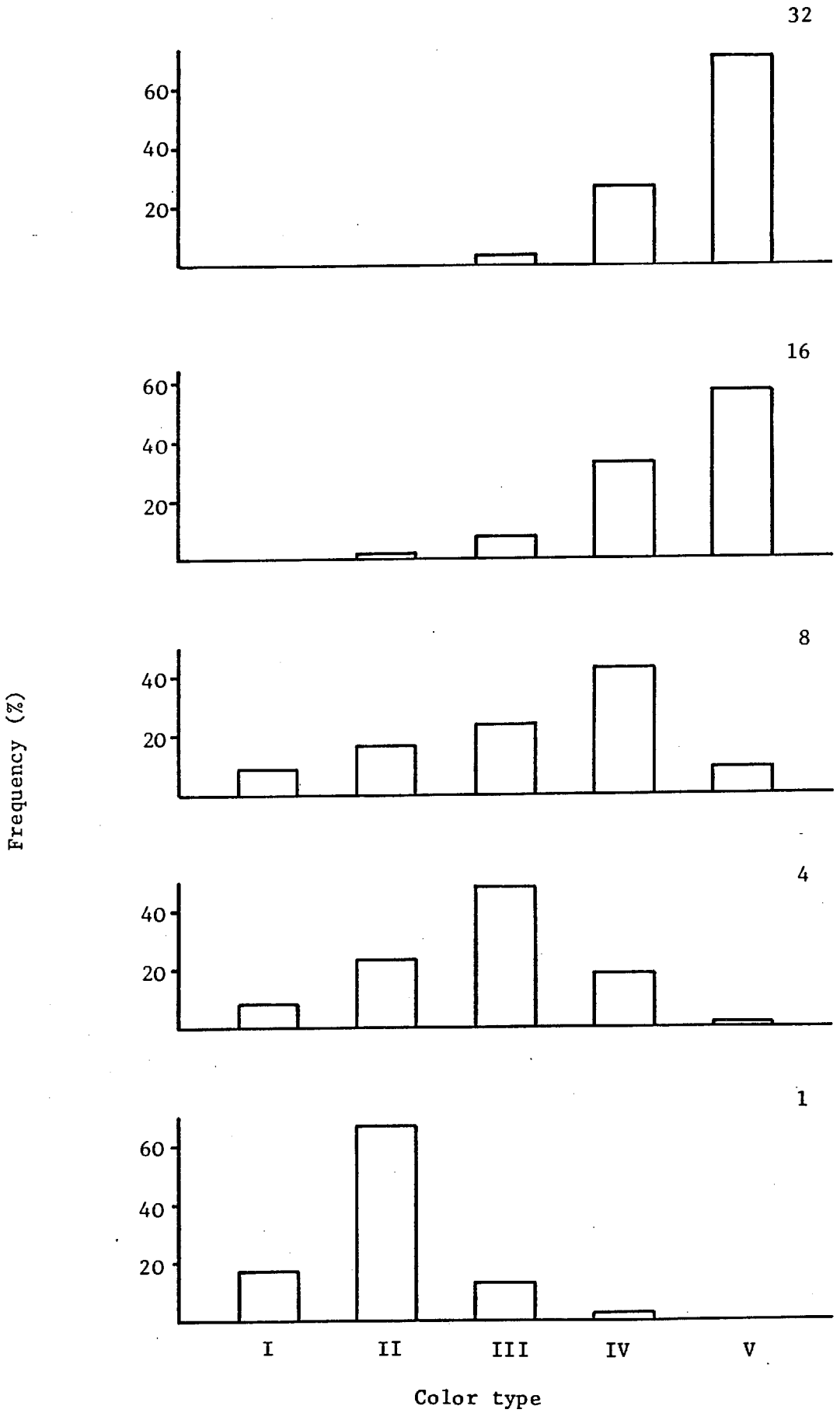


Figure 2.1. Frequency distribution of colour types of two days-old sixth instar *M. brassicae* larvae reared at various densities (Numerals in the figure indicate the rearing density).

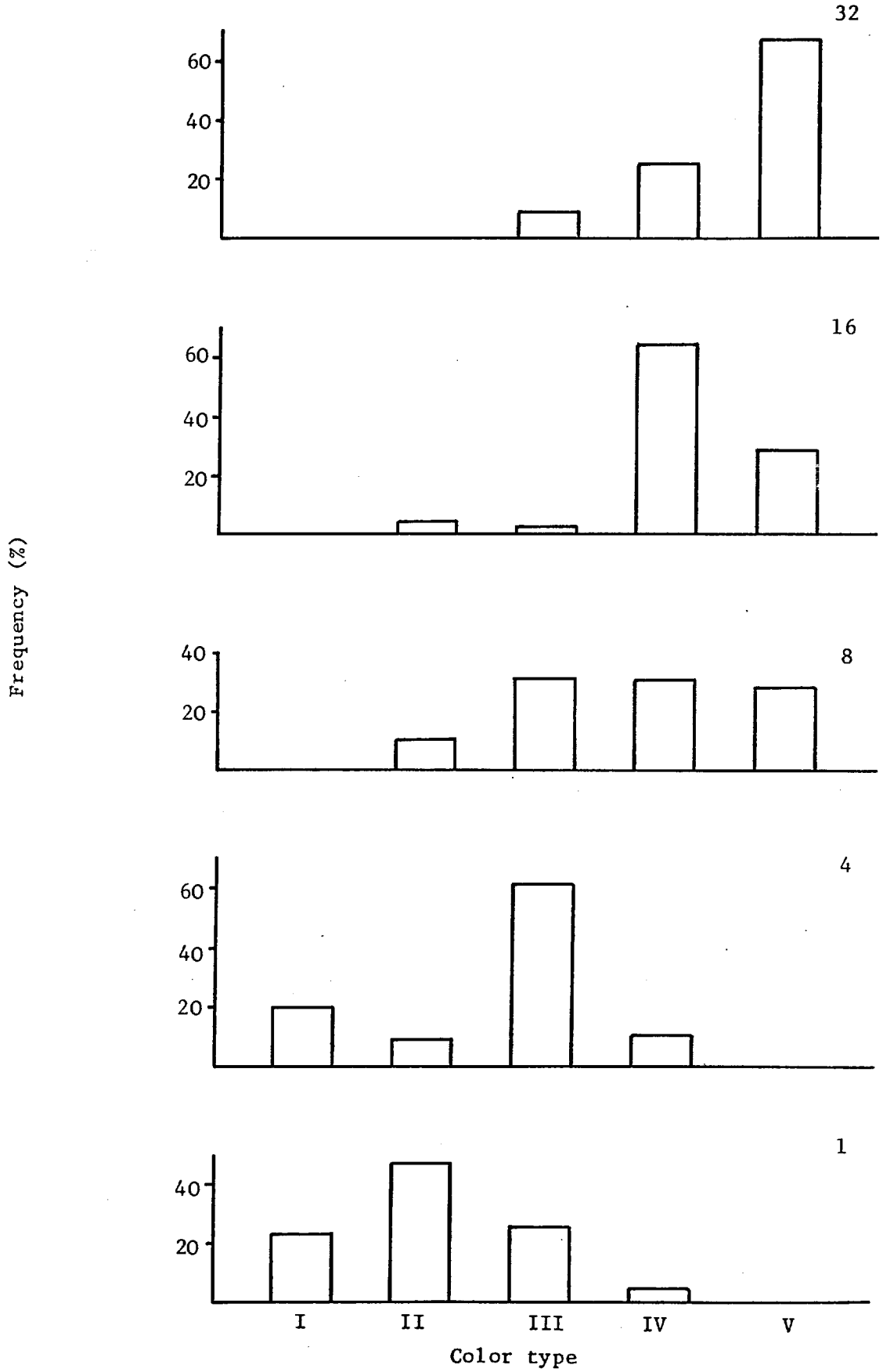


Figure 2.2. Frequency distribution of colour types of two days-old sixth instar *M. brassicae* larvae reared at various densities. (Numerals in the figure indicate the rearing density) (Data obtained from experiment shown in Figure 2.5).

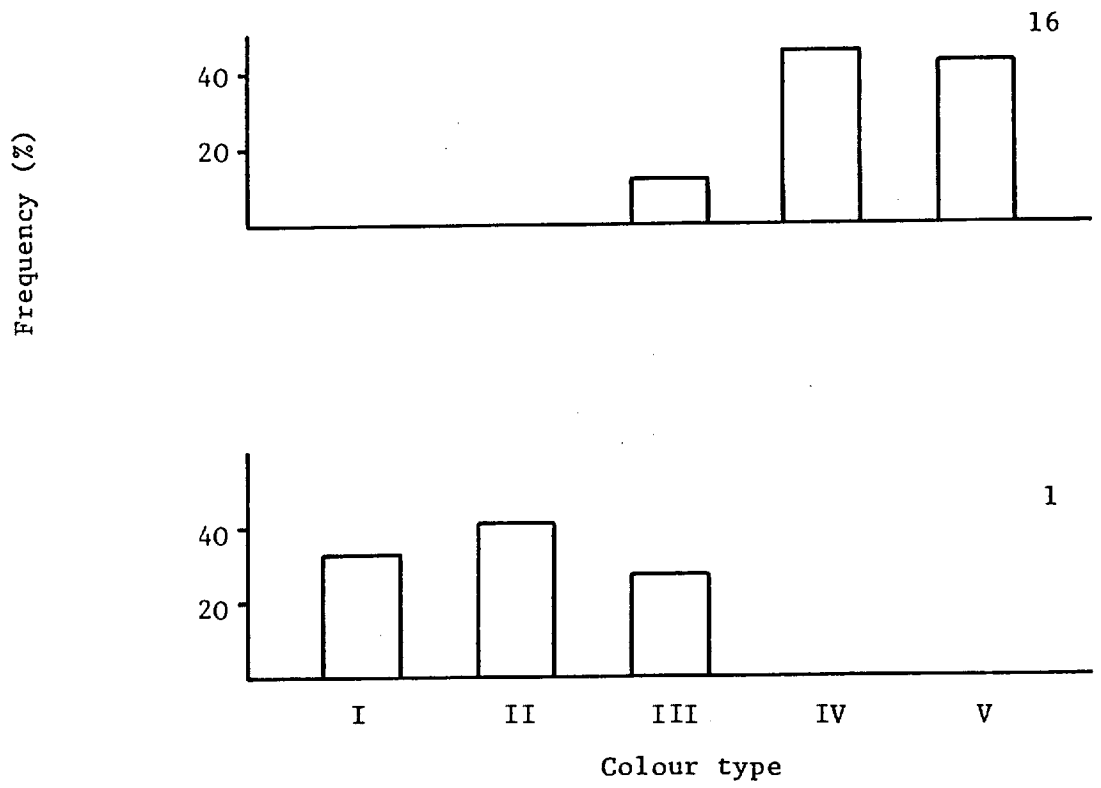


Figure 2.3. Frequency distribution of colour types of two days-old sixth instar *M. brassicae* larvae reared at various densities. (Numerals in the figure indicate the rearing density) (Data obtained from experiment shown in Table 2.3).

2.4.2 The pattern of larval and pupal developments

2.4.2.1 The duration of larval development

The larvae of M. brassicae developed significantly more rapidly when they were reared four or more individuals to a container (Table 2.1).

The length of the larval stage was shorter in males than in females at every density tested (Table 2.1) and the differences were statistically significant.

The peaks of pupation of isolated individuals occurred on days 18 and 19 for males and females respectively, and with increasing density they were moved to the left; the effect is noticeable even at a density of 4 individuals per container (Fig. 2.4).

The differences in development rates between the different densities first became noticeable during the 4th instar (Fig. 2.5). It can be seen that the percentage of larvae reaching a particular moult followed a different pattern. In reaching 4th moult the isolated and the four larvae density took a somewhat longer time than the rest. The gap continued to widen for the isolated cultures which on entering prepupal stage were clearly separated from the others.

The tendency towards a less pronounced peak in the frequency curves of prepupation seems to be associated with bimodality arising from sexual differences, with the peak of the males being at about one day earlier than in the females. This is evident in the frequency curves of total development time to the pupal stage (Fig. 2.4).

TABLE 2.1 The Duration of Larval Development of M. brassicae Among Individuals Reared at Various Densities

Density reared	Larval duration (days)			
	n*	males	n	females
1	22	18.23 ± 0.16**	16	18.81 ± 0.19
4	37	17.51 ± 0.10	37	18.19 ± 0.15
8	34***	17.58 ± 0.14	32	18.22 ± 0.13
16	32	17.34 ± 0.12	34	18.21 ± 0.16
32	68	17.66 ± 0.10	65	18.22 ± 0.12

* Number of surviving larvae

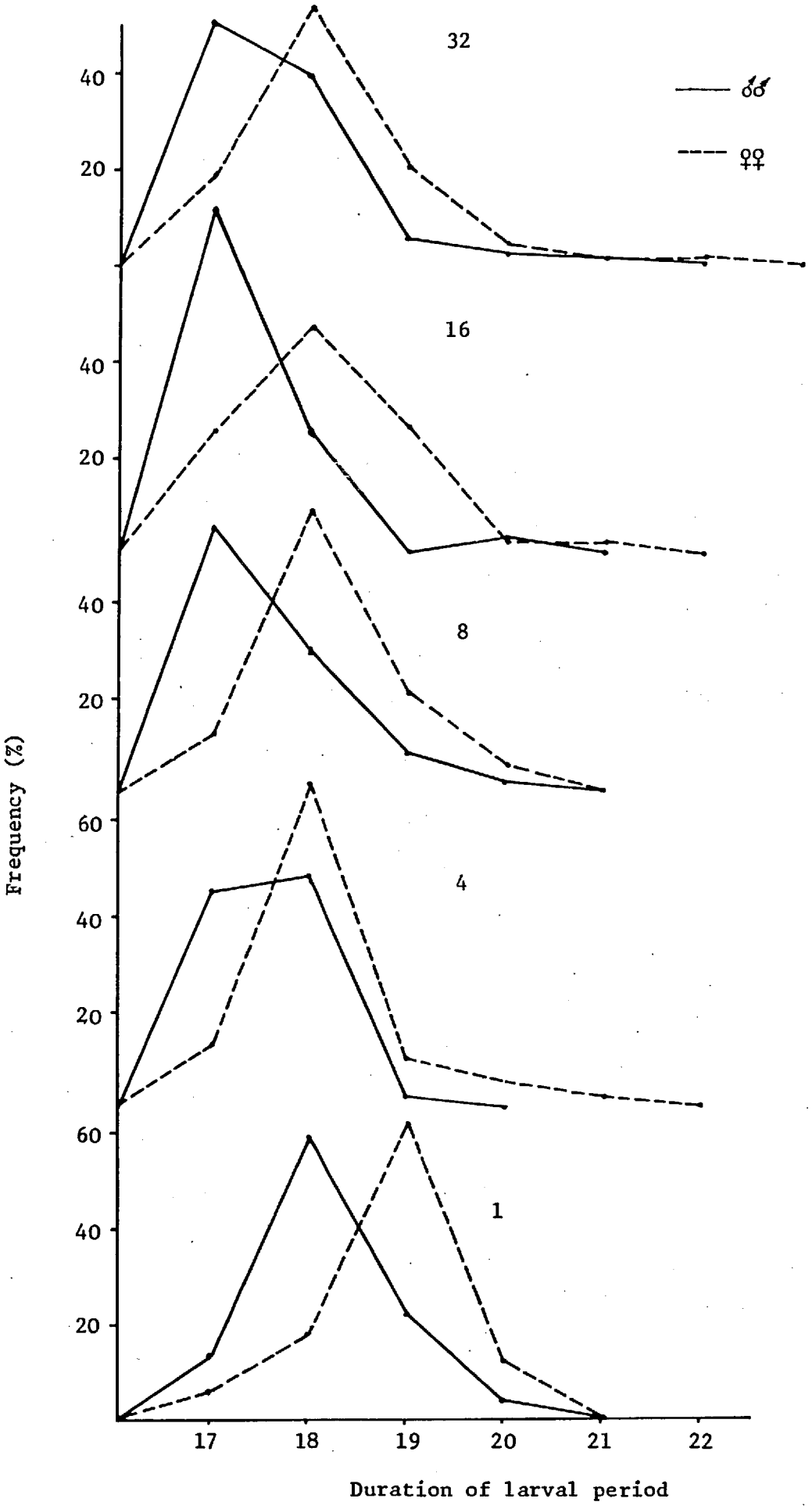
** Mean ± Standard error

*** One larvae was left out for the calculation of the larval duration because of its protracted development through the larval period.

Although the frequency peaks were displaced to the left as density increased the displacement seems maximum at about 16 larvae per container which might indicate an optimum density in terms of development rate. The effect might be mediated by mutual stimulation which has been described for several other insect species (Long, 1955; Sharov cited by Long, 1955; Iwao, 1962)

Various effects of rearing density on larval development of M. brassicae have been reported. Our results agree with those of Hirata (1954, 1956 and 1957) Bonnemaison (1962a) but differ from those obtained by Burov and Mokruosova (1970) and Ishikura and Ozaki (1958). Although Burov and Mokruosova, found an increase in length of the larval period associated with increased density, their data show that at a moderate density, 5 larvae per

Figure 2.4. Sequential frequency curves of pupation incidence of *M. brassicae* larvae reared at different densities (numerals in the figure indicate the rearing density).


32
16
8
4
1
♂♂
♀♀
Frequency (%)
40
20
60
17
18
19
20
21
22
Duration of larval period

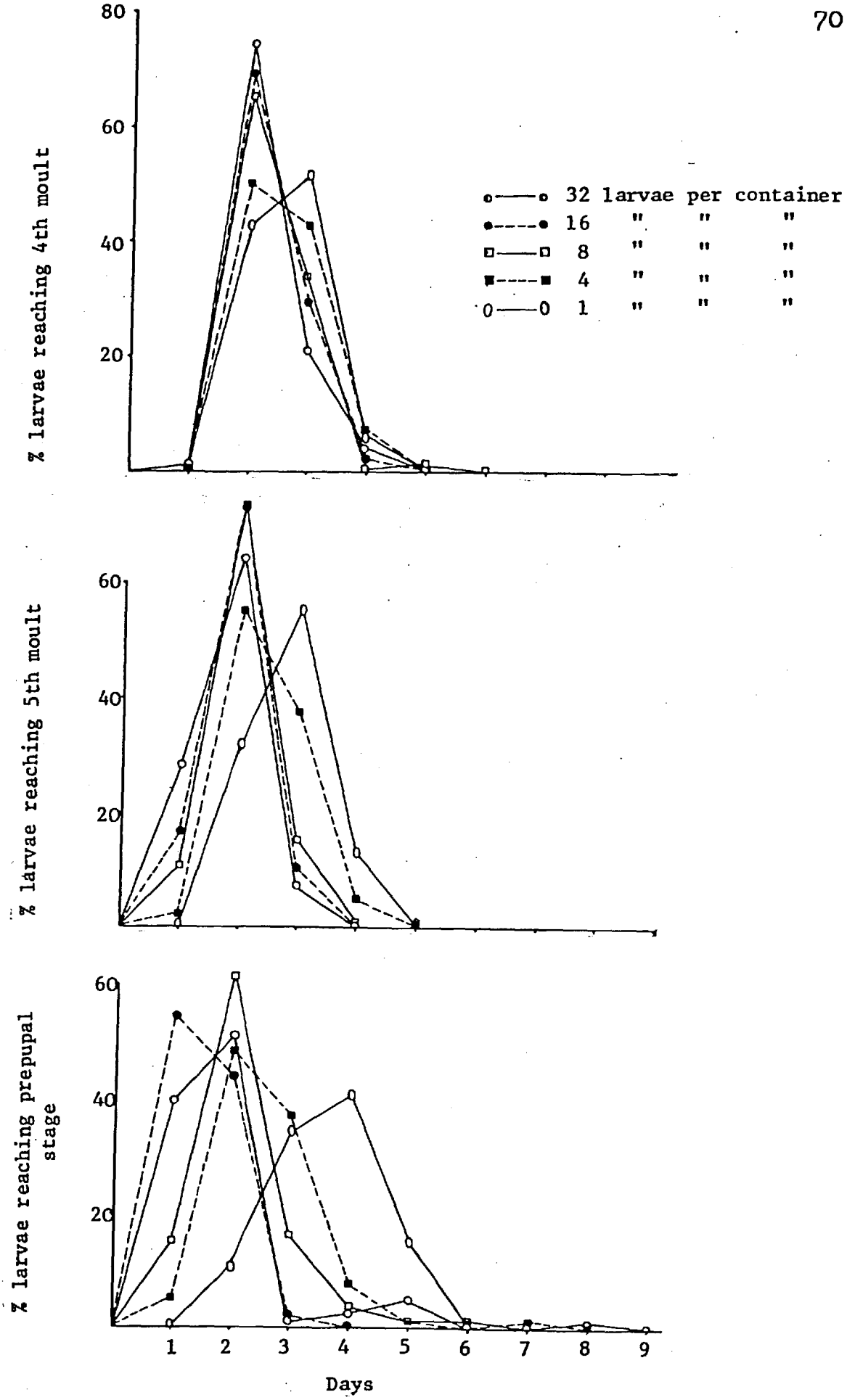


Figure 2.5. Frequency distribution curves of larvae reaching 4th and 5th moults and prepupal stage when kept at different densities.

container, the larvae did develop faster than isolated ones. Unfortunately, they did not state the size of the container used but some of their results might be attributable to overcrowding since development time was extended at the highest density. Ishikura and Ozaki, did not specifically compare isolated with grouped individuals but rather rearing densities of 10, 20 and 40 larvae to investigate problems associated with mass rearing. They conclude that at the higher densities the larval period is increased. Their results show that the duration of the last two instars was 9.4 days at a density of 10 caterpillars per container and 11.6 at a density of 40, which accounts for most of the observed increase in the larval period. Very high density during the last two instars, especially the last one, probably has a marked detrimental effect on development time since it is during this last instar that about 87%* of the food intake occurs.

2.4.2.2 The pattern of larval growth

A measure of larval growth is final pupal weight and was used to compare the growth of isolated and crowded larvae.

The weights of pupae decreased as larval density was increased (Table 2.2). At all densities the female pupae were significantly heavier than the males ("t" test, all cases $P<0.001$) and, with the exception of pupae reared as larvae four per container, all groups were significantly lighter than the isolated individuals. The decrease in weight with density for M. brassicae has been observed by previous workers (Hirata, 1954, 1956; Bonnemaison, 1963; Burov et al., 1970; and Ishikura et al., 1958).

*Calculated from Hirata's data (1963a)

The effect of density on larval growth was analysed by measuring the larval weights of successive instars in both isolated and grouped cultures (maintained constantly at 16 individuals per container, throughout the developmental period). Fresh body weights of the 2nd, 3rd and 4th instars were greater in grouped larvae than in isolated individuals (Table 2.3) but the differences were significant only for the 2nd and 3rd instars. The opposite was true of the 5th and 6th instars and thus, although it can be seen that during the 2nd and 3rd instars grouped larvae had a higher growth ratio than isolated individuals (Table 2.3), during the 4th, 5th and 6th instars the reverse was true. This trend could be interpreted in the sense that during the early instars the effect of density acts to promote growth and that in later instars, as individuals grow and presumably as "free" space becomes less, overcrowding effects begin to show.

2.4.2.3 The duration of prepupal and pupal periods

The males had a significantly shorter prepupal period than the females, at all densities between 4 and 32 larvae per container (Table 2.4). No clear significant density trends were observed.

There was a slight tendency for females to develop faster as pupae than the males, however, the differences were not significant and so the data for both sexes were pooled (Table 2.5). Rearing density did not have a significant effect on pupal development agreeing with the results of Bonnemaison (1962a), although Hirata (1956) observed a longer pupal period in crowded cultures.

TABLE 2.2 The Effect of Larval Density on Pupal Weight of M. brassicae

Density reared	Pupal weight (mgs)			
	n*	males	n	females
1	22	441.4 ± 9.41**	15	496.0 ± 8.71
4	37	420.8 ± 5.99	36	474.1 ± 8.47
8	34	402.8 ± 7.51	32	470.4 ± 7.45
16	32	378.5 ± 7.34	34	450.7 ±10.59
32	68	363.5 ± 4.33	63	398.3 ± 4.98

* Number of surviving pupae

** Mean ± Standard error

TABLE 2.3 Growth in Weight of M. brassicae Larvae Reared in Isolation or in Groups

INSTAR	Larval rearing			
	ISOLATED		GROUPED	
	Weight (mgs)	Growth ratio	Weight (mgs)	Growth ratio
1	0.5746 ± 0.0096*	4.30	0.5688 ± 0.0085	4.68
2	2.4723 ± 0.06	4.06	2.6624 ± 0.05	4.10
3	10.026 ± 0.23	4.40	10.928 ± 0.19	4.13
4	44.10 ± 0.82	4.54	45.13 ± 0.80	3.87
5	200.08 ± 6.24	2.45	174.43 ± 3.41	2.26
6	490.93 ± 9.21		393.58 ± 5.65	

* Mean ± Standard error

TABLE 2.4 The Duration of Prepupal Development of M. brassicae Among Individual Reared at Various Densities

Density reared	Prepupal duration (days)			
	n*	males	n	females
1	22	2.91 ± 0.09**	16	3.07 ± 0.12
4	37	2.68 ± 0.10	36	3.06 ± 0.07
8	34	2.87 ± 0.10	32	3.33 ± 0.09
16	32	2.78 ± 0.12	34	3.32 ± 0.09
32	68	3.09 ± 0.05	65	3.26 ± 0.06

* Number of larvae surviving prepupal stage

** Mean ± Standard error

TABLE 2.5 The Duration of Pupal Development of M. brassicae Reared at Various Densities

Density reared	n*	Pupal duration (days)
1	35	15.2 ± 0.15**
4	69	14.9 ± 0.10
8	56	15.1 ± 0.14
16	60	15.5 ± 0.12
32	128	15.4 ± 0.09

* Number of larvae surviving during pupal stage

** Mean ± Standard error

2.4.2.4 Larval and pupal mortality

Mortality during the larval period increased with larval density from 5.0% in isolated cultures to 30.7% at a density of 32 individuals per container (Table 2.6). During the pupal period the mortality was low (Table 2.7) and seemed to be unrelated to rearing density during the previous stage.

2.4.2.5 Sex ratio

The sex ratio did not differ significantly from unity (Table 2.8) (Chi-square = 2.01 for 4 d.f., $0.9<P<0.5$). With the biggest deviation arising in the isolated culture. Since the sex ratio was not affected by density then both sexes seem to be equally affected by density.

2.4.2.6 Diapause incidence in the pupae

Under the rearing condition used, 25°C constant temperature and 16:8 hours light:dark periods, considered as diapause preventing (Bonnemaison, 1959), the rate of diapause observed was very low (Table 2.9). Density did not have any effect on this rate agreeing with the findings of Hirata (1956) and Bonnemaison (1962a).

2.4.3 The behaviour pattern of larvae

2.4.3.1 Introduction

It has long been noted for many insects that when in groups, there is a tendency for an increase in activity, for example locust (Uvarov, 1966), armyworm (Faure, 1943). This part describes two experiments to examine

TABLE 2.6 Mortality of M. brassicae Larvae Reared at Various Densities

Density	Initial number	Number dying	%
1	40	2	5.0
4	80	6	7.5
8	72	6	8.3
16	80	14	17.5
32	192	59	30.7

TABLE 2.7 Pupal Mortality of M. brassicae from Larvae Reared at Various Densities

Density	n	males	females	total (%)
1	38	0	1	2.6
4	74	1	1	3.0
8	66	1	0	1.5
16	66	1	1	3.0
32	133	2	4*	4.5

* including two killed during handling

TABLE 2.8 The Effect of Larval Density on the Sex Ratio of M. brassicae

Density	males	females	ratio F/M
1	22	16	0.73
4	37	37	1.00
8	34	32	0.94
16	32	34	1.06
32	68	65	0.96

TABLE 2.9 The Effect of Larval Density on the Incidence of Pupal Diapause in M. brassicae

Density	n	Number entering in diapause			
		males	females	total	%
1	38	0	1	1	2.6
4	74	0	2	2	2.7
8	66	1	2	3	4.5
16	66	0	3	3	4.5
32	133	1	1	2	1.5

differences in behavioural pattern between individuals reared isolated and in groups.

2.4.3.2 General activity level

a) Materials and methods

16 larvae from isolated (coloure Types I-II) and grouped (colour Types IV-V) cultures reared at 25°C were transferred to isolated conditions in container type A; and a further batch of 16 grouped larvae was divided into two groups of 8 larvae. All larvae had moulted into the last instar two days previous and were fed on Spring greens leaves.

Observations were made at intervals of 15 minutes during 8 hours, 4 during the day and 4 at night, therefore, for each of three treatments a total of 544 observations were obtained. The behaviour of each larva was simply recorded as follows: R = resting, F = feeding, including masticatory movements and, W = walking or any other form of activity except feeding.

At night, a lamp fitted with a red filter was used, as most insects seem to be insensitive to red (Wigglesworth, 1972). When active larvae were suddenly illuminated with the red light their activity did not change and therefore it was assumed that normal activity would not be affected during night observations.

The temperature during the experiment was 20 ± 1°C.

b) Results and discussion

The results are presented as percentage of each kind of behaviour to

the total number of observations (Table 2.9a). The data for day and night observations were not pooled as differences between behaviour during both periods were evident.

TABLE 2.9a The Behaviour of Isolated and Grouped Larvae of M. brassicae During an 8-hours Observation Period (4 hours during the day and 4 during the night)

	Density during experiment	Behaviour during the night (in percentage)		
		Resting	Feeding	Walking
Isolated	1	83.1	16.2	0.7
Grouped	1	77.6	20.2	2.2
Grouped	8	68.7	23.9	7.4
	Density during experiment	Behaviour during the day (in percentage)		
		Resting	Feeding	Walking
Isolated	1	98.2	1.8	0.0
Grouped	1	96.5	3.1	0.4
Grouped	8	93.4	6.2	0.4

It can be seen that the larvae reared in groups showed a higher level of activity than those reared in isolation, which continued even when they were transferred to isolated conditions. Individuals from isolated rearing spent 17.3% more time resting, also walking was reduced. In contrast, the larvae of the other two treatments devoted more time to feeding and walking. This demonstrates the restlessness of grouped larvae as distinct to the rather sluggish isolated-reared individuals. It is interesting to note that even during the day the individuals of grouped cultures were more active.

Similar increased activity of grouped larvae has also been reported in P. gamma (Long, 1952), L. separata (Iwao, 1962), S. littoralis (Hodjat, 1970) and in some other species.

Although the results show that grouped larvae spent more time feeding than their isolated counterparts Hirata (1963a) found no significant differences in food consumption of the final instar, however, his data show that grouped larvae consumed slightly more food. It could be that grouped individuals have shorter feeding periods due to disturbance by neighbouring larvae, and subsequently try to make up lost feeding time later. This would give the impression of an increased total feeding period, and thus of greater food intake, however, even when isolated, grouped individuals still show an increase in time devoted to feeding.

2.4.3.3 Response to physical disturbance

a) Materials and methods

2-3 days-old sixth instar larvae from isolated (colour Types I-II) grouped (colour Types IV-V) (16 larvae per container) cultures were used for this experiment, which was carried out at 25 ± 1°C and the light conditions provided by four 125-watts flourescent tubes hanging at a height of 75 cms.

Each larva to be tested, was dropped from a height of 10 cm onto the centre of a petri dish of 9 cm diameter, 1 cm in height. When disturbed or dropped a larva takes a characteristic c-shaped curled position for some time before regaining normal posture and beginning to walk away. For each larva the following records were taken: (a) time elapsed from dropping until it straightened itself, and (b) time since it straightened until it crawled out of the dish.

The experiment was run on two days between 8.30p.m. and 11.30p.m. and the separate days data pooled. A total 31 grouped and 34 isolated-reared larvae were used. All records were grouped in frequency tables.

The test is almost identical to that used by Iwao (1962) with L. separata, except that he only took into account the overall time to escape from the dish.

b) Results and discussion

It can be seen clearly that about 94% of the grouped larvae regained normal positions during the first three minutes while only 5% of the isolated individuals did so within the same period of time (Table 2.10). Further, it was observed that 93% of the grouped larvae crawled out of the dish within a period of 6 minutes, in comparison only 29% of the isolated ones managed to escape (Table 2.11). The latter, once straightened, showed less activity and remained motionless for long periods of time unlike their counterparts that almost in all cases began walking as soon as they straightened.

As a result of these two different component responses, the overall time required to escape after being dropped is very different for the two types of larvae (Table 2.12). L. separata showed similar differences in activity between crowded and isolated reared larvae (Iwao, 1962).

TABLE 2.10 Response of Isolated and Grouped Reared Larvae when Dropped in a Petri Dish. I. Time taken from dropping until the larvae straightened themselves

Class (min.)	Grouped larvae	Isolated larvae
0 - 3	29	12
3 - 6	1	9
6 - 9	1	3
9 - 12	0	2
12 - 15	0	1
15 - 18	0	3
>18	0	4

TABLE 2.11 Response of Isolated and Grouped Reared Larvae when Dropped in a Petri Dish. II. Time required to escape from the dish after the larvae straightened themselves

Class (min.)	Grouped larvae	Isolated larvae
0 - 3	23	6
3 - 6	6	3
6 - 9	0	2
9 - 12	1	2
12 - 15	0	2
15 - 18	0	2
>18	1	14

TABLE 2.12 Response of Isolated and Grouped Reared Larvae when Dropped in a Petri Dish. III. Overall time required to escape from the dish after the dropping

Class (min.)	Grouped larvae	Isolated larvae
0 - 3	18	1
3 - 6	7	4
6 - 9	4	4
9 - 12	0	2
12 - 15	0	1
15 - 18	1	1
>18	1	18

2.4.4 The resistance of the final instar larvae to stress factors

2.4.4.1 Introduction

It is well known that under outbreak conditions the larvae of several species of lepidoptera are mainly composed of blackened individuals and are often cited as attacking a wide range of plants, and migrating in great numbers to adjacent fields. This raises the question as to whether larvae from dense populations are more resistant to stress factors such as starvation, desiccation, food changes, insecticide, solar radiation etc.

In this part we will deal only with an analysis of response to starvation and desiccation and briefly to insecticide.

2.4.4.2 Resistance to starvation

a) Materials and methods

Just after moulting into 6th instar, larvae which had been reared in isolation (colour Type I-II) and in groups (colour Type IV-V) were confined singly in 76.2 x 25.4 mm glass tubes; both ends of which were covered with pieces of terylene and secured by rubber bands. The experiment was done in a constant temperature room at 20 ± 1°C, with a 16:8 hours light : dark cycle. The relative humidity was adjusted to 75 percent by keeping the tubes in a desiccator over a saturated solution of sodium chloride.

Each larva was weighed before and at intervals of two days during starvation. The tubes were inspected daily for mortality and when the insects began to show signs of weakness the observations were made every twelve hours. To avoid unnecessary disturbance of the larvae which often led to the regurgitation of a green liquid with ensuing loss of water, they were weighed in the tube. Death was regarded as the time when no movement was observed after a larva was prodded.

b) Results and discussion

Larvae reared in groups lived longer, 7.26 days on average, compared with the isolated ones, 6.62 days on average (Table 2.13). The difference was highly significant ("t" test, $P<0.01$).

The weight losses after the first two and four days of starvation are shown as percentage of the initial weight (Table 2.14).

During the first two and four days the grouped larvae lost a lower

percentage of their weight than the isolated larvae. When the ratio survival time (days) to body weight (mgs) is plotted against frequency for both types of larvae, two distinct curves emerged (Fig. 2.6). The higher ratio shown by the grouped individuals indicating that they may withstand starvation better than their counterparts.

TABLE 2.13 The Resistance to Starvation of Isolated and Grouped Larvae of M. brassicae

Treatment	Number of larvae	Av. weight of larvae at the beginning of test (mgs)	Survival time (days)	Av. ratio survival/ weight
Isolated	33	208.62 ± 4.07*	6.62 ± 0.17	3.19
Grouped	35	200.94 ± 3.77	7.26 ± 0.13	3.64

* Mean ± Standard error

TABLE 2.14 Weight Losses in Isolated and Grouped Larvae of M. brassicae Kept in Starvation Conditions

Treatment	Number of larvae	% weight losses	
		after 2 days	after 3 days
Isolated	33	9.71 ± 0.28*	17.71 ± 0.57
Grouped	35	7.89 ± 0.35	15.42 ± 0.55

* Mean ± Standard error

Further studies are needed to clarify the better performance of the black individuals from grouped cultures. Nevertheless, a likely explanation

may be found by looking at differences in chemical composition, especially fat content. In general although other substances such as protein, glycogen, etc., can be utilized during periods of starvation, fat reserve seems to be the most important (Wigglesworth, 1972). Fat, although not analysed in this experiment, have been shown to be higher in many species of Lepidoptera where crowded larvae show colour changes, for example: S. exempta, and S. abyssinia (Mathhee, 1945); P. gamma (Long, 1953) and L. separata (Okauchi, cited by Iwao, 1968). In S. exigua (Hanna et al., 1973) crowded larvae had a higher, although not significant, percentage of fat content (dry weight) than solitary larvae in the summer generation but significantly less in the autumn generation. However, it should be mentioned that Zaher et al., (1961, 1962) found that individual larvae in crowded cultures of Agrotis ypsilon and Spodoptera littoralis contained less fat than individuals reared alone. Iwao (1967) stated that the longer survival time of dark larvae from crowded cultures as compared to pale, solitary reared individuals, was due primarily to their greater fat content.

2.4.4.3 Resistance to desiccation

a) Materials and methods

This experiment was carried out in similar conditions to those of the previous experiment, with the difference that the relative humidity inside the desiccators was kept about 5% by using phosphorus pentoxide. The general experimental procedure was the same as in the preceding experiment.

b) Result and discussion

No difference was found between larvae reared under crowded and isolated conditions (Table 2.15).

TABLE 2.15 The Resistance to Desiccation of Isolated and Grouped Larvae of M. brassicae

Treatment	Number of larvae	Av. weight of larvae at the beginning of test (mgs)	Survival time (days)	Av. ratio survival/ weight
Isolated	35	214.75 ± 4.44*	5.64 ± 0.12	2.64
Grouped	35	189.40 ± 3.35	5.76 ± 0.11	3.06

* Mean ± Standard error

TABLE 2.16 Weight Losses in Isolated and Grouped Larvae of M. brassicae under Condition of Desiccation

Treatment	Number of larvae	% weight loss	
		after 2 days	after 3 days
Isolated	35	21.64 ± 0.57*	27.97 ± 0.84
Grouped	35	21.95 ± 0.43	30.58 ± 0.64

* Mean ± Standard error

After 3 days, the percentage of weight loss was higher for the grouped larvae (Table 2.16). Compared with the preceding experiment the isolated larvae were heavier than those grouped, and perhaps part of the difference in % weight loss could have resulted from this.

When the data on survival were compared on a weight basis, the ensuing ratio favoured the grouped individuals (Fig. 2.7), indicating that notwithstanding their smaller size, the dark larvae from grouped cultures were more

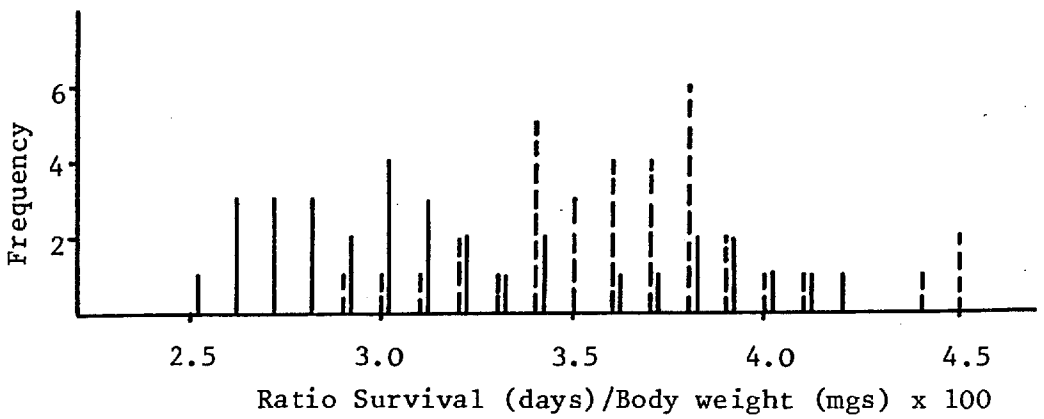


Figure 2.6. The distribution of the survival/body weight ratio between individuals reared from isolated and grouped cultures and kept under starved conditions (——— : larvae from isolated cultures; ----- : larvae from grouped cultures).

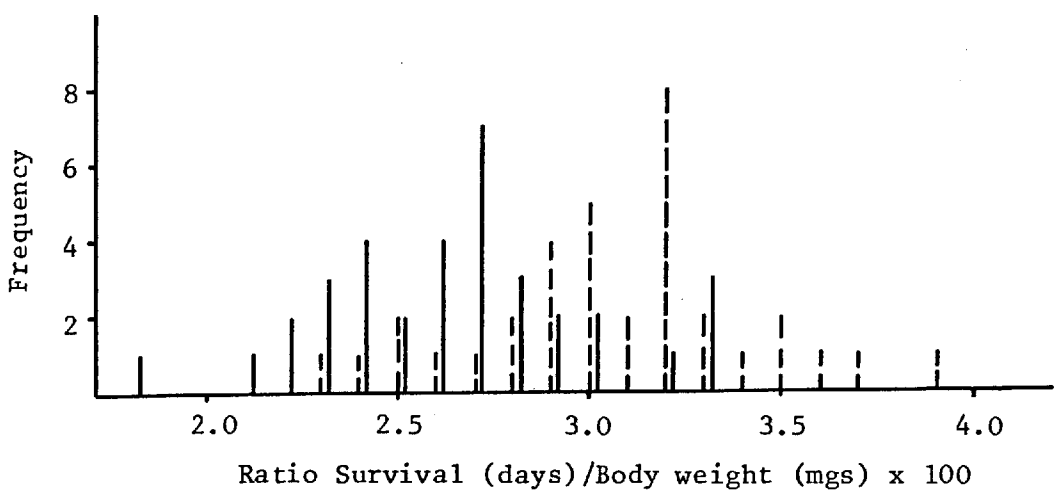


Figure 2.7. The distribution of the survival/body weight ratio between individuals reared from isolated and grouped cultures and kept under condition of dessication (——— : larvae from isolated cultures; ----- : larvae from grouped cultures).

resistant to desiccation. This confirms the results of the previous experiment in which the ratio of survival time (days) to weight (mgs) also showed a higher value for the grouped larvae.

2.4.4.4 Resistance to D.D.T.

a) Material and methods

Larvae that had been reared either isolated (colour type I-II) or in groups (colour type IV-V) at 25°C were weighed and assigned to containers of type A. Each larva was given a topical dose of 30 µg in one µl of acetone + 5% risella oil. A preliminary experiment indicated that this was close to the LD-50. The dose was applied to the dorsal part of first thoraxic segment with an electrically operated Arnold microapplicator fitted with an agla syringe.

Treated larvae were held at 20°C with fresh cabbage leaves supplied daily. Mortality counts were made every 24 hours. Death was considered when after prodding, a larva showed no reaction.

b) Results and discussion

Unfortunately the dose given was not adjusted to the weight of the caterpillars and turned out to be too high producing 100% mortality in both treatments (Table 2.17). However, the treatment differed greatly in survival times, for example, the black individuals of the grouped cultures survived up to 11 days, in contrast with only 6 days for the isolated-reared individuals. This suggests that the larvae from the high density cultures, although also killed, were more resistant than individuals of the isolated cultures. Working with an organophosphorous compound (EPN), Ishikura et al.,

(1958) showed that the resistance of M. brassicae increased in larvae reared at densities of 20 and 40 per container as compared with 10 larvae.

TABLE 2.17 Preliminary Test on Differential Susceptibility between Larvae Reared in Groups (Colour Type IV-V) and Larvae Reared in Isolation (Colour Type I-II) to D.D.T.

Density	Colour type	No. tested	Av. Weight (mgs)	Daily accumulated mortality (%)										
				1	2	3	4	5	6	7	8	9	10	11
G (16)	IV-V	25	620.0	0.0	4.0	28.0	44.0	52.0	64.0	76.0	80.0	84.0	92.0	100.0
I	I-II	22	651.4	0.0	4.5	54.5	68.2	77.3	100.0	-	-	-	-	-

G = Grouped I = Isolated

On the present evidence there cannot be definite conclusions. However, the differences showed by the two groups might be explained by one of two, or both of the following reasons: (a) a thicker cuticle and for the presence of pigments in the cuticle, and (b) a higher lipid content or changed lipid characteristics.

Reay-Jones (1971) studying the physiological aspect of the blackening of S. littoralis in response to crowding, suggested that changes other than increased melanin deposition occur in the cuticle, for example increased sclerotization, and which, could improve water conservation. In the black larvae, of our experiment, the penetration of the insecticide might have been affected by a thicker cuticle. Additional evidence is presented by Gast (1961) who demonstrated that light yellow larvae of the Corn Earworm (Heliothis zea (Boddie)) were approximately twice as susceptibe to DDT as black larvae and that the former absorbed greater quantities of DDT through

the integument. It should be noted that the larvae used by Gaston in his tests were all collected from Corn fields and not from laboratory grouped cultures.

A number of workers show that higher lipid content, or changed lipid characteristics (saturated or unsaturated) reduce susceptibility to chlorinated hydrocarbon insecticides (Fast 1964). As mentioned earlier, higher fat content has been found in several lepidoptera, mainly Noctuidae when reared in groups as compared with isolated-reared individuals.

These aspects of mechanism of resistance require further study.

2.4.5 The effect of density during hatching and first larval instar

2.4.5.1 Introduction

The eggs of M. brassicae are laid in a mass, and after hatching the larvae remain in aggregates for some time. Such a habit might have some beneficial effect such as observed in other species with colonial habit throughout or at the beginning of their larval development (Ghent, 1960; Hitchcock, 1961; Sigura, 1961; Morimoto et al., 1962; Lyons, 1962).

To investigate such possible effects certain observations were made and are described in this part, namely synchronization of hatching, the pattern of larval growth during the first instar, and the effect of the leaf, through its toughness, on the initiation of feeding of the hatchlings.

2.4.5.2 The synchronization of larval hatching

a) Materials and methods

An experiment was carried out to make preliminary observations on the effect of density on the distribution of hatching, by taking one half of an egg mass and separating each egg to be kept singly until hatching and then comparing it with the other half which was left to hatch as a natural mass.

Two main problems were encountered (1), it was difficult to detach the eggs from the substrate without causing some damage to the chorion , (2) when the egg mass was left to hatch undisturbed, after some time the aggregation of larvae on top of the mass made counting very difficult and inaccurate. Hatching of the isolated eggs was less rapid, although this might have been partly caused by some injuries to the eggs while detaching them.

The first problem was solved by removing a larva from the egg mass as soon at it had about $\frac{3}{4}$ of its body length out of the egg; fine-tipped forceps were used for this purpose. The second problem was overcome by taking a photograph every 5 minutes and counting the larvae on enlarged prints. With these modification, an experiment was set up where an egg mass was divided approximately in two halves. One half was left to hatch undisturbed, except by the flash lightings every 5 minutes (Treatment A), and in the other, the hatching larvae were removed (Treatment B). Two replicates of each treatment were made.

The temperature during the experiment varied between 19 and 21^{o}C.

b) Results and discussion

The egg masses used in both replicates were very uniform in their

characteristics (Table 2.18).

TABLE 2.18 Characteristics of the Egg Masses used in the Experiments

	Replicate			
	1		2	
	Treatment A	Treatment B	Treatment A	Treatment B
Initial No. larvae	140	137	120	115
No. larvae hatched	138 (98.6)*	131 (95.6)	118 (98.3)	109 (94.8)
Infertile eggs	0 (0.0)	3 (2.2	1 (0.8)	4 (3.5)
Unhatched	2 (1.4)	3 (2.2)	1 (0.8)	2 (1.7)

* percentage

The cumulative frequency distributions of hatching between treatments in both replicates (Figs. 2.8 & 2.9) were significantly different (Kolmogorov-Smirnov test, two-sampled test, one-tailed test, $X^2 = 19.9$ for d.f. = 2, $P<0.01$, and $X^2 = 18.4$ for d.f. = 2, $P<0.01$ for replicates 1 and 2 respectively).

The results suggest that hatching within an egg mass is well synchronized and that disturbance, in this case by the larval removal, may slow down the process. The mechanism of such synchronization is uncertain but it might be due to the activity of larvae on top of the egg mass and also to the gnawing of the larvae while escaping from or eating the chorion. If a suitable method for detaching the eggs is found, the results could be more striking, as shown in the preliminary experiment.

Synchrony of hatching within an egg mass has been observed in Euproctis pseudoconspersa Strand (Sigiura, 1961) and Chilo suppressalis

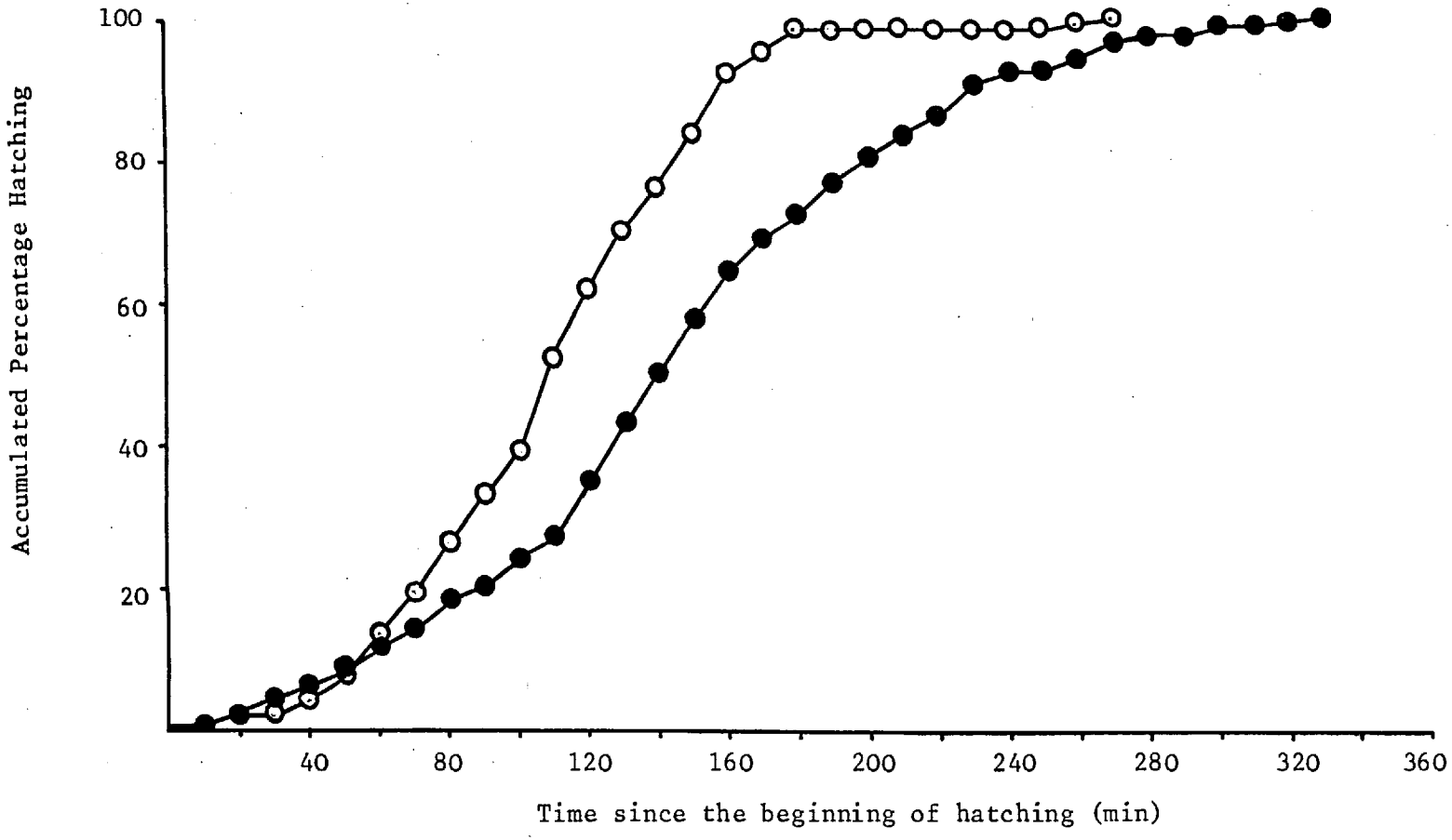


Figure 2.8. Accumulative percentage curves of hatching. Comparison between an egg mass hatched undisturbed (o-o), and one where the hatching larvae were removed (•-•).

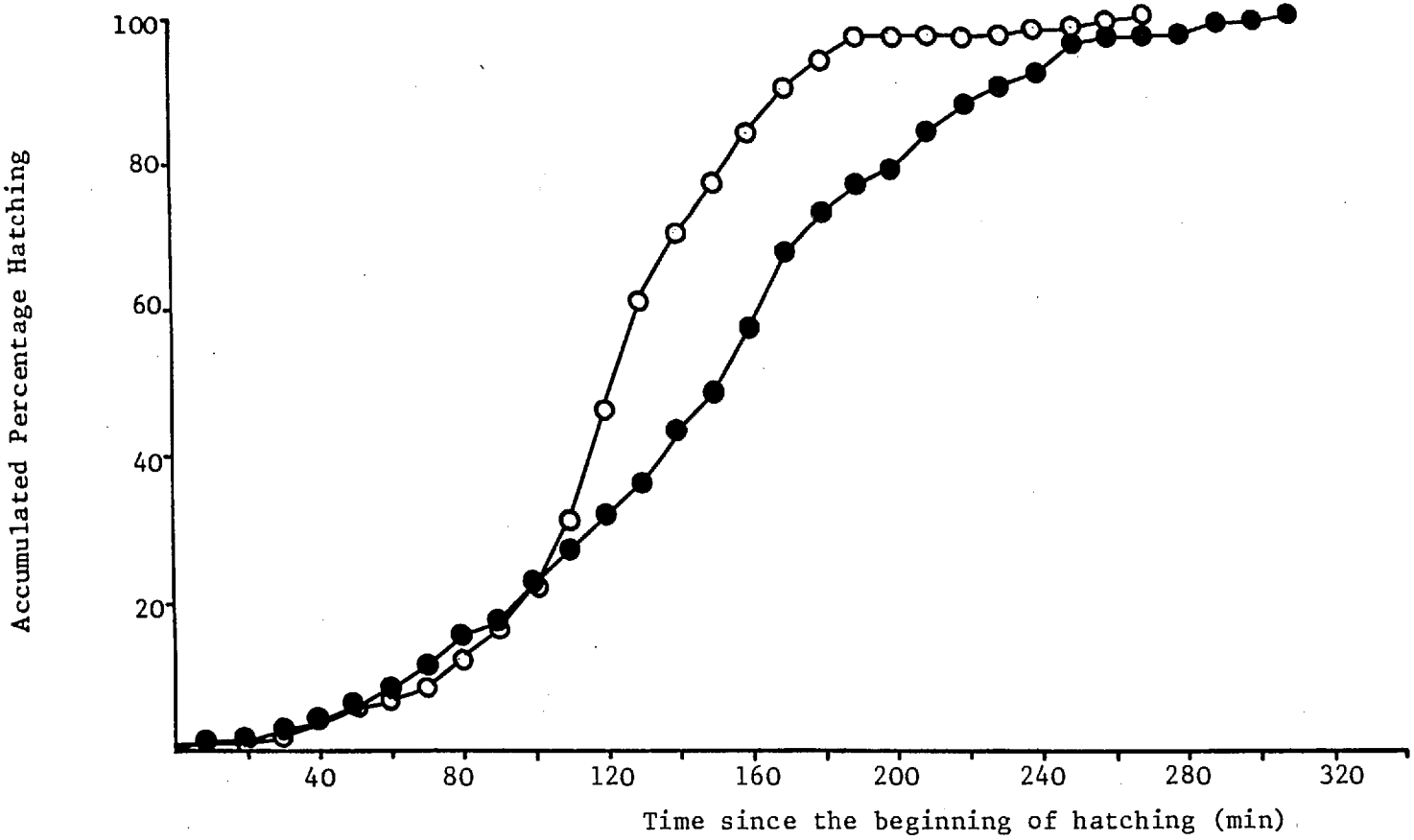


Figure 2.9. Accumulative percentage curves of hatching. Comparison between an egg mass hatched undisturbed (o-o), and one where the hatching larvae were removed (•-•).

Walker (Morimoto et al., 1962) and in both cases it was important to the formation of the larval aggregation and to survival.

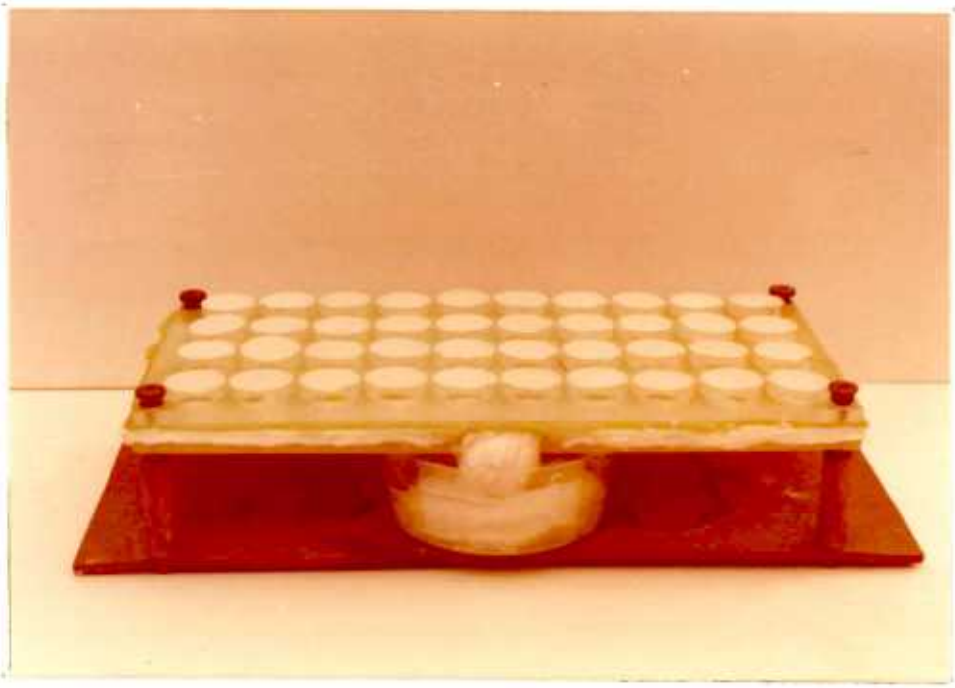
2.4.5.3 The pattern of larval growth during the first instar

a) Materials and methods

Larvae hatched within one hour were confined singly or in groups of 16, 32 or 40. The confining cage were part of an apparatus comprising 40 cage units (Fig. 2.10A & 2.10B) similar to that used by Murdie (1965). It has four rows of ten circles, 220 mm diameter, cut out of a 305 x 152 x 6 mm perspex sheet. A 16 mm flange milled out of the wall of each circle to a depth of 3.2 mm provided a shelf upon which a 10.2 mm high, 22.2 mm internal diameter, perspex ring rests. Each ring was closed at the upper end with muslin. A sheet of perspex placed below the perforated sheet provides a floor for the cages; the two sheets are bolted together at each corner. Although a moistened filter paper placed between the sheets was sufficient to keep broad beans leaf discs fresh for at least 72 hours (Murdie, 1965), this proved unsatisfactory for cabbage leaf discs, furthermore, the hatchlings tended to feed at the edges giving a misleading result. A layer of cotton wool was laid on the base perspex sheet, on top of which a 4 mm foam rubber sheet with holes made to match those of the perforated sheet was placed. The leaf discs, 27 mm diameter, were placed between the cotton layer and the rubber sheet, with their underside (adaxial) surfaces uppermost facing the holes. A cotton wool wick dipped into a water reservoir supplied moisture.

The larvae were handled with a fine camel hair brush and their weight was taken just after entering the first moult.

A.



B.

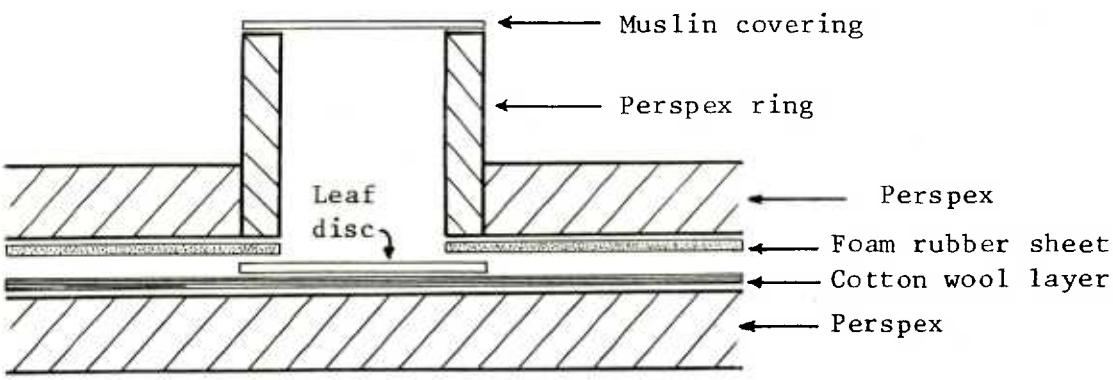


Figure 2.10. A. Apparatus used to cage *M. brassicae* hatchlings on individual leaf disc. (After Murdie, 1965).

B. Cross-section of single leaf disc cage (modified after Murdie, 1965).

The experiment was conducted at 25°C, with 16 : 8 hours light : dark cycle. Leaf discs were cut from frech leaves of the cabbage variety June star. From the second day these were changed daily.

b) Results and discussion

The larval weight during the first instar is affected by the rearing density (Table 2.19).

TABLE 2.19 The Weight of M. brassicae First Instar Larvae Reared at Various Densities

Density	Number of replicates	Number weighed	Larval weight (mgs)
1	16	13	0.5178 ± 0.0240*
16	3	24	0.5730 ± 0.0120
32	3	24	0.4953 ± 0.0206
40	2	32	0.4282 ± 0.0084

* Mean ± Standard error

Individuals kept at a density of 16 were significantly heavier than those kept isolated or in densities of 32 or 40 larvae per cage ($P<0.05$, $P<0.01$, $P<0.01$ respectively).

The results suggest that the first instar larvae of M. brassicae may perform better when in groups with an optimum density about 16 larvae per cage.

The mortality observed during this experiment is considered later (Page 104).

2.4.5.4 Influence of leaf toughness on the initiation of feeding by newly-hatched larvae

a) Materials and methods

The experiments used the leaf disc cage apparatus as in the previous experiment with the addition that leaves of two different toughness were presented to densities of 1 or 16 larvae per cage.

Two methods were used to measure toughness of the leaves:

(1) General appearance of the leaf

(2) Penetrometer

(1) General appearance of the leaf

This criterion of toughness is a subjective one; the leaves were considered tough when they were thick and hard as found in mature plants, in our case they were given some water stress; their colour was dark blueish green and were covered with a wax layer. Leaves were considered tender when they were soft and turgescent, green in colour, and normally found on young and middle aged plants which had been well watered; the wax layer not as conspicuous as in the mature leaves.

(2) Penetrometer

Measurement of toughness were made with a penetrometer modified from the type described by Williams (1954).

A leaf disc was placed between two blocks of perspex (130 x 60 x 8 mm

each) (Fig. 2.11), which were located together by means of three pins. Two common binder clips kept the blocks fastened together. The upper block had a hole through which an 18.5 mm diameter and 12.0 mm length perspex cylinder is housed. Through a small hole in the cylinder was placed a steel needle to the upper end of which a lightweight box made of celulose-acetate (sand reservoir) was attached. The sand reservoir was gradually filled with sand at a constant rate from a funnel connected to a rubber tube until the needle pierced the leaf and a reading of the amount of sand required was made. The sand was poured very near to the bottom and to the centre of the reservoir to prevent it from spinning, which would have led to an underestimated leaf toughness. The lower block had a 7 mm hole which allowed observation of the needle as soon as it penetrated the leaf disc, and was illuminated by light reflected from a mirror placed underneath the blocks. To facilitate observation a hole was bored in the front part of the upper block. The needle was rounded with an aloxite hone to avoid piercing when positioning the reservoir.

The advantages of this version over Williams' model are: (1) because the disc is held taut between the blocks, and also that the hole in the lower block is small, there is less chance of the leaf sagging giving an inaccurate reading, (2) there is less probability of damaging a disc when several consecutive readings are made of one leaf disc, (3) the use of a needle honed to give a circular point, avoids premature piercing, and (4) when a sharp needle is used, the observation tunnel facilitates positioning of the needle on the leaf.

Three test readings were made, and the average figure taken on each of ten discs for both tender and mature leaves. The average relative toughness for each type was taken from the ten averaged disc readings. The discs were

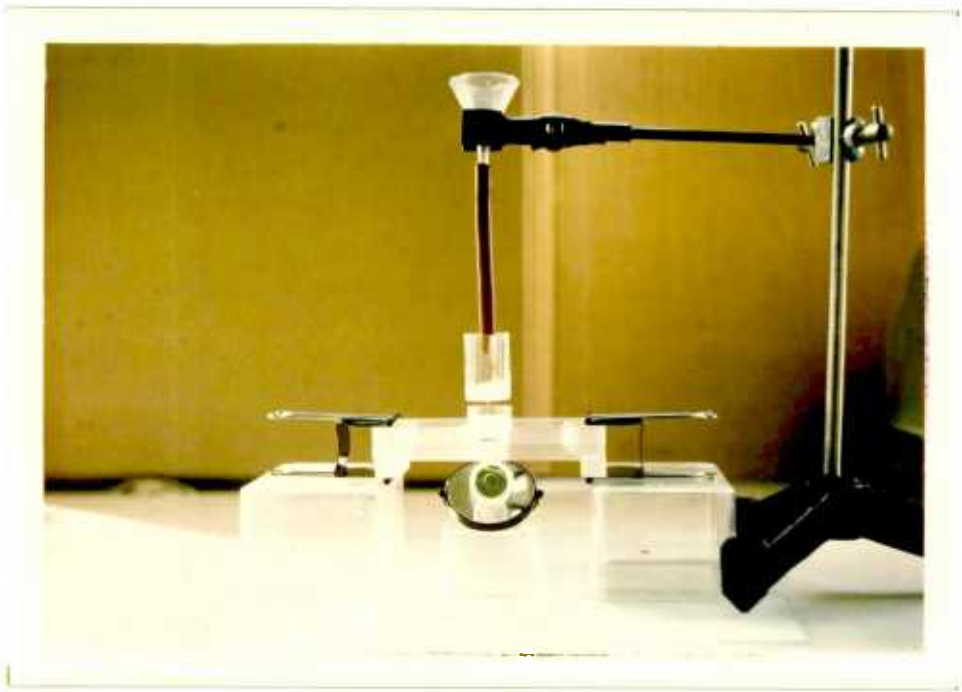


Figure 2.11. Penetrometer.

randomly selected from each of the two types of leaves that were to be used in the experiment. It was not feasible to assess the toughness of the same disc on which the insect were caged.

The design in the first method consisted of two sets of 16 isolated and 4 groups of 16 larvae and was replicated three times. The third replicate included a variation in which the wax layer of tough disc leaves was rubbed off, thus allowing some observation of its effect on the initiation of feeding. The first observation was made 8 hours after the start of the experiment and then subsequently every 4 hours, for a total period of 24 hours. An additional observation was taken at 33 hours. In the second method, the design consisted of 32 isolated and 4 groups of 16 larvae presented to the two different leaf toughnesses; this was replicated twice. The first observation was taken six hours after the experiment was set up and subsequently every three hours.

Fed larvae were readily distinguished because of their change in colour from reddish brown to green, due to food plant pigments.

b) Result and discussion

Penetrometer reading of tender and tough leaves as judged by the general appearance method showed substantial differences (Table 2.20).

Leaf toughness affected the time necessary for the initiation of feeding in newly hatched larvae of M. brassicae (Figs. 2.12, 2.13, 2.14, 2.15 and 2.16) but was modified by the influence of larval density. Thus in grouped larvae, for both tender and tough leaves, about 90% of the hatchlings had settled down and fed when the first observation was taken, seemingly not affected by the leaf toughness. In contrast, isolated individuals on

TABLE 2.20 Penetrometer Readings from Tender and Tough Leaves of Cabbage Plant, Variety June Star

Leaves general appearance	Penetrometer readings in grs. of sand		
	replicate 1		replicate 2
Young (tender)	8.09 ± 0.23*		9.62 ± 0.23
Mature (tough)	19.44 ± 0.59		20.73 ± 1.24

* Mean ± Standard error

tough leaves took longer to begin feeding. The isolated larvae on tender leaves were less affected and when the first observation was made between 53 and 81% of the larvae had already fed.

The third replicate of the first method showed that the wax layer on tough leaves seems to have no effect on the feeding ability of the young larvae (Fig. 2.14).

It may be said that leaf toughness interferes with the initiation of feeding of M. brassicae hatchlings and that it is largely modified by larval density. Solitary individuals have greater difficulty to begin feeding on tough leaves than on tender ones. The high percentage of fed larvae observed in the grouped larvae may be attributable to the tendency of the hatchlings to join and enlarge feeding sites started by another larva. Although solitary individuals are able to grow under either conditions of toughness, aggregative feeding would seem to be advantageous for the hatchlings.

2.4.5.5 Larval mortality

A summary of the mortality recorded from the two previous experiments is given in Tables 2.21 and 2.22.

TABLE 2.21 Larval Mortality Observed in the Experiment Shown in Table 2.19

Density	Number of larvae	Number dying	%
1	16	3	18.8
16	48	1	2.1
32	96	9	9.4
48	96	38	39.6

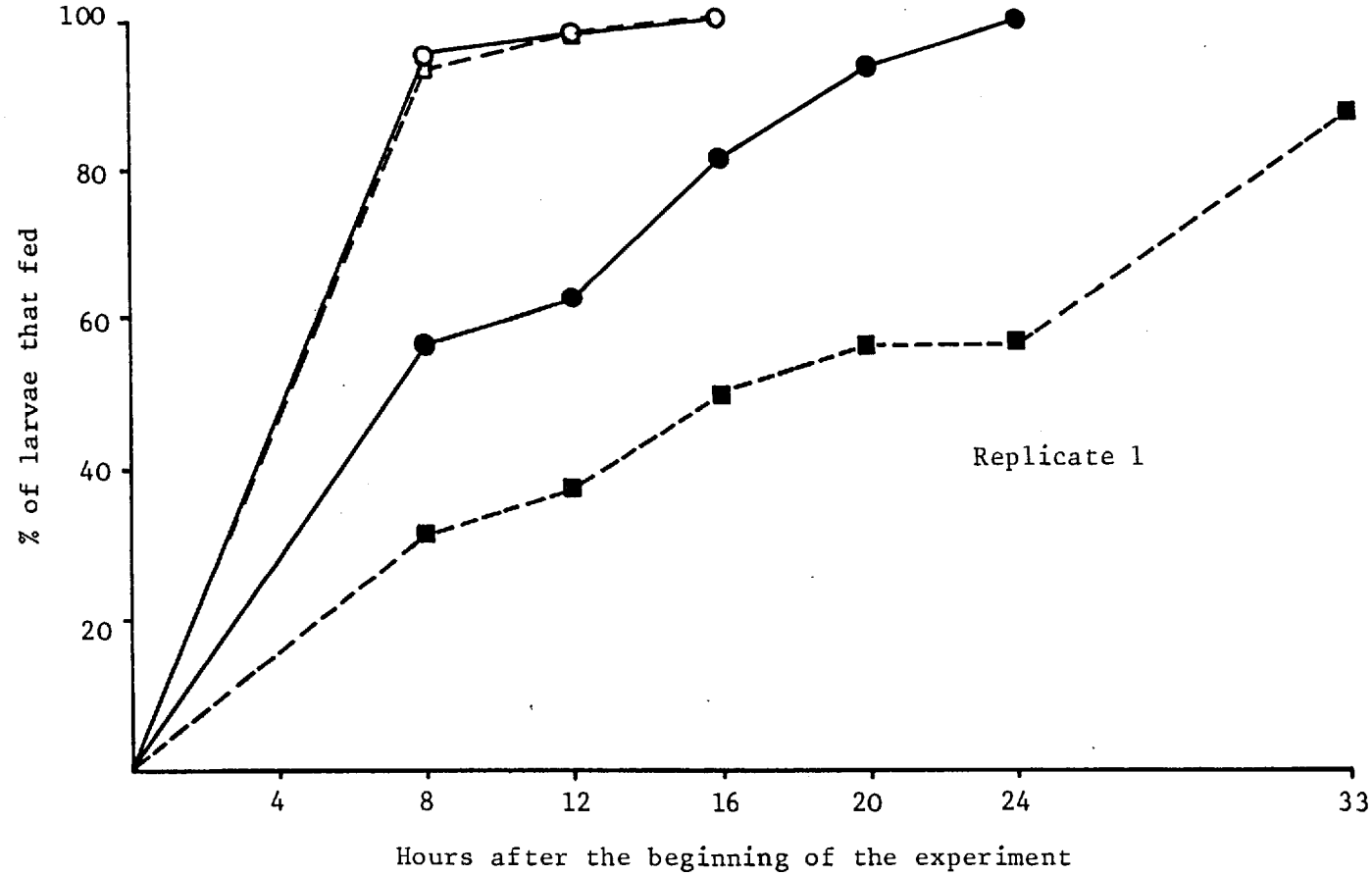


Figure 2.12. The influence of leaf toughness on the initiation of feeding of *M. brassicae* hatchlings (●-● : isolated larvae on tender leaves; 0-0 : grouped larvae on tender leaves; ■---■ : isolated larvae on tough leaves; □---□ : grouped larvae on tough leaves.

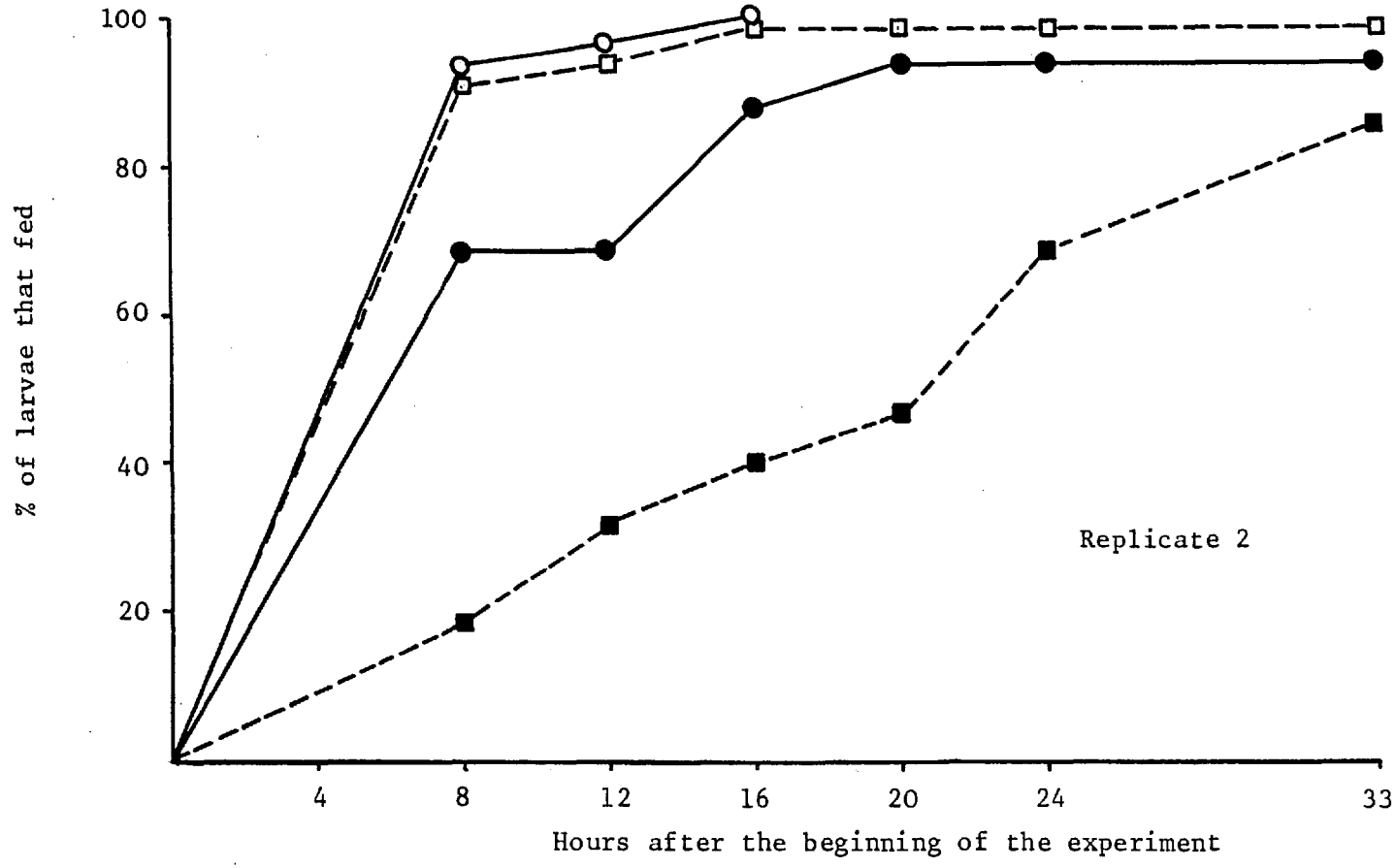
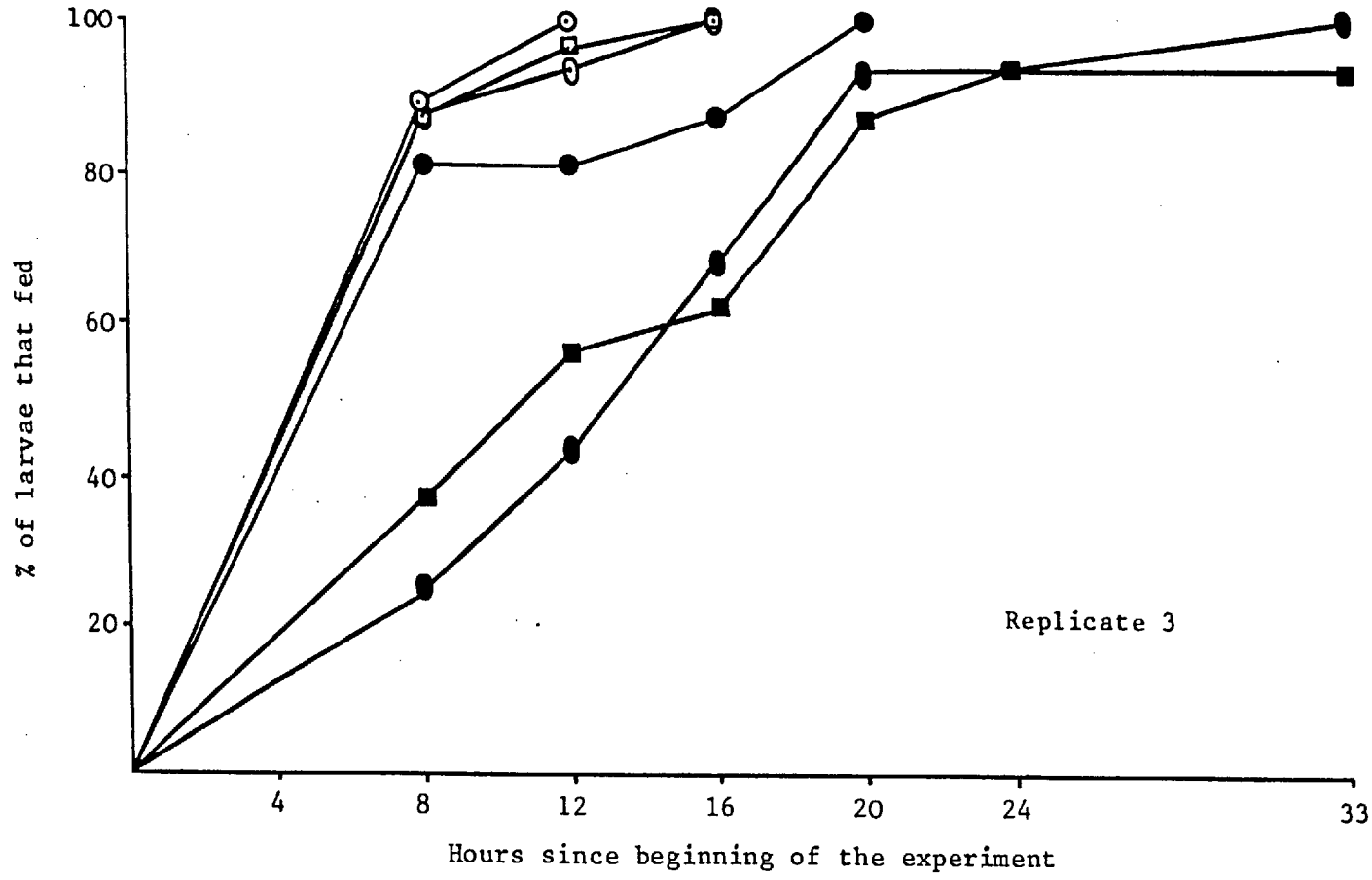


Figure 2.13. The influence of leaf toughness on the initiation of feeding of *M. brassicae* hatchlings (●-● : isolated larvae on tender leaves; O-O : grouped larvae on tender leaves; ■---■ : isolated larvae on tough leaves; □---□ : grouped larvae on tough leaves).

Figure 2.14. The influence of leaf toughness on the initiation of feeding of *M. brassicae* hatchlings, ●-● : isolated larvae on tender leaves; ○-○ : grouped larvae on tender leaves; ■-■ : isolated larvae on tough leaves; □-□ : grouped larvae on tough leaves; ◐-◐ : isolated larvae on tough leaves without wax layer; ◯-◯ : grouped larvae on tough leaves without wax layer.


100
80
60
40
20
% of larvae that fed
Replicate 3
4
8
12
16
20
24
33
Hours since beginning of the experiment

Figures 2.15 (Replicate 1) and 2.16 (Replicate 2). The influence of leaf toughness on the initiation of feeding of *M. brassicae* hatchlings (●-● : isolated larvae on tender leaves ; O-O : grouped larvae on tender leaves; ■---■ : isolated larvae on tough leaves; □---□ : grouped larvae on tough leaves).

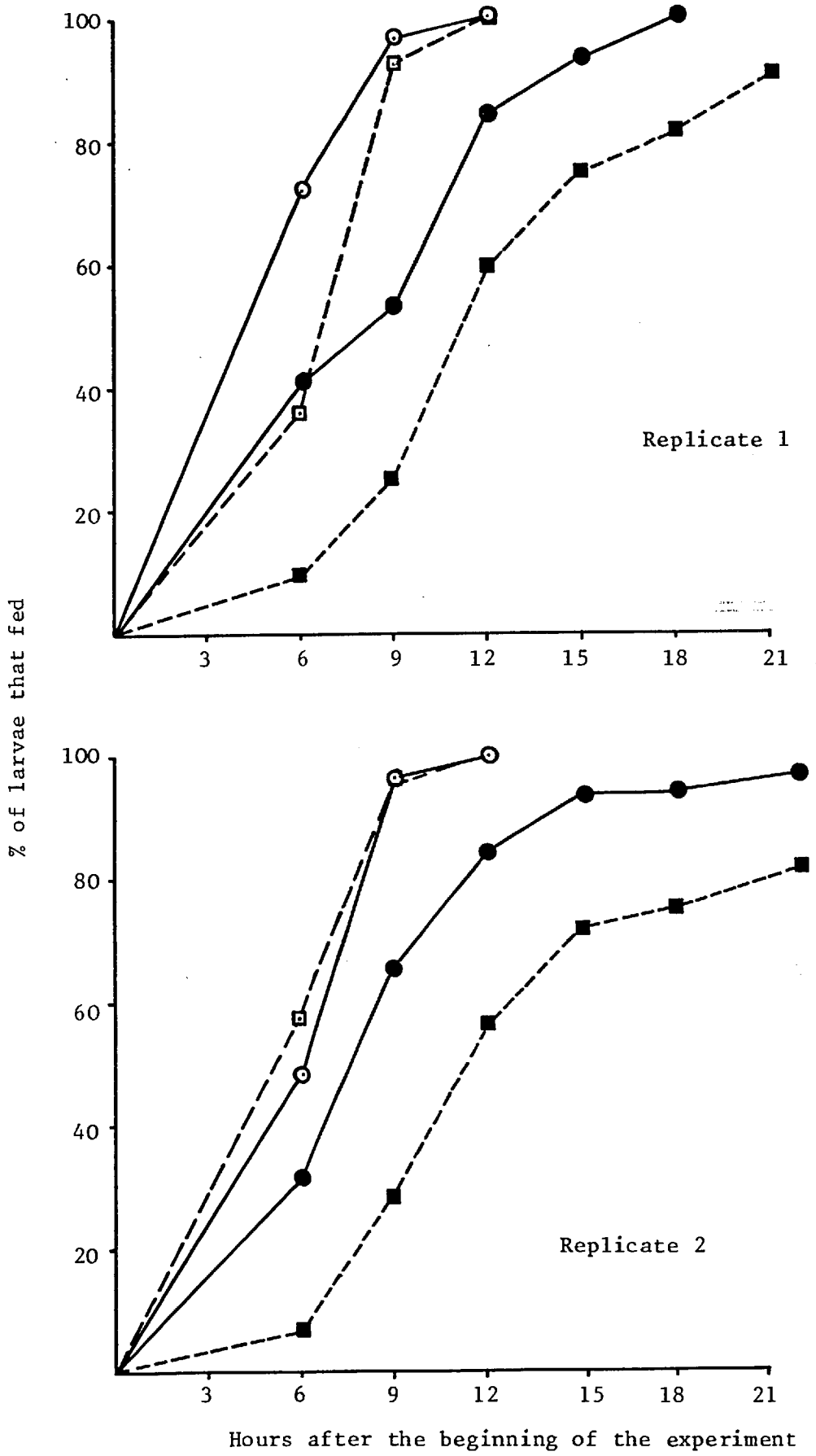

100
80
60
40
20
% of larvae that fed
3
6
9
12
15
18
21
Replicate 1
Replicate 2
Hours after the beginning of the experiment

TABLE 2.22 Larval Mortality Observed in the Experiments Shown in Figs. 2.12, 2.13, 2.14, 2.15 and 2.16

	Replicate	Rearing condition			
		Isolated		Grouped	
		tender	tough	tender	tough
Experiment Fig. 2.12	1	0 (0.0)	2 (12.5)	0 (0.0)	0 (0.0)
Experiment Fig. 2.13	2	1 (6.3)	2 (12.5)	0 (0.0)	1 (1.6)
Experiment Fig. 2.14	3	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
	3a*	-	1 (6.3)	-	0 (0.0)
Experiment Fig. 2.15	1	0 (0.0)	3 (9.4)	0 (0.0)	0 (0.0)
Experiment Fig. 2.16	2	1 (3.1)	6 (18.8)	0 (0.0)	0 (0.0)

* Corresponds to the tough leaves where the wax layer was rubbed off

Mortality tended to be higher for solitary individuals than for grouped larvae, especially where individuals were isolated on tougher leaves. Observations showed that the mortality occurred mainly among those larvae that failed to settle down to feed, or that after starting feeding seemed to have been unable to cope with the continued resistance offered by the tough leaves.

With overcrowding, however, mortality rose again, (Table 2.21).

2.5 Section General Discussion

It has been pointed out that the grouping of individuals, even in small numbers may have important influences upon the biology of the species concerned (Grasse, 1946; Chauvin, 1952). Studies of these influences are necessary

to the understanding of animal population dynamics, and often with added important when the species are pests.

The manifestations of the effects of density in a particular species is related with its mode of life. In lepidopterous insects that lay single eggs, grouped individuals, which otherwise would develop with very little influence on each other, might show strong responses such as increased mortality, retarded development, decreased weight, as found in Parnara guttata Bremer et Grey and Maliatta signifera Walker (Iwao, 1962). At the other extreme, as in the tea-tussock moth, Euproctis pseudocompersa Strand which is typically colonial, when the larvae are kept singly or in pairs, most of them wander and die without feeding. The larval duration and the number of ecdysis are increased by isolation of young larvae (Mizuta, 1960). In those lepidoptera that lay egg masses, the degree of aggregation of ensuing larvae hatched from an egg mass varies according to species. Some live in compact groups throughout larval life dispersing shorly before pupation (as seen in E. pseudocompersa), while the hatchlings of some species disperse as soon as they hatch, as in Epiphyas postvittana (Walker) (Danthanarayana, 1975b) where a low density crowd (2-4 larvae per container) can markedly reduce pupal weight as well as fecundity. An extreme case is Adoxophyes orana F.R (Ankersmit et al., 1971), where after dispersing a solitary habit of life is adopted. If crowding does occur, one larva can be seen to guard the food and chase off all intruders.

Between these extremes, there are many species of intermediate type in which the aggregative habit persists until some stage and diminishes gradually as development proceeds. For example larvae of the rice stem borer, Chilo suppressalis Walker aggregate up to 3rd instar and then disperse. Group rearing of the larvae after dispersing can cause high mortality, protracted

development and reduced size of ensuring pupae (Morimoto, 1960b).

Mamestra brassicae may be included in the intermediate category, although this species responds to crowded conditions by a functional polymorphism (phase variation) not observed for example in C. suppressalis.

The hatchlings of M. brassicae remain aggregated during the first days after hatching and although the aggregation becomes loose with time it can be maintained in general up to the 2nd instar. However, this varies with the conditions; for example an undisturbed aggregate on a large leaf might not disperse until the leaf is well damaged.

With Mamestra, the beneficial effect of the aggregation can be observed during the first instar period, hatching is very well synchronized within an egg mass which might provide the opportunity for aggregation. Although young larvae are capable of growing in conditions of isolation, they perform better when in groups. Mortality is less and, consistent with Hirata's (1963a) results, were heavier at the first moult. However, overcrowding during the first instar is harmful significantly decreasing larval weight and increasing mortality.

The density dependent changes observed in M. brassicae followed, in general, the same pattern as other species showing "phase variation". Together with darkening, there was an increase in the rate of development, which was apparent from the 4th moult onwards. The weight of pupae decreased significantly at high density, whereas sex ratio, the rate of diapause and length of the pupal period were not influenced. Analysis of the pattern of larval growth showed that crowding promoted growth during early stages but led to a reduction of weight during later instars.

Larvae from crowded cultures were more active and reacted readily to external disturbance when they dropped to the ground. Dark coloured individuals of M. brassicae showed a stronger resistance to starvation and desiccation, which might be of survival value after exhaustion of suitable food plants and during mass larval migrations. Furthermore, larvae reared in crowded conditions can tolerate and survive on a wider range of plant species (Hirata, 1963b). There is also evidence that crowded larvae can tolerate some artificial stresses, for example D.D.T., better than their pale counterparts from sparse populations.

Some characters found in adults yielded from crowded cultures seem to be more adapted for dispersal than those reared from solitary culture as found in Plusia gamma and Pieris brassicae L. (Long, 1959), Leucania separata (Iwao, 1962), which are also known as migratory species (Johnson, 1969; Iwao, 1962).

In Mamestra, results are contradictory, since although Hirata (1956) observed that larval crowding enhances flying activity and produces smaller wing loading accompanied by higher fecundity, Burov et al., (1970) reported a higher wing loading, and Bonnemaison (1962b) obtained a decrease in fecundity. The significance of those findings is not clear, because this species matures on emergence, has a short preoviposition period and the females can lay eggs without feeding. Furthermore, the inherited photoperiodic adaptations of the local populations limit the possibilities of movements within the species' range, this is so remarkably observed in M. brassicae, that northerly and southerly populations behave as if they were distinct species (Masaki, 1956). No evidence of migration has been found in the literature.

Iwao (1968) has regarded the phase variation in Lepidoptera as a

switch-over mechanism between two modes of larval life. One is well suited for sparsely populated conditions and the other is adapted to epidemic conditions. From the above-mentioned considerations, the density-induce changes observed in M. brassicae seems to be explained by the mechanism suggested by Iwao, above.

Summing up, the habit of egg laying of M. brassicae seems to be beneficial during hatching and first instar, thereafter the larvae disperse on the plant. The reaction of the larvae to subsequent environmental conditions will probably depend on the population density. If it is high, then dark coloured individuals may develop while, in sparse population, the pale forms develop. It is of interest to note that in M. brassicae, the possibility of encountering another individual is high even when population density is low since on a host plant like cabbage or brussels sprout the larvae tend to move to the upper part of the plant, especially the head. In laboratory conditions, interactions are evident even at low densities (4 larvae per container) when the rate of development increased, while mortality and pupal weights were not changed significantly.

SECTION 3

FIELD STUDIES ON THE MORTALITY OF EGG AND LARVAL STAGES AND DISPERSAL OF FULLY-GROWN LARVAE

3.1 Introduction

As already stated previously, the cabbage moth, Mamestra brassicae L, is mainly found on Brassicas, and that its pest status varies from one place to another. It is considered a major pest in eastern Europe (Ionescu, 1966; Camprag, 1970 and Dochkova, 1969) while, for instance in Britain it is regarded as a secondary pest.

Although it is known from the literature that predators, parasites, diseases, and other factors can kill many eggs, larvae and pupae, there is little information on the differential effect of various mortality factors on population trends in the field. Recently some information on these aspects provided by Japanese work has become available (Oku et al., 1973b; Oku et al, 1974a, b, c, d, e).

A series of experiments was done in order to determine the mortality factors acting on the egg and larvae stages of M. brassicae in a brussels sprouts experimental plot. For the larval stage, some of the factors e.g., ground predators were excluded by means of various devices and the trends of the populations observed. The dispersal of fully-grown larvae once they leave the host was also investigated.

3.2 Studies on Egg Mortality

3.2.1 Materials and methods

Mated females were taken to the field plot during the afternoon and caged on brussels sprouts leaves in a terylene sleeve (Fig. 3.1). The next morning they were examined and if an egg mass was found, the female and the sleeve were removed leaving the egg mass exposed. The eggs were counted with a magnifying glass. The egg masses were subsequently re-examined. When about to hatch the egg masses were taken to the laboratory for recounting and observation for possible parasites. Sterile eggs, masses or abnormal ones i.e., eggs disorderly laid etc., were removed from the plant.

A total of five infestations were made; one in 1975 and four in 1976.

Feeding tests with possible predators were carried out by confining both the predator and the eggs in a petri dish, 9 cm diameter and checking after 24 hours for predation.

3.2.2 Results and discussion

3.2.2.1 Characteristics of the egg mass infestations

There were some differences in the egg mass size (number eggs/egg mass), total number of eggs and number of egg masses (Table 3.1). The number of egg masses during the last two infestations was increased in order to obtain information about the egg mass losses in relation to their position on the leaf.

Figure 3.1. Positioned terylene sleeve used to cage *Mamestra brassicae* females.

TABLE 3.1 Characteristics of the Egg Mass Infestations Carried out During 1975 and 1976

Year	Infestation Number	Date	Number of egg masses	Total No. eggs	Mean number eggs per mass
1975		3/VII	15	2085	139.5 ± 10.9*
1976	1	22-23/VI	20	1881	94.1 ± 10.1
	2	7-8/VII	32	3129	97.8 ± 10.6
	3	22-23/VII	46	3151	68.5 ± 5.9
	4	6-7/VIII	40	3469	86.7 ± 8.5

* Mean ± Standard error

3.2.2.2 Frequency of egg mass losses in relation to egg mass size

The assumption that bigger egg masses would be more likely to suffer losses when compared with small ones, was tested by classifying the egg masses within each infestation into three size categories according to the number of eggs per mass (Table 3.2).

TABLE 3.2 Frequency of Egg Mass Losses in Relation to Egg Mass Size

Egg mass size	Number of egg masses with losses	Total
0 - 50	27	41
51 - 100	35	55
>101	30	42
TOTAL	93	138

The infestation carried out in 1975 was left out as it was composed almost exclusively of large egg masses (>101 egg per mass). Both total and partly attacked egg masses were included as losses.

A chi-square test did not show significance ($x^2 = 1.7$ with 2 d.f., $0.50 < P < 0.10$), and thus we can conclude that the proportion of egg masses subject to losses is unaffected by size of the mass.

3.2.2.3 The effect of date of infestation on rate of loss in egg masses

The percentage of egg masses presenting either partial or total losses during 1976 did not show a consistent trend through the period of infestation (Fig. 3.3).

TABLE 3.3 Frequency of Egg Mass Losses Through the Infestation Carried Out in 1976

Infestation Number	No. egg masses with losses	Total observed	% losses
1	12	20	60.0
2	22	32	68.8
3	30	46	65.2
4	30	40	75.0
TOTAL	93	138	

3.2.2.4 The frequency of egg mass losses in relation to their position on the leaf

It was noticed that in the first and second infestation many of the

egg masses with total or partial losses were located near the edges of the leaves. To confirm this the leaves used during the 3rd and 4th infestation were brought to the laboratory and the relative position of the egg masses recorded and measured (see page 15) (Fig. 3.2).

It can be seen that there is a tendency to bimodality which as stated before (p. 15) was probably due to the fact that the females also use the midrib area for oviposition, particularly the distal third of the leaf. However the histograms differ from that in Fig. 1.6 in the fact that the highest frequency of egg masses in both infestations was located in the range 0.0 - 1.0 cm, while in the natural population it was observed in the 1.1 - 2.0 cm range. It is possible that the sleeve used for confining the females modified their oviposition behaviour.

The largest proportion of egg masses with losses was in the first two centimetres from the edges of the leaves decreasing towards the midrib area (Table 3.4). When the percentage of losses within each range is computed, there seems to be also a tendency for higher losses near the edges (Table 3.4), this is more clearly shown when the group size is increased to two centimetres (Table 3.5).

3.2.2.5 Egg mortality factors

Mamestra brassicae eggs suffered mortality from various sources. Some mortality causes were more easy to recognise than others. Parasitized eggs were uniform black while in healthyones, when about to hatch, although black, the larvae could be seen through the corium. Sucked eggs appeared as shrivelled eggs usually at the edges of an otherwise normal egg mass. Coccinellids were either seen on the eggs or were detected by the excrements

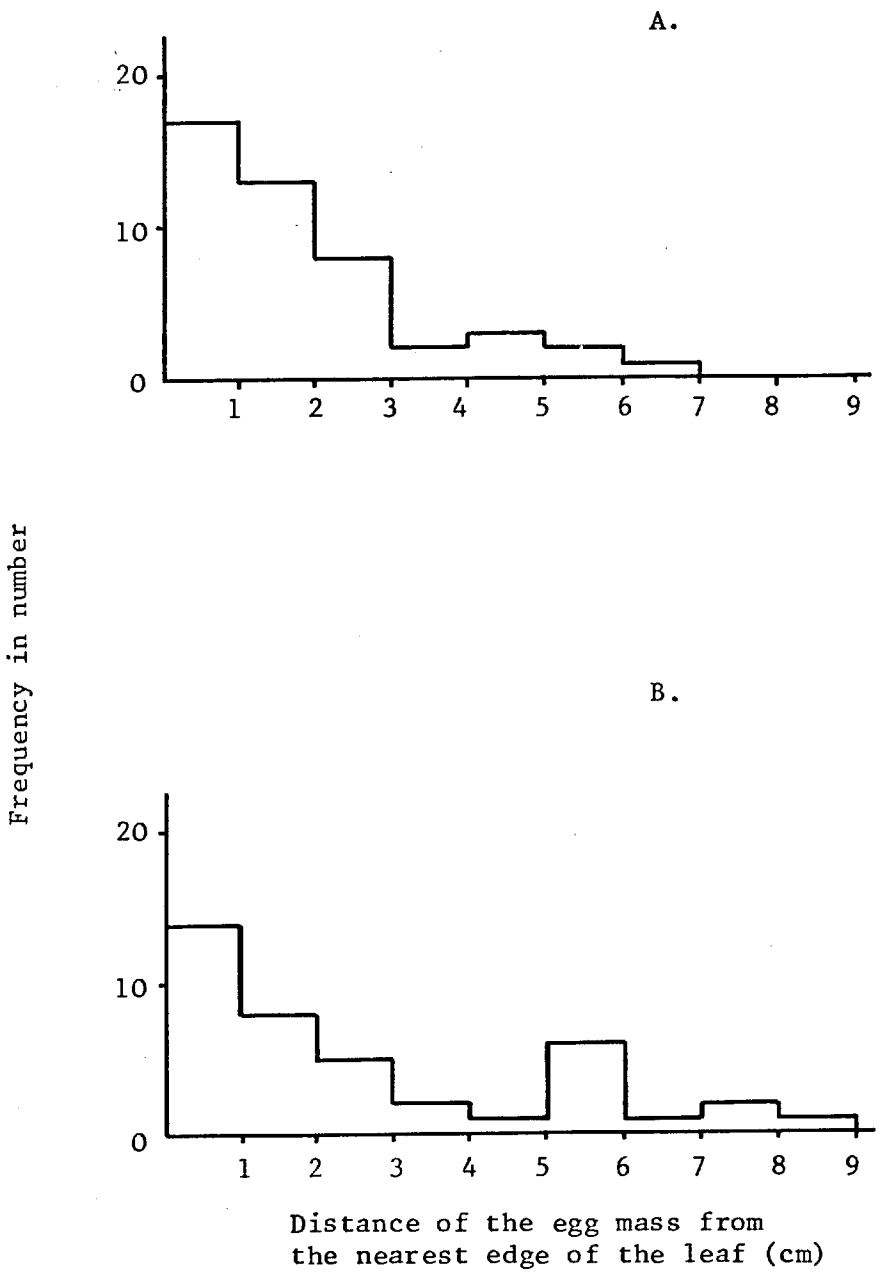


Figure 3.2. The distribution of the egg masses over the leaf surface.

A. third infestation

B. fourth infestation

TABLE 3.4 The Frequency of egg Mass Losses in Relation to their Distribution over the Leaf Surface

Infestation number	Distance from the edge (range in cm)	No. egg masses with:		Total	% egg mass losses within the range	% losses from the total
		no losses	losses			
3	0 - 1	6	11	17	64.7	23.9
	1.1 - 2	3	10	13	76.9	21.7
	2.1 - 3	3	5	8	62.5	10.9
	3.1 - 4	1	1	2	50.0	2.2
	4.1 - 5	1	2	3	66.7	4.3
	5.1 - 6	1	1	2	50.0	2.2
	6.1 - 7	1	0	1	0.0	0.0
	TOTAL	16	30	46	-	65.2
4	0 - 1	2	11	13	84.6	27.5
	1.1 - 2	1	8	9	88.9	20.0
	2.1 - 3	1	4	5	80.0	10.0
	3.1 - 4	0	2	2	100.0	5.0
	4.1 - 5	1	0	1	0.0	0.0
	5.1 - 6	2	4	6	66.7	10.0
	6.1 - 7	1	0	1	0.0	0.0
	7.1 - 8	1	1	2	50.0	2.5
	8.1 - 9	1	0	1	0.0	0.0
	TOTAL	10	30	40	-	75.0

TABLE 3.5 Percentage of Egg Mass Losses Within each Range when the Range is Increased to 2 cms

Infestation	Range	No. egg masses with:		% losses within the range
		no losses	losses	
3	0 - 2.0	9	21	72.4
	2.1 - 4.0	4	6	60.0
	4.1 - 6.0	2	3	60.0
	>6.1	1	0	0.0
4	0 - 2.0	3	19	86.4
	2.1 - 4.0	1	6	85.7
	4.1 - 6.0	3	4	57.1
	6.1 - 8.0	2	1	50.0
	>8.1	1	0	0.0

left by them on the place where the preyed egg mass was attached to the leaf. Thrips were seen rasping on eggs which later collapsed, usually one to three in an egg mass. Dislodgement was attributed as the cause in those egg masses that showed loss of contact with the leaf in one or two places and that were later lost. Under the term "disappearance" were included all those eggs lost to uncertain reasons; here we included some eggs that might have been eaten by coccinellids, but on which no visible signal of their activities was observed. Also some masses probably dislodged but of which we were not sure of, and certainly unknown predators. The number of sterile eggs varied among the masses and were not computed as it was a variable introduced by the laboratory reared females.

The observed mortality factors during the egg stage were tabulated in the form of a life table (Table 3.6).

a) Parasitism

The egg parasites collected during the present study were Trichogamma sp and Telenomus sp.

The number of egg parasitized by Trichogramma was low in the 1975 season only reaching 1.4%. During the 1976 season the percentage rose from 2.0 to 6.8% (Table 3.6) and the percentage of attacked masses also increased with time (Table 3.7).

The total amount of eggs parasitized by Trichogramma might have been higher because adults of the parasite were observed on top of some egg masses which were later lost to coccinellids, disappearance and other reasons. To balance this one adult parasite was observed on one egg mass which later hatched normally and produced no parasites.

In the 3rd and 4th infestations the egg masses most parasitized by Trichogramma were located on the edges of the leaves (Table 3.8).

The genus Trichogramma is often of considerable value in the control of M. brassicae and other Lepidoptera. In many cases, high percentage of field parasitism (some times up to 100%) have been recorded for Mamestra (Oku et al., 1973b; Petrukha, et al., 1967; Luchnic, 1926; Voelkel, 1925). It is frequently cited that Trichogramma occurs relatively late in the season being then more important during the second generation of M. brassicae (Adashkevich, 1975; Oku et al., 1973b; Nikolova, 1945). Our data suggests

TABLE 3.6 Egg Mortality Factors Acting on *Mamestra brassicae* on Brussels Sprouts Plants at Silwood Park during 1975 and 1976

Year	Infest. No.	Lx	dxF	dx	100qx
1975		2085	Dislodgement	379	18.2
			Disappearance	160	7.7
			Trichogramma	29	1.4
			Telenomus	38	1.8
			Sucking insects	37	1.8
			TOTAL	643	30.9
1976	1	1881	Dislodgement	277	14.7
			Disappearance	244	13.0
			Trichogramma	37	2.0
			Coccinellids	121	6.4
			Sucking insects	49	2.6
			TOTAL	728	38.7
	2	3129	Dislodgement	390	12.5
			Disappearance	348	11.1
			Trichogramma	143	4.6
			Telenomus	16	0.5
			Coccinellids	771	24.6
			Sucking insects	46	1.5
			Thrips	3	0.1
			Larval feeding	17	0.5
			TOTAL	1718	54.9
	3	3151	Dislodgement	146	4.6
			Disappearance	659	20.9
			Trichogramma	174	5.5
			Coccinellids	597	18.9
			Sucking insects	7	0.2
			Thrips	2	0.1
			Accidental dislodgement	12	0.4
			TOTAL	1597	50.6
	4	3469	Dislodgement	140	4.0
			Disappearance	862	24.8
			Trichogramma	237	6.8
			Coccinellids	503	14.5
			Sucking insects	54	1.6
			Thrips	5	0.1
			TOTAL	1801	51.8

TABLE 3.7 Changes in the Percentage of Egg Masses Parasitized by *Trichogramma*

Year	Infestation number	No. egg masses parasitized	Total egg masses	% egg masses parasitized
1975	-	2	15	13.3
1976	1	1	20	5.0
	2	4	32	12.5
	3	10	46	21.7
	4	10	40	25.0

that parasitism by *Trichogramma* increased as the season progressed, especially in 1976.

The other egg parasite, *Telenomus* parasitized only 3 egg masses during the two years; 2 in 1975 and one in 1976. This genus has also been found to attack *Mamestra* on the continent (Karadzhov, 1970; Birova, 1973) and in Japan (Oku *et al.*, 1973b). In Japan it seems to attack early in the season in contrast with *Trichogramma*.

b) Predation

In the field the predators of egg masses were coccinellids, heteropterous bugs and thrips.

Coccinellids, particularly *Coccinella 7-punctata* L., were very important egg predators during 1976 in contrast with 1975 when no predation by coccinellids was detected (Table 3.6). This heavy predation in 1976 coincided with the outbreak of coccinellids, which reached very high numbers during

TABLE 3.8 Analysis of the Frequency of Egg Mass Losses in Relation to Their Position over the Leaf Surface in Infestations Nos. 3 and 4 (Pooled Data)

Distance from the leaf edge (cm)	No. of egg mass with losses attributed to:					Total* egg mass losses	Total egg masses
	dislodgement	disappearance	Trichogramma	Coccinellids	sucking insects		
0 - 1	0	8	7	9	2	26	31
1.1 - 2	5	3	8	3	1	20	21
2.1 - 3	0	7	2	0	0	9	13
3.1 - 4	0	2	0	1	1	4	4
4.1 - 5	0	2	0	0	0	2	4
5.1 - 6	0	3	3	0	0	6	8
6.1 - 7	0	0	0	0	0	0	2
7.1 - 8	1	1	0	0	0	2	2
8.1 - 9	0	0	0	0	0	0	1

* the total number of egg mass losses is inflated because sometimes more than one factor acted on an egg mass, each factor was computed separately.

the period from late June until August.

Coccinellids tend to walk at the leaf edges (Michelakis, 1973) and at the thick part of the midrib, and it was on egg masses near the leaf edges that predation by these insects was mainly observed (Table 3.8). Laboratory feeding tests showed that adult C. 7-punctata can eat large numbers of Mamestra eggs (Table 3.9).

Egg predation by C. 7-punctata and other coccinellids has recently been recorded in Bulgaria (Trenchev et al., 1975). Observations are needed to establish importance of coccinellids on Mamestra during periods of normal population density, as 1976 was an exceptional year for coccinellids.

TABLE 3.9 Results of Laboratory Feeding Tests with Possible Mamestra egg Predators

Species	No. of trials	No. eggs offered	No. eggs eaten after 24h
Coleoptera			
Coccinellidae			
Coccinella 7-punctata L.	1	182	129
	2	200	113
	3	205	99
	4	192	81
Hemiptera			
Nabidae			
Nabis fuscus (L.)	1	128	96
	2	201	102
	3	150	41
Miridae			
Anthocoris nemorum (L.)	1	16*	16
	2	11	11

* A rather low number was offered because of reduced egg availability

Predation by sucking insects was rather low and did not exceed the 2.6% observed during the first infestation of 1976 (Table 3.6) and for all five infestation only averaged 1.5%.

One species, Nabis fuscus L., was commonly seen in the field and in feeding tests readily fed on the presented eggs (Table 3.9). This species proved very voracious and, as noted later (p.172), also attacked larval stages. Anthocoris nemorum (L.) was rarely found in the plot, however, adults preyed upon egg masses in the laboratory (Table 3.9).

During the third infestation of 1976, a fourth instar Mamestra larva was observed feeding on an egg mass and it consumed a total of 17 eggs. It seemed that the larva came across the egg mass while wandering and no other evidence of feeding was observed. Hirata (1965) and Oku et al., (1973b, 1974a) reported that the feeding activities of older larvae is often one of the causes of the disappearance of eggs because leaf bearing egg batches can be eaten by them. This kind of loss has also been cited for Tyria jacobaeae L. (Dempster, 1972; Isaacson, 1973) and might be important in late season in places where egg batches and older larvae coincide.

Last in order of importance were the thrips. Some eggs were damaged by them but so few as to be relatively unimportant.

c) Dislodgement

One of the main reasons for egg losses were attributed to the dislodgement of the egg masses from the leaf surface. As mentioned earlier (p.124), the edges of the egg masses were seen to have lost contact with the leaf and subsequently fell off.

In 1975, 18.2% of the egg losses were allocated to this cause. During 1976 the losses to dislodgement were higher during the first two infestations (Table 3.6). It is believed that in the very dry summers of 1975 and 1976 the plants suffered water stress, and the daily changes in turgor might have been responsible for the dislodgement. Oku et al. (1973b, 1974a) also observed losses by dislodgement of M. brassicae egg masses in Japan, and they attributed them to the rapid growth of the sugar beet leaves which resulted in the masses falling off. In our case the brussels were not growing very fast because of drought observed during those periods.

It was thought that large egg masses might suffer a higher proportion of dislodged, which was not supported by the data (Table 3.10).

TABLE 3.10 Frequency of Egg Mass Dislodgement in Relation to Egg Mass Size

Egg mass size	No of egg masses dislodged	Total	% dislodged
0 - 50	2	41	4.9
51 - 100	9	55	16.4
>101	4	42	9.5
TOTAL	15	138	10.9

d) Disappearance

Egg disappearance was observed in both years in all the infestations. It amounted to 7.7% in 1975 and in 1976 increased through the different infestations to reach 24.8% in the last one (Table 3.6).

No clear association between disappearance and egg mass size was

observed (Table 3.11).

It is likely that wind, through the leaf rubbing, helped in some of the dislodgement and disappearance cases.

e) Other causes of mortality

A few eggs were accidentally dislodged while counting (Table 3.6).

TABLE 3.11 Relation Between Egg Mass Disappearance and Egg Mass Size

Egg mass size	No. egg masses that disappeared	Total	% disappeared
0 - 50	16	41	39
51 - 100	9	55	16
>101	10	42	24
TOTAL	35	138	

3.3 Studies on Larval Mortality

3.3.1 Materials and methods

3.3.1.1 The plot

The field experiments were all carried out in the "hill bottom" area at Imperial College Field Station, Silwood Park, Ascot, Berkshire.

The soil of Hill bottom is an acidic Bagshot sand under a crop rotation of potatoes, field beans and brassicas.

The plants Brussels sprouts, var. "Irish Elegance" was chosen because the shape of the plants and distribution of leaves allowed relatively easy handling of the leaves without too much risk of damage during the observations. The plants were set out 1 m apart in the rows with 1 m between the rows.

The size of the plots were 64 x 22 m (1408 m^2) in 1975 and 52 x 40 m (2080 m^2) in 1976.

3.3.1.2 The exclusion devices

Cages and metal enclosures were used in the field experiments in order to obtain information about the importance of predators, parasites and rain acting on M. brassicae larvae.

To exclude all parasites, predators and rain a wooden frame 0.75 x 0.75 x 1.50 m was covered with terylene netting (440 mesh/square inch). The roof was made of a transparent polythene sheet and a door was provided to allow inspection of the plants. The cages were dug into the soil to about 6 cm and in addition an aluminium enclosure (1.0 x 1.0 x 0.20 m) was put around the cages, dug about 10 cm into the ground and coated on the edge with I.C.I. fruit tree grease. Finally, two pitfall traps were set up; one between the cage and the enclosure, on one corner, and the other inside the cage. Guy wire was used to secure the cages (Fig. 3.3).

To exclude only ground predator, aluminium metal enclosure, measuring 1.90 x 1.90 x 0.40 m enclosing five plants, were sunk about 10 cm into the soil and the edges were also coated with I.C.I. fruit tree grease. Flying parasite and predators could easily reach the plants as no other barriers

were used (Fig. 3.4).

To exclude birds, fruit caging net (19 mm square mesh) was supported on aluminium frames 3.0 x 3.0 x 2.0 m. This bird-proof cage was placed over a enclosure similar to that above described (Fig. 3.4). The net had holes big enough to let flying arthropod parasites and predators go freely in and out but too small for birds (Fig. 3.5).

3.3.1.3 The setting up of the field experiments

Suitable brussels sprouts plants of similar size and appearance were selected for the field plots.

All the natural enemies in "all excluded" treatment and those of ground alone in the treatments excluding ground predators and birds, were eliminated before the experiment by hand-picking and pitfall-trapping. In the "all exluded" treatment the plants were sprayed with 0.1% Nicotine to kill Brevicoryne brassicae (L.) which could easily build up to large numbers on the completely enclosed plants. Residual insecticides were not sprayed on the ground because of the danger of killing any caterpillars that fell off the plants.

Pieces of paper bearing egg masses which were about to hatch were taken to the field where they were glued to the lower surface of leaves using gum tragacanth.

After hatching the larvae were counted every two or three days.

Figure 3.3. Cage used to exclude predators, parasites and rain.

Figure 3.4. Enclosure used to exclude ground predators.

Figure 3.5. Caged enclosure used to exclude birds and ground predators.

3.3.1.4 Associated laboratory studies

a) Precipitin test

This serological technique was used to detect predation of M. brassicae only on a qualitative basis. The technique involves the injection of M. brassicae antigen into rabbits in order to produce a specific antibody. This is then used to test the gut contents of possible predators when a positive precipitin reaction would indicate that Mamestra antigen was present in the gut of the predator. Details of the method used are given in Appendix 2.

The serum gave no reaction with material from the sprout plant, nor with the following other Lepidoptera : Pieris rapae (L.), P. brassicae L., Pionia forficalis L., Plutella xylostella (Curtis). It did, however, react strongly with Noctua pronubra L., Plusia gamma L. and Agrotis spp. P. gamma was rarely seen in the plot, however, N. pronubra and three species of Agrotis (A. segetum Denis & Schiff, A. exclamationis L, and A. ipsilon Hufn.) were rather common. Furthermore while doing trial-testing on 5 Pterostichus melanarius Illiger caught inside one of the enclosures to exclude ground predators before the setting of the experiments, 3 gave strong positive reactions which indicates that carabids prey on cutworms thus making the test of limited usefulness for Mamestra. Nevertheless some syrphids and spiders from the natural population were tested when observed on plants bearing young Mamestra larvae.

b) Feeding tests

They were also designed to determine, qualitatively, the identity of possible predators of M. brassicae larvae.

Predators gathered from pitfall trapping and hand-picking were starved overnight before being placed in an arena. In the case of large predators i.e., large carabids, the arena consisted of container type A, provided with a thin moist layer of silver sand and with vaseline smeared on the upper third of the walls. Mamestra larvae were provided with a piece of brussels sprout leaf and allowed to settle down before the candidate predator was introduced. For small predators i.e., syrphid larvae, a petri dish of 9 cm diameter and 1.0 cm in height was used. It was provided with a damp filter paper and a small piece of leaf.

The containers were examined after 24 hours to record larvae killed by the predator.

Except for Episyrphus balteatus Deg., the rate of food consumption was not determined, as the experimentswere run only for 24 hours. Regardless of the predator size a fixed number of larvae per instar was offered : either 40 I; 20 II; 10 III; 5 IV; 2 V; or 1 VI.

c) Rearing of field collected material

To obtain additional information on parasitism and diseases field collected larvae from the experimental plot but mainly from a plot of cabbages and brussels close by, were brought to the laboratory and reared individually in containers of type A. They were fed with brussels leaves which were carefully inspected and cleaned to avoid infestation by tachinids flies which lay their eggs on foliage of the host plant, which can then be swallowed by the caterpillars. All containers were sterilized with sodium hypocloride.

3.3.1.5 Details of the 1975 and 1976 field experiments

The mortality factors assessed during 1975 were ground predators, flying predators, parasites and rain.

The plants were transplanted on the 27th of May and were artificially infested on the 20th July. Four plants were used for each treatment. The effect of the factors excluded was assessed by comparison with that of the population of larvae, artificially infested, on uncaged plants fully-exposed to all mortality factors.

During early summer 1976 apart from the treatments previously described a "bird excluded" treatment was set up with, as before, 4 replicates of each treatment. The plants were transplanted much earlier, on the 11th May and the infestation was done on the 17th July.

A second experiment was started on the 2nd September. For this experiment, the plants previously used in the treatments to exclude ground predators and birds and ground predators during the first experiment were re-used, to avoid loss of time to set up the cages and the need to remove natural enemies. Four replicates were used for each treatment except for the "all factors excluded" where only two replicates were set up.

3.3.1.6 Meterological data

Daily mean air temperature (°C) and daily rainfall (mm) for each year were obtained from the Meterological Station at Silwood Part (Appendix 3, Figures 1 and 2).

3.3.2 Results and discussion

3.3.2.1 Survivorship curves and life tables

The results for the 1975 and 1976 experiments are summarised in Figs. 3.6, 3.7 and 3.8; Tables 3.12 to 3.22. The life tables shown in the above mentioned tables were prepared by pooling the records of mortality of the replicates within each treatment.

Because the treatments were all started simultaneously and also because the higher numerical mortalities occurred in the first two instars, it was generally not difficult to record the number of larvae that entered each instar, this was, however, easier at some times of the larval period than at others. For each replicate the number of unhatched eggs was counted and subtracted from the initial number and the result was taken as initial number of larvae. Unless the larval aggregation on the leaf were disturbed by some factors e.g., syrphids attacks, it was difficult to count the number of hatchlings during the first or second day. Sometimes during routine counts larvae were overlooked, to be found during the next count. During the last instar some larvae left the host, especially in those plants that were small in size, but stayed hidden under fallen leaves or partially buried underneath the plants or neighbouring ones. This made the counts more time-consuming, however, they were probably reliable, and as it will be seen in the next sub-section the larvae do not disperse far from the original plant. During the 6th instar, those fully-grown larvae ready for pupation, that were missing in the next count were recorded as pupating successfully, especially in the Ground predators excluded (GPE) and Birds and ground predators excluded (BGPE) treatments.

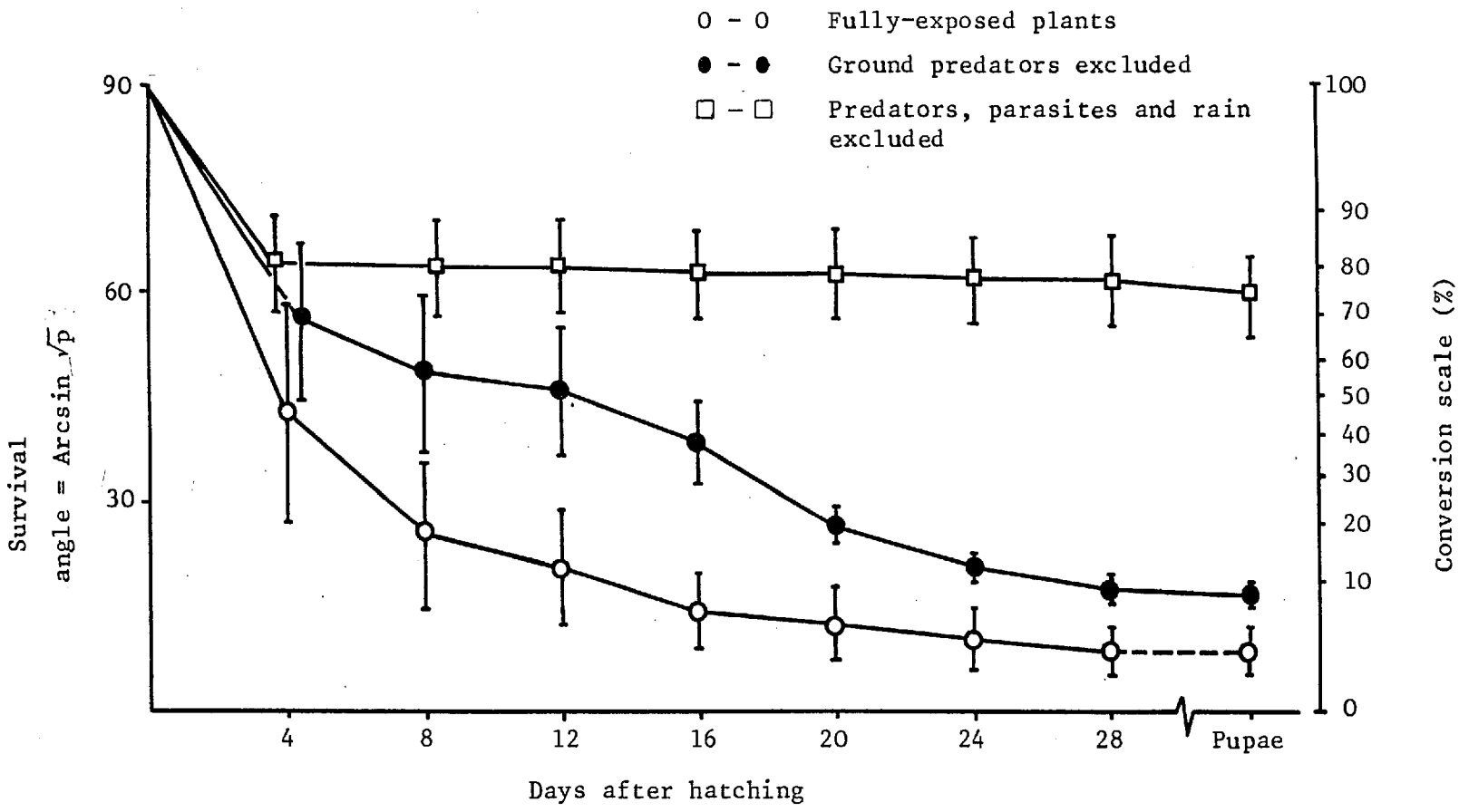


Figure 3.6. Survivorship curves for *M. brassicae* larval stage at Silwood Park. 1975 (Vertical lines indicate standard error).

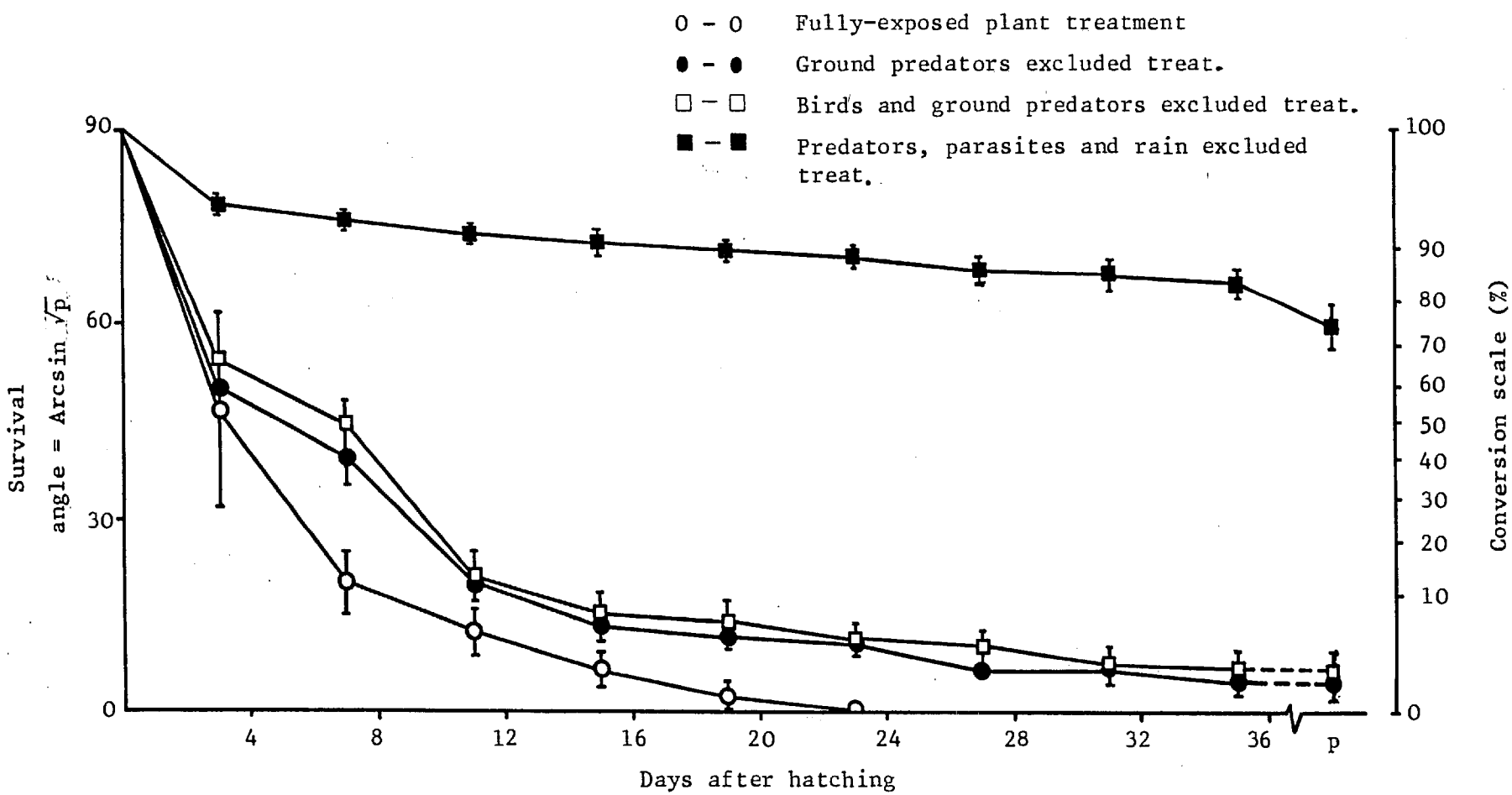


Figure 3.7. Survivorship curves for *M. brassicae* larval stage at Silwood Park. 1976. Early summer. (Vertical lines indicate standard error).

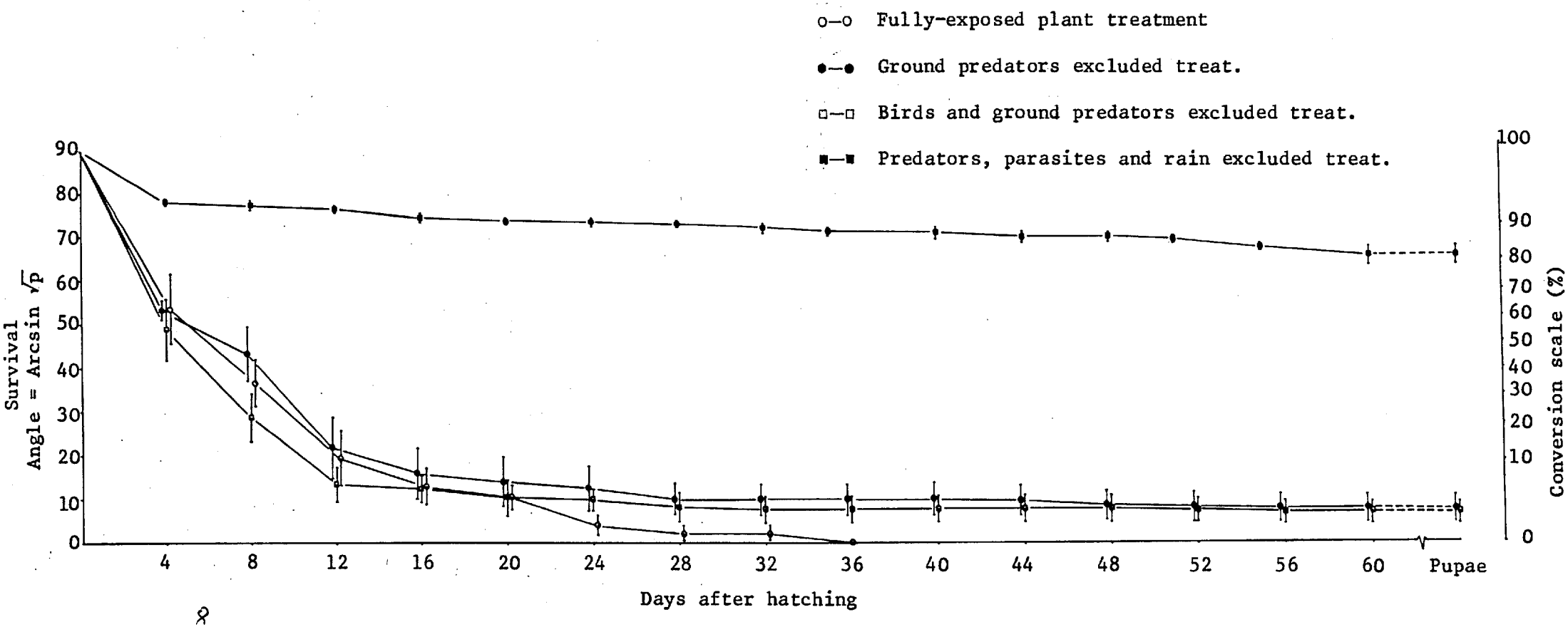


Figure 3.8. Survivorship curves for *M. brassicae* larval stage at Silwood Park. 1976. Late summer.

(Vertical line indicate standard error)

TABLE 3.12 Life Table for M. brassicae Larval Stage at Silwood Park, 1975. Fully-exposed Plants Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	459	Syrphids	164	35.7	
		Spiders	2	0.4	
		Failed at moult	1	0.2	
		"Illness"	3	0.7	
		Unknown causes	169	36.8	
			339	73.9	73.9
Instar II	120	Syrphids	8	6.7	
		Killed by observer	1	0.8	
		Unknown causes	30	25.0	
			39	32.5	8.5
Instar III	81	Wasps	1	1.2	
		Unknown causes	31	38.3	
			32	39.5	7.0
Instar IV	49	Wasps	1	2.0	
		Unknown causes	13	26.5	
			14	28.5	3.1
Instar V	35	Wasps	2	5.7	
		Carabids	1	2.9	
		Unknown causes	7	20.0	
			10	28.6	2.2
Instar VI	25	Wasps	4	16.0	
		Carabids	3	12.0	
		Unknown causes	3	12.0	
			10	40.0	2.2
Pupae	15				
		TOTAL	444		96.7

TABLE 3.13 Life Table for *M. brassicae* Larval Stage at Silwood Park, 1975. Ground Predators Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	448	Syrphids	151	33.7	
		Spiders	2	0.4	
		"Illness"	2	0.4	
		Unknown causes	51	11.4	
			206	46.0	46.0
Instar II	242	Syrphids	2	0.8	
		"Illness"	1	0.4	
		Unknown causes	18	7.4	
			21	8.7	4.7
Instar III	221	Unknown causes	41	18.6	
Instar IV	180	Wasps	4	2.2	
		Eulopha ?bicolor	1	0.6	
		Disease	1	0.6	
		Unknown causes	52	28.9	
			58	32.2	12.9
Instar V	122	Wasps	2	1.6	
		Failed at moult	1	0.8	
		Disease	3	2.5	
		Unknown causes	39	32.0	
			45	36.9	10.0
Instar VI	77	Wasps	3	3.9	
		Disease	3	3.9	
		Unknown causes	35	45.5	
			41	53.2	9.2
Pupae	36				
		TOTAL	412		92.0

TABLE 3.14 Life Table for M. brassicae Larval Stage at Silwood Park, 1975. Predators, Parasites and Rain Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	375	Syrphids	49	13.1	
		Failed at moult	2	0.5	
		"Illness"	2	0.5	
		Unknown causes	30	8.0	
			83	22.1	22.1
Instar II	292	Unknown causes	2	0.7	0.5
Instar III	290		0	0.0	0.0
Instar IV	290	Unknown causes	1	0.3	0.3
Instar V	289	Failed at moult	1	0.3	
		Unknown causes	2	0.7	
			3	1.0	0.8
Instar VI	286	Killed by observer	3	1.0	
		Disease	5	1.7	
		Unknown causes	2	0.7	
			10	3.5	2.7
Prepupae	276	Unknown causes	3	1.1	0.8
Pupae	273				
		TOTAL	102		27.2

TABLE 3.15 Life Table for *M. brassicae* Larval Stage at Silwood Park, 1976. Early Summer. Fully-exposed Plants Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	436	Syrphids	46	10.6	
		Rain	5	1.1	
		Coccinellids + Unknown causes	335	76.8	
			386	88.5	88.5
Instar II	50	Syrphids	1	2.0	
		Coccinellids + Unknown causes	28	56.0	
			29	58.0	6.7
Instar III	21	Unknown causes	15	71.4	3.4
Instar IV	6	Wasp	1	16.7	
		Unknown causes	5	83.3	
			6	100.0	1.4
Instar V	0		0		
Instar VI	0		0		
Pupae	0		0		
		TOTAL	436		100.0

TABLE 3.16 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Early Summer. Ground Predators Excluded Treatments

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	451	Syrphids	12	2.7	
		Rain	4	0.9	
		"Illness"	2	0.4	
		Spiders	3	0.7	
		Coccinellids + Unknown causes	286	63.4	
			307	68.1	68.1
Instar II	144	Syrphids	2	1.4	
		"Illness"	1	0.1	
		Coccinellids + Unknown causes	106	74.2	
			109	75.7	24.2
Instar III	35	Unknown causes	15	42.9	3.3
Instar IV	20	Unknown causes	7	35.0	1.6
Instar V	13	Wasps	2	15.4	
		Disease	1	7.7	
		Unknown causes	4	30.8	
			7	53.8	1.6
Instar VI	6	Wasps	1	16.7	
		Unknown causes	1	16.7	
			2	33.3	0.4
Pupae	4				
		TOTAL	447		99.1

TABLE 3.17 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Early Summer. Birds and Ground Predators Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	404	Syrphids	41	10.1	
		Rain	6	1.5	
		"Illness"	4	1.0	
		Killed by observer	1	0.2	
		Failed at moult	1	0.2	
		Coccinellids + Unknown causes	241	59.7	
			294	72.8	72.8
Instar II	110	Syrphids	3	2.7	
		Coccinellids + Unknown causes	77	70.0	
			80	72.7	19.8
Instar III	30	Syrphids	2	6.7	
		Unknown causes	10	33.3	
			12	40.0	3.0
Instar IV	18	Failed at moult	1	5.6	
		Unknown causes	3	16.7	
			4	22.2	1.0
Instar V	14	Wasps	2	14.3	
		Unknown causes	2	14.3	
			4	28.6	1.0
Instar VI	10	Wasps	1	10.0	
		Unknown causes	1	10.0	
			2	20.0	0.5
Pupae	8				
		TOTAL	396		98.0

TABLE 3.18 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Early Summer. Predators, Parasites and Rain Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	280	Failed at moult	1	0.4	
		"Illness"	2	0.7	
		Killed by observer	2	0.7	
		Unknown causes	13	4.6	
			18	6.4	6.4
Instar II	262	Killed by observer	1	0.4	
		"Illness"	1	0.4	
		Unknown causes	5	1.9	
			7	2.7	2.5
Instar III	255	Failed at moult	1	0.4	
		Unknown causes	4	1.6	
			5	2.0	1.8
Instar IV	250	Failed at moult	1	0.4	
		Unknown causes	4	1.6	
			6	2.0	1.8
Instar V	245	Disease	2	0.8	
		Killed by observer	3	1.2	
		Unknown causes	1	0.4	
			6	2.4	2.1
Instar VI	239	Disease	29	12.1	
		Unknown causes	4	1.7	
			33	13.8	11.8
Prepupae	206		1	0.5	
Pupae	205		1	0.5	0.4
		TOTAL	75		30.5

TABLE 3.19 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Late Summer. Fully-exposed Plants Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	440	Syrphids	187	42.5	
		Spiders	2	0.5	
		"Illness"	15	3.4	
		Rain	3	0.7	
		Unknown causes	190	43.2	
			397	90.3	90.3
Instar II	43	Syrphids	5	11.6	
		Unknown causes	29	67.4	
			34	79.1	7.7
Instar III	9	Unknown causes	9	100.0	2.0
Instar IV	0		0		
Instar V	0		0		
Instar VI	0		0		
Pupae	0		0		
		TOTAL	440		100.0

TABLE 3.20 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Late Summer. Ground Predators Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	435	Syrphids	308	70.8	
		Spiders	8	1.8	
		"Illness"	3	0.7	
		Failed at moult	1	0.2	
		Rain	1	0.2	
		Unknown causes	41	9.4	
			362	83.2	83.2
Instar II	73	Syrphids	11	15.1	
		Spiders	1	1.4	
		Unknown causes	18	24.7	
			30	41.1	6.9
Instar III	43	Failed at moult	1	1.7	
		Unknown causes	17	39.5	
			18	41.9	4.1
Instar IV	25	Unknown causes	7	28.0	1.6
Instar V	18	Unknown causes	4	22.2	0.9
Instar VI	14	Disease	2	14.2	
		Low Temperature	1	7.1	
			3	21.4	0.7
Pupae	11				
		TOTAL	424		97.5

TABLE 3.21 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Late Summer. Birds and Ground Predators Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	423	Syrphids	272	64.3	
		"Illness"	4	0.9	
		Spiders	2	0.5	
		Rain	4	0.9	
		Unknown causes	106	25.1	
			388	91.7	91.7
Instar II	35	Syrphids	3	8.6	
		Failed at moult	1	2.9	
		Unknown causes	17	48.6	
			21	60.0	5.0
Instar III	14	Disease	1	7.1	
		Unknown causes	2	14.3	
			3	21.4	0.7
Instar IV	12	Unknown causes	2	16.7	0.5
Instar V	0		0		
Instar VI	10	Low Temperature	1	10.0	0.2
Pupae	9				
		TOTAL	415		98.1

TABLE 3.22 Life Table for M. brassicae Larval Stage at Silwood Park, 1976. Late Summer. Predators, Parasites and Rain Excluded Treatment

Age inter. (x)	Number entering stage (lx)	Cause of death (dxF)	Number dying (dx)	% of stage dying (100qx)	% of initial no. ($100qx_1$)
Instar I	159	Failed at moult	1	0.6	
		Unknown causes	10	6.3	
			11	6.9	6.9
Instar II	148	Unknown causes	3	2.0	1.9
Instar III	145	Unknown causes	4	2.8	2.5
Instar IV	141	Unknown causes	3	2.1	1.9
Instar V	138	Unknown causes	2	1.4	1.3
Instar VI	136	Disease	2	1.5	
		Low Temperature	5	3.7	
			7	5.1	4.4
Pupae	129				
		TOTAL	30		18.9

In 1975 the pupae of the Predators, parasites and rain excluded (PPRE) and the GPE treatments were dug up, but only those of the PPRE treatment (early summer) during 1976. In the other treatments the number were estimated as above.

The category "illness" refers to those individuals showing sluggishness or protracted development, sometimes with a pinkish colour. Under unknown causes are indluded those larvae that disappeared from one count to another. "Wasps" includes those cases when they were seen preying or evidence of their attacks were found.

Except for the PPRE in both years, and the 1975 GPE treatments, all survivorship curves obtained showed basically similar features i.e., remarkably high mortality during early instars (1st to 3rd). The shape of the curves is thus concave. As we will see later arthropod predators were the main factors causing this high mortality, although not always the same type of predators were involved.

An analysis of variance (App. 4, Tables 1, 2 and 3) confirmed significant differences among treatments, and also between days ($P<0.01$ on each experiment), mainly due to the high survival rate in the PPRE treatments in contrast with the rather uniform mortality trend observed among the other treatments. The interaction treatment by days was significant in both experiments during 1976 but not in 1975 (App. 4, Tables 1, 2 and 3).

In 1975, syrphids and ground predators accounted for most of the mortality during early instars. It is interesting to note that in the GPE treatments the curve, although with less mortality than that of the fully-exposed plant (FEP) treatment, dropped ending with few pupae but signifi-

cantly more than the FEP treatment. The difference in mortality was 4.7% while both started with a comparable initial number of larvae (Fig. 3.6; Tables 3.12 and 3.13). This might suggest that the high larval density might have attracted airborne predators which partially compensated for the lower mortality in early instars.

The trend of the curves for all treatments in 1976 were similar (Figs. 3.7 and 3.8), however, the mortality agents acting in each treatment were different in their intensities. In early summer the fall was attributed partially to predation by ladybirds, which were in such an unusual number that this year has been called by some "the year of the Ladybirds", nevertheless they did not account for all the mortality in the FEP treatment which was possibly due to ground predators.

Syrphids and, to a lesser extent, ladybirds were responsible for the high mortality observed in the survivorship curves in late summer (Fig. 3.8).

In 1976, in both experiments the mortality in the FEP treatments was 100%, and was probably due to invertebrate predators, especially ground ones.

3.3.2.2 Mortality factors

a) Predators

It is very difficult to measure quantitatively the effect of predators on the host population by direct observation. Exclusion techniques help in this respect, although they give only information on the kind of predators involved i.e., ground or airborne predators and indicate the impact that they

have. However, mortality due to certain predators may be quantified with some accuracy in those cases in which the predators or prey leave particular marks. For example the emptied and distorted bodies of young Mamestra larvae are left stuck on the leaf surface after being attacked by syrphids larvae.

Syrphid larvae were important predators during both 1975 and 1976 especially during late summer of 1976. (Table 3.23)

The species of syrphidae most frequently found on the brussels plant were Episyrphus balteatus Deg., Metasyrphus latisfaciatus Macquart, M. corollae F., Sphaerophora scripta (L.) and Scaeva pyrastri L.. Of these, the first, second and fourth species were seen preying on Mamestra in the field (Table 3.27) with E. balteatus the commonest and most important species.

TABLE 3.23 Percentage of Mamestra Larvae Killed by Syrphids During 1975 and 1976

Treatment	1975	1976	
		Early summer	Late summer
Fully-exposed plants	37.5	10.8	43.6
Birds and ground predators excluded	-	11.4	65.0
Ground predators excluded	34.2	3.1	73.3
Predators, parasites and rain excluded	13.1*	0.0	0.0

* In two replicates of this treatment syrphid larvae overlooked during the removal of natural enemies killed 13.1% of the larvae before being removed.

In feeding trials E. balteatus and other species readily fed on Mamestra larvae up to the third instar (Tables 3.24 and 3.29). The feeding rate of E. balteatus was high, consuming an average of 30.1 larvae per day (Table 3.25).

TABLE 3.24 Results of Feeding Trails with Syrphid Larvae Supplies with Different Instars of M. brassicae during a 24 hours period

Species	Instar offered	No. of trials	Number offered per trial	Total eaten in all trials
Episyrphus balteatus	2	1	20	15
	3	3	10	10
	4	2	5	0
Metasyrphus latisfaciatus	1	2	40	79
	2	1	20	20
	3	1	10	1
	4	2	5	0
M. corollae	1	1	40	19 *
Sphaerophoria scripta	1	1	40	38
	2	3	20	31**

* Pupated after eating the 19 larvae

** One pupated after eating 5 larvae

In view of the high syrphid predation observed in the 1975 experiment, where 5 out of 8 replicates of the ground predators excluded (GPE) and

fully-exposed plant (FEP) treatments suffered from their attacks, some additional information was sought to check whether these results were a true reflection of field conditions.

TABLE 3.25 The Daily Consumption Rate of E. balteatus on M. brassicae First Instar Larvae in Laboratory Feeding Trials

Specimen	No. larvae offered daily	No. of larvae eaten in day				Total	Daily consumption
		1	2	3	4		
A	40	29	37	35	-	101	33.7 ± 4.2*
B	40	40	31	22	17	110	27.5 ±10.1

* Mean ± Standard deviation

A survey carried out on the natural population showed that 12 (57.1%) out of 21 hatching places examined gave evidence of having been attacked by syrphids.

By following the procedure described in the study of egg mortality (p.117) several egg masses were obtained of which 4 were selected, one per plant on leaves of comparative sizes. The plants were enclosed within a metal enclosure similar to that used in the PPRE treatment. The ground inside the frame was searched for ground predators and also provided with two pitfall traps, and in addition a band of ICI fruit tree grease was put around the base of the plants. All plant-dwelling insects were removed. A plastic container 28.0 x 15.9 x 9.0 cm with the inside smeared with ICI fruit tree grease was placed directly underneath each egg mass-bearing leaf to collect any falling larvae. On the night that hatching was due 4 large and two medium size field collected larvae of E. balteatus were distributed on

each of the two plants, leaving the remaining two plants as controls. The high number of syrphid larvae per plant allowed for possible pupation or death of the larvae. The experiment was conducted for five days.

The larval aggregation of plant B was attacked on the first night. On the second day 2 syrphids had pupated on each of the plants.

It can be seen (Table 3.26) that syrphid larvae can have a great impact on a Mamestra larval aggregation. At the end of the experiment a total of 60.6% of larvae had been preyed upon by syrphids, leaving only 6.7% alive while in the "controls" 79.9% of the larvae were still alive on the plants. It is noteworthy that 25.4% of the larvae were trapped in the plastic containers which suggests considerable disturbance by the syrphids. Although in this case falling larvae were caught in the container, in natural conditions such larvae will fall to the ground and/or to the lower leaves where they may have a high risk of getting preyed by ground predators. It seems reasonable to assume that disturbance of larval aggregation by any factor will lead to increased mortality. Perhaps the mortality attributed to ground predators and unknown factors during the first instar, which was always high in any of the FEP treatments may in part have been enhanced by the syrphid and coccinellids attacks. In some of the GPE and BGPE treatments, larva were found on lower leaves because either they dropped or climbed up after falling to the ground; later some moved to the upper part of the plant. In the case of the FEP treatments, those observed on lower leaves were almost always soon lost.

During September 1976, the syrphid population on the brussels plants was large. It is possible that increased syrphid egg-laying on brussels took place in preference to field beans and other crops, because for example

TABLE 3.26 : The Effect of Syrphid Predation on First Instar Larvae of *M. brassicae*

INFESTED PLANTS	Plant A	Plant B	Total	%
Initial number of larvae	185	158	343	
Final number of larvae on the original leaf	7	8	15	4.4
Number of head capsules recovered	124	84	208	60.6
Number of larvae in container	31	56	87	25.4
Number of larvae on other leaves	5	3	8	2.3
Other losses (i.e. weak larvae, diseased)	6	3	9	2.6
Unknown	12	4	16	4.7
CONTROL PLANTS	Plant C	Plant D	Total	%
Initial number of larvae	154	135	289	
Final number of larvae on the original leaf	118	89	207	71.6
Number of head capsules recovered	0	0	0	0.0
Number of larvae in container	2	7	9	3.1
Number of larvae on other leaves	1	23	24	8.3
Other losses	3	3	6	2.8
Unknown	30	13	43	14.9

in the beans plot the coccinellids seemed to have decimated the aphid population while in brussels, small colonies of Brevicoryne brassicae (L.) were to be found. The adult coccinellids cannot move about on sprouts as easily as on field beans giving some protection from predation. Rain had a striking effect on the syrphid population since after rain many hundreds of larvae could be counted dead on the brussels plants, especially in pockets of water formed on some leaves.

In 1975 very few coccinellids were seen on the plot and it was thought that they were feeding on Brevicoryne brassicae whereas during 1976 an unusually large number occurred. The species most abundant were Coccinella 7-punctata and C. 11-punctata. The populations rose to peaks, for both species in mid-July over most of Southern England. C. 7-punctata was exceptionally abundant in places like Silwood Park (Bowden, 1977).

The high mortality observed during early summer in 1976 was thought to have been caused by Ladybirds especially C. 7-punctata. They were observed feeding on 1st and 2nd instar Mamestra larvae (Table 3.27).

The two treatments with metal enclosures (GPE and BGPE treatments) showed similar trends in their mortalities (Fig. 3.7) which might have been due to a comparative build up of coccinellids inside the enclosures. In addition some attacks by syrphids disturbed some of the aggregation which might have also facilitated ladybird predation.

In feeding test trials the adults of C. 7-punctata readily preyed upon 1st and 2nd instars and were even able to attack 3rd instar larvae (Table 3.28 and 3.29).

TABLE 3.27 Natural Enemies Observed Preying on M. brassicae in the Field

Species	Egg	Larval instar						
		I	II	III	IV	V	VI	
INSECTA								
Coleoptera								
Coccinellidae								
Coccinella 7-punctata L.	+	+	+					
Propylea 14-punctata (L.)			+					
Carabidae								
Pterostichus melanarius Illiger							+	1
Hymenoptera								
Vespidae								
Paravespula vulgaris (L.)				+		+	+	
P. germanica (F.)						+	+	
Diptera								
Syrphidae								
Episyrphus balteatus Deg.		+	+					
Metasyrphus latisfaciatus Macquart			+					
Sphaerophoria scripta (L.)		+						
Thysanoptera								
Thripidae	+							
ARACHNOIDEA								
Araneae								
Theridiidae								
prob. Theridion vittatum Clk.		+	+					2
poss. T. sisyphium (Clerk)		+						
Argiopidae								
Meta segmentata (Clerk)		+	+					3
poss. Araneus cucurbitinus Clk.		+	+					4
Thomisidae								
Philodromus sp		+						
Xysticus sp		+						

1. The specimens were not seen feeding but engorged by a killed Mamestra

6th instar larvae

2, 3 and 4 Not seen preying on 2nd instar but dead 2nd instar larvae in their webs.

Broadly speaking, there are two types of spiders, those that spin webs and wait for the prey to arrive and those that hunt for them. The first group was very common on brussels plants, most with their webs located on the lower part of the plant. Almost invariably all Mamestra larvae found in webs were on those lower leaves.

Spiders were seen handling first instar larvae, and remains of first, second and even of a fourth instar (of the natural population) were recovered from webs. The number of larvae killed by web-spinning spiders was rather low in the experiments (see life tables), and in the natural population by examination of webs near to hatching places showed that probably few larvae were taken. Although there are no records, it is possible that hunting spiders might have made up part of the losses attributed to ground predators in the FEP treatment.

Spiders of the families theridiidae and Argiopidae were the main predators in this group. Two species of Thomisidae, Philodromus sp and Xysticus sp were seen handling first instar larvae with the later eating its prey (Table 3.27). Philodromus and Xysticus fed on Mamestra larvae in feeding trials (Tables 3.28 and 3.29).

One unidentified Linyphiidae and one Xysticus sp caught by hatching places in the natural population were positive when precipiting-tested. Two other Xysticus specimens gave no reaction.

Ground beetles are among the most common arthropod predators, however, little evidence was obtained to show their importance during this two year study.

Feeding tests revealed that carabids preyed readily upon the different instar of Mamestra (Tables 3.28 and 3.29). Two species, Pterostichus melanarius Illiger and P. madidus F. were able to kill fully-grown caterpillars with ease.

Carabids are nocturnal and rarely observed during the day, however, some evidence of their attacks on older larvae in the field was obtained. Larvae that left the plants and stayed hidden beneath the plants under fallen leaves etc. were attacked. On two occasions, adults of P. melanarius were found by the remains of dead 6th instar larvae, and in each case the beetles had full guts. In 1975 some remains of larvae were found near to the FEP treatments and these deaths were attributed to carabids as the remains resembled those of larvae killed by carabids in the laboratory.

During 1976, the FEP treatments were subject to such a high mortality that no larvae reached the late instars. It is possible that carabids may have taken a share in that mortality as they are known to be important during the early instar of other brassica pest, Pieris rapae (L.) (Dempster, 1967). It should be mentioned, however, that the activity of the beetles was very much reduced during the dry and hot summers observed in those two years (Paiva, 1977). Some additional information will be given in the next sub-section.

In 1975, there was a reduction in the number of larvae of the GPE treatment. This was thought to be due either to wasps or birds. It is

TABLE 3.28 Results of Feeding Trials with Possible Predators Supplied with *M. brassicae* Larvae

Species	Instar offered	Number of trials	Number offered per trial	Total eaten in all trials
INSECTA				
Coleoptera				
Carabidae				
Pterostichus melanarius Illiger	4	2	5	10
	5	3	2	6
	6	5	1	5
P. madidus F.	4	1	5	4
	5	1	2	2
	6	3	1	3
Harpalus rufipes Deg.	5	6	2	3
	6	6	1	1
H. aeneus F.	3	2	10	13
	4	1	5	0
Calathus fucispes Goeze	5	5	2	5
	6*	2	1	2
	6**	2	1	0
Nebria sp	3	3	10	12
	4	2	5	5
Amara sp	3	1	10	0
Staphylinidae				
Platydrocus stercorarius (Oliver)	4	1	5	5
Coccinellidae				
Coccinella 7-punctata L.	1	2	40	43
	2	2	20	11
	3	1	10	2
Hemiptera				
Nabiidae				
Nabis ferus (L.)	1	1	40	26
	2	2	20	13
	3	1	10	2

Continued .....

TABLE 3.28 - Continued

Species	Instar offered	Number of trials	Number offered per trial	Total eaten in all trials
ARACHNOIDAE Aranae Thomisidae				
Xysticus sp	2	1	20	7
Philodromus sp	2	1	20	4

* young 6th instar

** old 6th instar

possible that wasps were responsible for most of the losses as they were frequently seen foraging through the day and on several occasions were observed attacking and killing Mamestra larvae (Table 3.27).

In general, wasps seem to prefer larger caterpillars (5th and 6th) or perhaps they are found more easily. However, they also attack middle instars (3rd and 4th) because on one occasion a 3rd instar larva was observed whilst being attacked and killed by a wasp. Wasps were also seen preying on middle size P. rapae.

In 1976, in an attempt to find out the importance of wasps, a new treatment was introduced using nets to keep birds away from the metal enclosure plants.

With the small number of larvae left during the last instars it is difficult to obtain good estimates of the relative importance of wasps and birds, nevertheless, by using the life table data (tables 3.13; 3.16;

TABLE 3.29 Summary of Results of Feeding Tests of Different Insect Predators Supplied with M. brassicae eggs and Larvae

	Egg	Larval instar						
		I	II	III	IV	V	VI	
Coleoptera								
Stphylinidae								
Platydrocus stercorarius (Oliver)					+			
Carabidae								
Pterostichus melanarius Illiger					+	+	+	
P. madidus F.					+	+	+	
Harpalus rufipes Deg.						+	+	1
H. aeneus F.				+	−			
Calathus fuscipes Goeze						+	+	2
Nebria sp.				+	+	−	−	
Amara sp.		−	−	−				
Coccinellidae								
Coccinella 7-punctata L.	+	+	+	+	−			
Diptera								
Syrphidae								
Episyrphus balteatus Deg.		+	+	+	−			
Metasyrphus latisfaciatus Mcquart		+	+	+	−			
M. corollae F.		+						
Sphaerophoria scripta (L.)		+	+					
Hemiptera								
Nabiidae								
Nabis ferus (L.)	+	+	+	+	+			3
Cimicidae								
Anthocoris nemorum (L.)	+							
Neuroptera								
Chrysopidae								
Chrysopa carnea Stephens		+	+	+				
Thysanoptera								
Thripidae	+							

TABLE 3.29 Continued

	Egg	Larval instar					
		I	II	III	IV	V	VI
Araneae Thomisidae							
Xysticus sp.		+	+				
Philodromus sp.		+	+				

\+ Indicates feeding

\- Indicates that the predators did not feed on the offered prey

1 and 2 Only one day-old 6th instar larva are taken

3 Preyed only young 4th instar larva.

3.17; 3.20; and 3.21) the mortality from 3rd instar until pupal stage was calculated (Table 3.30).

During 1976, in early summer the disappearance of larvae in both treatments was approximately similar (87.1 to 70.4%) thus agreeing with the observations that wasps were very active during that period. In late summer it was more likely that the losses in the GPE treatment were due to birds as the activity of wasps was observed to be very much reduced or at least less wasps were seen foraging. Although birds were seen on the plot on no occasion were they seen taking caterpillars of Mamestra or any other Lepidoptera. It is possible that a good deal of the 82.3% mortality observed in 1975 in the GPE treatment was due to wasps.

Paravespula vulgaris (L.) and P. germanica (F.) were the species of wasps observed preying in both years (Table 3.27).

TABLE 3.30 Estimation of Mortality Caused by Wasps and Birds during 1975 and 1976

	1975	1976			
		Ground predators excluded		Birds and ground predators excluded	
		Early summer	Late summer	Early summer	Late summer
Number entering 3rd instar	221	35	43	30	14
Number lost to other causes than wasps birds (i.e. diseases)	9	1	4	3	2
Number observed lost to wasps	9	3	-	-	-
Corrected value*	203	31	39	27	12
Number larvae entering pupal stage	36	4	11	8	9
% mortality	82.3	87.1	71.8	70.4	25.0

* Obtained by subtracting the values in rows 2 and 3 (known larval losses) from row 1 in each column

Birds have been cited attacking M. brassicae. Gyory et al. (1964-65) reported on birds preying on Mamestra larvae in outbreak areas. Bird attacks, along with other factors, were shown to have brought to an end an outbreak of Mamestra (Valch, 1913, 1914). Oku et al. (1973a, b) found predatory activities of birds to be important and related to the disappearance of older larvae. They noticed that their experimental field was located in an area where birds were more abundant than usual.

Severe predation by wasps and birds has been reported in other Lepidoptera for example, Hyphantria cunea Drury (Ito and Miyashita, 1968;

Morris, 1972).

Under special circumstances that is a plot near to woods, bird predation can be very high as found with P. rapae (Dempster, 1967).

Other predators of Mamestra were Nabis ferus L. and Chrysopa carnea Stephens. N. ferus, a predatory bug of the family Nabiidae, was tested in the laboratory and readily preyed on the offered larvae (Tables 3.28 and 3.29). They were common in the field in both years and it is possible that they took a share in the mortality observed in the FEP treatments. A C. carnea larva was tested for predation, being capable of attacking up to 3rd instar larvae. Very few were seen in the field.

Observation on predation by small mammals was not attempted. Scanty evidence of their predatory activities was obtained in an experiment on the dispersal of the fully-grown larvae using radioactive tagged larvae. This will be dealt with in the next sub-section.

b) Parasites

Very few parasites were obtained during the two years study. In 1975 three 5th instar larvae; one from the GPE treatment and two from the natural population were seen bearing clusters of larvae of the parasitic insect Euplectrus ?bicolor (Swed) (Hymenoptera : Eulophidae). In 1976, two larvae from the field collected material were found parasitized by another species of the above-mentioned family Eulophus pennicornis Nees.

In 1976, four 6th instar larvae collected in the field bore eggs laid on the head and thorax (probably tachinid eggs). They were taken to the laboratory and reared but Mamestra adults successfully emerged from the pupae.

The only tachinid fly obtained during the whole study emerged from a pupa formed from a larva collected in the field in 1976 (Table 3.31), unfortunately just after emergence, it was trapped between the cotton plug and the wall of the rearing sample tube and it was impossible to identify.

TABLE 3.31 Results of Field Collection of M. brassicae Larvae During 1975 and 1976

Year	Date	Number of larvae collected	Disease	Larval parasite	Pupal parasite	Number of larvae that pupated
1975	2-4 August	28	1	1	0	26
	11-12 August	20	1	0	0	19
	19-22 August	15	0	1	0	14
	26-28 August	15	2	0	0	14
1976	30 June	5	0	0	0	5
	3-4 July	18	0	0	0	18*
	17-18 July	14	0	1	0	13
	9-11 August	7	0	1	0	6
	14-15 August	23	1	0	0	22
	18 September	5	0	0	1	5

* Three sixth instar larvae had tachinid fly eggs laid on their head and thorax, however, adults successfully emerged from the pupae

Although the number of species of parasites cited for M. brassicae is relatively high, for instance Thompson (1945) listed 32 species of parasites (excluding egg paraiste), and also 18 parasites have been recorded in

Britain (App. 5), they seem to occur in low numbers in the field and have little numerical effect. Nevertheless in some places of eastern Europe some parasites like Ernestia consobrina Mg. are frequently cited as important mortality factors reaching high level of parasitism (Zorin, 1936; Serebrovski et al., 1944; Birova, 1973). While in Japan, parasitism was very low even under outbreak conditions (Oku et al., 1973b).

c) Diseases

During the course of the experiments larvae showing symptoms of diseases were found, and others already dead were on the plant or more frequently on the ground.

The number of larvae killed by diseases was low and only particularly high in two replicates of the 1976 PPRE treatment (early summer) where 11.1% of the total were lost to apparently two kind of diseases. In one case, the dead larvae were reddish black in colour with their tissues liquified, probably a virus infection. In the other, but less frequently, the caterpillars showed diarrhoea with faeces adhered to the anal aperture; the larvae typically ceased feeding and began to shrink until they died.

From field collected material only three larvae died in the laboratory with symptoms similar to the viruses mentioned above.

A fungus, probably Beauveria was recorded on one individual in 1975. The larva was covered with a white mycelial growth.

There is a possibility that the high number of larvae killed by disease in the PPRE treatment was due to accidental introduction of the

disease agents.

d) Weather

Of the components of weather, rainfall was the only one of which some information was gathered. This was done on one occasion for each of the two experiments carried out in 1976 by counting the number of first instar larvae before and after rainfall.

Table 3.32 shows that rainfall had little effect as a mortality factor in our experiments, and that was probably the case in the natural populations of 1975 and 1976 as these were, atypically, very dry summers.

Rainfall may be an important cause of mortality during early instars of lepidopterous larvae, as found by Harcourt (1963a, 1966) in Plutella xylostella and Pieris rapae. It is possible that in seasons with heavy and frequent rainfalls the mortality of early instar Mamestra larvae could be very high. This, however, should be less important in older caterpillars, as they are not easily disturbed or when dislodged are probably able to regain the plant.

During the experiments carried out in late summer a total of 7 larvae that had shown protracted developments were found dead. This was thought to have been caused by the drop in the temperature to near ^{o}C or below during the first days of November.

TABLE 3.32 Larval Counts Before and After Rainfall at Silwood Park 1976

Date	Rainfall (mm)	Treatments	Larval counts (total per treatment)		Missing larvae	%
			Before	After		
20/7	7.1	Fully-exposed plants	214	209	5	2.3
		Ground predators excluded	271	267	4	1.5
		Birds and ground predators excluded	261	255	6	2.3
		Predators, parasites and rain excluded	236	236	0	0.0
10/9	8.0	Fully-exposed plants	117	114	3	2.6
		Ground predators excluded	82	81	1	1.2
		Birds and ground predators excluded	174	170	4	2.3
		Predators, parasites and rain excluded	151	151	0	0.0

3.4 Studies on the Dispersal of Fully-grown Larvae

3.4.1 Introduction

In 1975, it was noted that some fully-grown larvae left the host and stayed hidden beneath the plant or neighbouring ones, underneath fallen leaves or even partially buried etc., and it was thought that they probably pupated near to their original host plant. This behaviour might be important because, if the larvae stayed on the ground for a long time before pupating,

they might be preyed upon by predators such as carabids and small mammals.

In order to obtain information on the dispersal distance of the fully-grown caterpillars, and also on their mortality during this period, an experiment was undertaken using larvae with radioactive tags.

3.4.2 Materials and methods

3.4.2.1 Tagging, release and recovery

An adaptation of the technique used by Baldwin and Cowper (1969) was used. One 2mm length of 0.33mm diameter Platinum-Iridium radioactive wire (1 μCi) (1 micro-Curie) was inserted beside the mid-dorsum of 6th instar larvae (weighing between 700-800 mgs). The tag wires were loaded using forceps into the tip of a 23 gauze by 1 inch needle fitted to a syringe. A nickel-chromium wire attached to the plunger of the syringe and inserted into the bore of the needle, was used to eject the tags underneath the cuticle. The larvae were first anaesthetised with carbon dioxide, and after treatment were placed individually in container type A for recovery and observation. Brussels sprouts leaves were provided as food.

Because of safety reasons the activity allowed per individual wire was 1 μCi, with a total of 20 μCi per release. In order to get the desired activity per length of wire, the material was irradiated in a thermal flux of 1.5×10^{12} neutron/cm^2. sec. for 25 min. using the facilities provided by the University of London Reactor Centre at Silwood Park. The short-lived isotopes (Ir^{194}, Ir^{192m}, Pt^{197} and Pt^{199}) were allowed to decay.

The search for radioactive caterpillars was made using a portable ratemeter type R.M.5 fitted with a probe head "Scintillation Crystal NaI (Ti)".

In the laboratory a radioactive wire was placed on the bottom of a beaker and covered with soil from the plot at different depths and the counting rates measured. It was found that the tags could be detected at a distance of 30 cm when lying on the soil surface, and at a depth of 10 cm when the probe was held 5 cm immediately above the spot where the wire was buried.

Two releases were carried out, the first one on the 23 September 1976 and the second on the 13 October 1976. 20 caterpillars were used per release.

A light frame with netting to avoid bird predation was placed over the release plant. This was necessary to avoid the losses of tagged larvae and also to prevent spread of the radioactive tags by birds.

After release the larvae were searched for every day, and once a positive reading was obtained, the place was marked with a stake for subsequent checking. The pupae were dug up after 15 days had elapsed after the time of release. Both the distance from the release point and the depth of pupation were measured.

3.4.2.2 Effect of tagging method on the insect

An experiment was conducted in the laboratory to determine whether the tagging method directly affected larval survival, and subsequent pupation,

emergence, mating and fecundity. Three treatments were compared, namely, larvae injected with radioactive wire, larvae injected with wire non-radioactive and the control. 10 larvae were used for each treatment. Longevity and fecundity of the emerged adults were studied in container type A at a temperature varying between 23 and 26°C. A 5% honey solution was given during the first three days to adults.

The possible effect of tagging on larval activity was assessed by using the test described in page 80. The light was provided in this case, by a 40W electric lamp. The test was carried out at 20°C. As before the time from dropping until they straightened and from there until they escaped from the petri dish, was measured. For this experiment only larvae injected with wire no radioactive were compared with the control insects; it was considered that the amount of radioactivity was so small that it could not produce any effect by itself so the mechanical effect of the injection and the wire would be the possible factors capable of altering larval activity.

3.4.3 Results and discussion

3.4.3.1 Effect of tagging on the insect

The tagging method seems to have no detrimental effect on survival of the larvae. Similarly, their pupation and emergence as adults in the laboratory were not affected by tagging (Tables 3.33 and 3.34). However, the data (Table 3.34) shows an effect on the fecundity of the ensuing females, but the sample being too small and the variation so great that statistical tests were inconclusive. Furthermore our stock culture shows high variability as far as fecundity is concerned. The mating and general activity seem to have been unaffected.

To ensure maximum survival in the field, the tagged larvae were observed overnight before releasing so that only healthy-looking individuals were taken to the plot. All the tagged individuals recovered from the soil had pupated successfully and all developed into adults in the laboratory with the exception of those damaged during the digging.

TABLE 3.33 Effect of Tagging Method on Pupation Success and Adult Emergence

Treatment	Number of larvae used	Surviving pupae	Emerging moth
Radioactive wire	10	10	10
No radioactive wire	10	10	9*
Control	10	10	9**

* one pupa entered diapause

** one pupa entered diapause

TABLE 3.34 Effect of Tagging Method on Adult Longevity and Fecundity

Treatment	Number of larvae used	Longevity (days)	Fecundity
Radioactive wire	5	♂ 10.6 ± 2.88*	
	5	♀ 10.8 ± 2.39	709.8 ± 589.9
No radioactive wire	4	♂ 9.5 ± 3.11	
	5	♀ 10.8 ± 4.32	879.2 ± 718.6
Control	5	♂ 8.4 ± 1.52	
	4	♀ 10.0 ± 1.41	1268.8 ± 358.7

* Mean ± Standard deviation

The effect of tagging on the larval activity did not seem important (Table 3.35) since the time from dropping until the larvae straightened and from there until the larvae escaped from the petri dish, followed similar patterns in both groups of larvae.

TABLE 3.35 Effect of Tagging on Larval Behaviour

Time (min.)	Number of larvae that straightened after dropping		Number of larvae that escaped out of the dish	
	Control	Wire	Control	Wire
0 - 3.0	5	3	1	2
3.1 - 6.0	3	4	3	2
6.1 - 9.0	1	2	3	2
9.1 - 12.0	2	2	0	3
12.1 - 15.0	1	0	0	0
>15.1	6	7	6	3
TOTAL	18	18	13	12

3.4.3.2 Tag recovery

In both releases the recovery of tags was very high being 95 and 90% for the first and second released respectively (Table 3.36). Most of the tags were in the recovered pupae. The rest were in the remains of larvae and also bare wire with no sign of larvae; the reason for this high percentage of recovery will be discussed later.

All recovered pupae were invariably beneath brussels sprouts plants, mainly in the area where senescent leaves touched the ground or fallen leaves

TABLE 3.36 Details of Tag Recovery

Release number	Number of larvae released	tags found in			Tags lost	% recovery
		pupae	rest of larvae	alone		
1	20	17	1	1	1	95.0
2	20	11	5	2	2	90.0

were present. This may have been due to the fact that the plot was relatively weed-free so the only shelter was provided by the brussels plants and the soil beneath the plants was also softer.

3.4.3.3 Larval dispersal and mortality

Once left on top of the release plant, the larvae soon hid away inside the head and neighbouring leaves. Some larvae abandoned the plant during the night, while others remained for at least two days. In the ground they stayed hidden during the day underneath fallen leaves, senescent ground touching leaves or partially buried, moving about at night during one or two days before setting down to pupate.

The average distances at which pupae were found from the release point were 256.8 and 229.0 cm for releases No. 1 and 2 respectively (Table 3.37).

The maximum distance was about 10 mts. A bare wire was recovered during the second release 1344 cm away.

TABLE 3.37 Larval Dispersal of M. brassicae Tagged with Radioactive Ir - Pt Wires

Release number	Number of larvae released	Number of pupae recovered	Dispersal from release point	
			$\bar{x}$ ± S.e	range
1	20	17	256.8 72.0	6.0 - 980.0
2	20	11	229.0 57.5	27.0 - 577.0

The distribution of the places of pupation or where wires were found are presented in Figs. 3.9 and 3.10, which together with the above-mentioned Table clearly show that the larvae tended to pupate near the release plant. It should be said that the dispersal was not hampered by ground vegetation as the plot was relatively weed-free.

Because of the satisfactory results obtained in the laboratory and the fact that only larvae in healthy condition were taken to the field, it was assumed that the mortality or disappearance of larvae was due to predators. Dispersal out of the plot was discounted as a cause of losses because of the low range of dispersal, however, an area two meters wide around the plot was also searched.

The remains of a total of six larvae were found in both treatments and in addition 3 bare wires were recovered; only three wires were lost (Table 3.36). Of the six larvae three had the appearance of those killed by carabids during feeding trials while the other three seemed to have been chopped, leaving in each case the rear end of the larva with the wire still inside. Near two of the larvae, excrements were found which were identified as probably belonging to shrews by Mr. L. Warner. It is not known why the

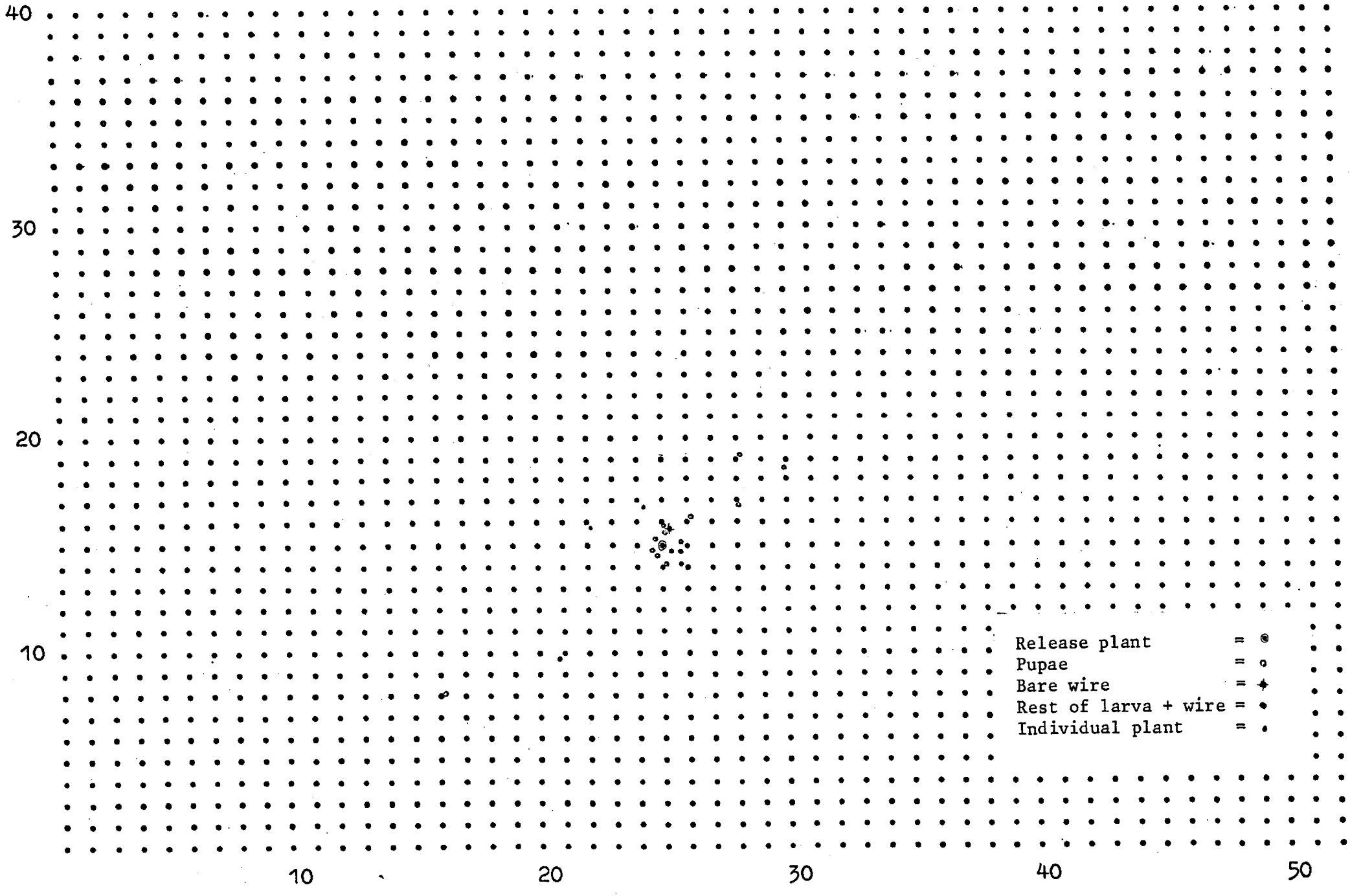


Figure 3.9. The distribution of radioactive tags in the brussels sprouts field. 1st release.

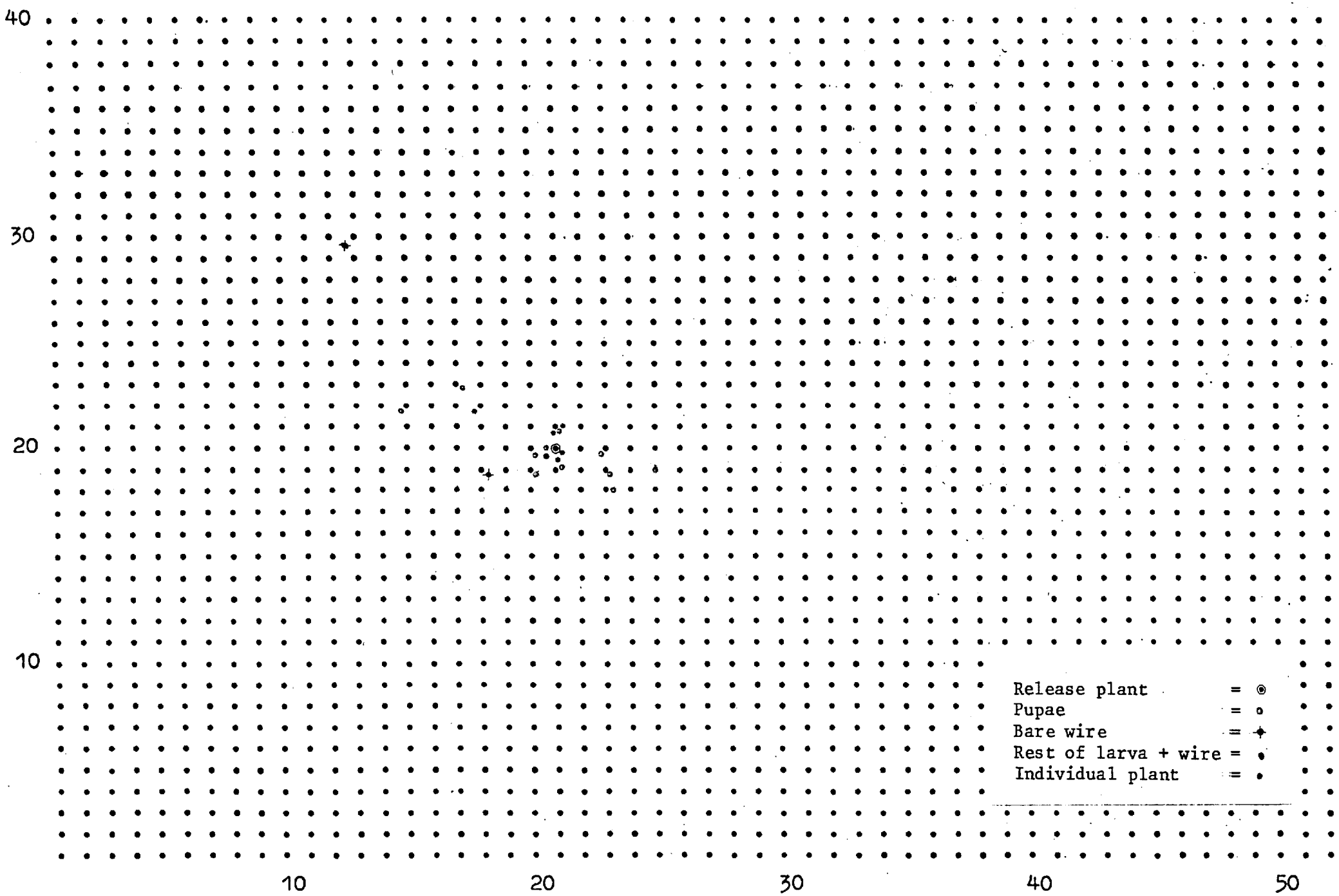


Figure 3.10. The distribution of radioactive tags in the brussels sprout's field. 2nd release

whole larvae was not consumed, but the voracious way of eating of the shrews perhaps might account for this. Shrew trapping was undertaken in an attempt to observe the way in which they attack and devour caterpillars; unfortunately, none was trapped.

In the case of the three bare wires found laying on the ground it is impossible to be certain of the kind of predators responsible. A carabid could have killed a caterpillar, consuming only part of it, leaving the rest to other predators until only the tag was left; perhaps carabids could not swallow the wire. If so then the missing wires might have been lost to small mammals, which after foraging inside the plot moved elsewhere.

In summing up, it may be said that according to our results, the dispersal distance of the fully-grown caterpillars after leaving the plant seem to be rather short. Predation of those caterpillars before entering the soil to pupate might be important, since a total loss of 30% could be attributed to them.

3.5 Section General Discussion

Populations of Mamestra brassicae (or any other insect) under field conditions are subject to a number of different mortality factors which interact and affect each other as well as M. brassicae. Those factors are responsible for the regulation of the population and hence for the greater or lesser importance of the species as a pest. It is difficult to isolate the actual effect of each factor; for instance temperature will affect the rate of development of M. brassicae and also that of its predators and parasites and the rate of growth of the host plant; therefore it is difficult to assess the direct effect of temperature alone. Nevertheless, estimates

of the effect of mortality factors may be obtained by isolating one or more factors. This "exclusion" technique was used in the present investigation to assess the importance of ground predators, airborne predators, parasites and rainfall. The advantage of this method is that by varying the characteristics of the devices certain enemies may be allowed in while others are excluded. However, this "exclusion" technique is criticised on the grounds that the dispersal of the prey is prevented, and the physical environment is modified by the exclusion devices (Kiritani and Dempster, 1972). The first drawback was in part ameliorated by using metal enclosures big enough to enclose 5 plants thus allowing some movement of the larvae from the original plant, if they happen to leave it, except for the "all excluded" treatment where only one plant was caged. Of the devices used only the cages excluding all natural enemies and rainfall may have altered the microclimate. In those cages light and wind speed were reduced but were acceptable (Salinas, 1972).

Some authors have reported on the general pattern of age-specific mortality of M. brassicae in field conditions (Ito and Miyashita, 1955; Hirata, 1963c, 1966b). More recently Oku and Kobayashi (1973b; 1974, a, b, c, d, e) published a more detailed study of the different mortality factors and its influences on the population trends in the field.

All previous authors and also our findings showed a remarkably high mortality during egg and early larval stages. The shape of the survivorship curves is thus concave, type C of Deevey (1947). This type of survivorship curve seems to be the most frequently observed for lepidopterous surface feeders which deposit many eggs in an egg mass (Kanamitsu, 1962; Kokubo, 1965; see Ito 1959 for further examples). This conspicuous decrease in number would be expected since the adult lays unprotected egg masses on the

surface of the host plant (Ito, 1959).

The average mortalities during the two years study were 45.5 and 84.2 per cent for the egg and first larval instar respectively.

Predation, parasites and climatic factors have been given as the causes for the egg mortality by those authors mentioned above.

Among the major egg mortality factors in our study was dislodgement of the egg masses. This varied from 4.0 to 18.2%, which was probably due to the egg masses falling off the leaves brought about by the daily changes in leaf turgidity, as the plants were subjected during both summers to very hot and dry conditions. Oku et al. (1973b, 1974a) have suggested that some of the egg disappearances found by them were attributable to dislodgement, in this case, caused by the egg masses falling off because of the fast growing rate of the leaf of the sugar beet plants.

Disappearance, partial or complete, of the egg masses was the major mortality factors. Several factors might have been operating but it was not possible to allocate the losses specifically; it is possible, however, that most of them were due to coccinellids, as the disappearances were higher during the peak period of coccinellids abundance. Dislodgement could also have made up some of these losses. Disappearance of egg masses have been found by Hirata (1965) and Oku et al. (1973b, 1974a) to be due in part to older larvae feeding on egg bearing leaves, this, however, was not our case.

Eggs parasitized by Trichogramma and Telenomus, mainly the former, were found during the study but the percentage of parasitism was rather low, not exceeding 6.8%. Of the egg parasites, Trichogramma is regarded as

important in eastern Europe and has been known to produce very high levels of parasitism, which has encouraged some attempts to use releases of the parasite in integrated control programmes against Mamestra, in some cases with success (Karadzhov, 1970; Degtyarev, 1970 and Garnaga, 1975).

Predation by coccinellids, sucking insects and thrips was detected, although only the first mentioned was important destroying in one case as much as 24.6% of the egg population. Mortality by coccinellids ranked second behind egg disappearance in importance.

As indicated, mortality in early instars, particularly the first instar, was very high. Ito and Miyashita (1955) suggested that predation and climatic factors can reduce the number of younger larvae. Oku et al. (1973b, 1974a) found that although total mortality during early instars exceeded over 70% every generation, they were not able to explain the causes of mortality and referred to them as "unknown". In our investigation however, a lot of the losses was caused by syrphids and coccinellids. The importance of syrphid predation during early instar caterpillars has also been reported in Pieris rapae by Dempster (1967) and Ashby (1974). Coccinellids were important mainly in 1976, during the first field experiment, as the population of the coccinellids, especially of C. 7-punctata was unusually high.

During this period other mortality factors like spiders and rain were acting at a very low intensity. However, this may not be the case under different circumstances, for instance, in Bulgaria Dochkova (1972) found a direct proportional dependence between the rain and the density of the 2nd generation during three consecutive years. However, a correlation does not imply a direct causal relationship between the two.

Mortality during middle and late instars was mainly due to predators (wasps, carabids, etc.) parasites and diseases but most of it was due to unknown causes. Nevertheless, comparison of treatments where ground predators were excluded with birds, ground predators excluded suggested that wasps were probably the main contributors to the unknown causes. Birds seemed to have been more important later in the season.

The dispersal of fully-fed caterpillars seems to be restricted. Our evidence suggests that they do not disperse over long distance but rather stay near the original host plant, however, this might not be so during outbreaks. Before settling down to pupate they remain on the ground for a period of time, in our case for a couple of days. This behaviour might allow certain predators like large carabids and small mammals to cause losses, which might be important.

This restricted dispersal could be one of the reasons why the population does not build up to considerable numbers in places where large plots are used. Most of the overwintering pupal population would be found inside the plot and during autumn might be destroyed by cultivation, and also by exposure to winter climatic conditions and predators, possibly by birds. Oku et al. (1973b) concluded that ploughing was the main cause of the breakdown of an outbreak population at Morioka, Japan. In small plots such as gardens, allotments and small horticultural holdings, where the ratios of perimeter to total area is large, there is greater chance of a high proportion of the population going to pupate outside the cultivated area which would ensure a higher proportion surviving. This is in part supported by Jones and Jones (1968) who cited Mamestra as most common in gardens and allotments. Minimal insecticide application in small plots might also be a contributory factor.

King (1968) working with Pionia forficalis L. suggested that the production of Brassica crops for seed presents a condition where numbers may build up to a temporary high level, primarily owing to the prerequisite of leaving the plants in the soil for a second season with no losses due to ploughing; this might also apply to M. brassicae.

GENERAL DISCUSSION

Mamestra brassicae L. has a wide geographic range. It is found almost everywhere in the paleartic and many subtropical regions. This common occurrence over such a vast area is undoubtedly a proof of its remarkable success in adaptation. This is especially noticeable in the inherited variation in the pattern and kind of diapause observed along a geographic gradient of climatic conditions.

In spite of the extreme diversity of climatic conditions the species is a serious pest almost everywhere. It has a high potential for increase which is observed in field conditions in the frequent mass outbreaks reported in the literature, thus its population density seems to fluctuate between wide ranges. In this respect M. brassicae seems to be also adapted to unfavourable conditions experienced in overpopulated areas through modification of its subsequent physiology and development. This functional adaptation (Phase variation) to varying population density may provide individuals with a better chance of survival as well of more effective reproduction. More extensive and detailed studies are needed to understand the nature of this type of variation and its relation to population dynamics.

It is not possible to formulate far-reaching conclusions on population regulation of M. brassicae in England because of the limitations of our study. For example the high mortality of the eggs and early larval instars may not necessarily be more important than low ones in its effects on population trends.

There was some indication that a decrease in mortality during early stages would probably be compensated for by an increase in

mortality during the middle and late instars, which would then help prevent wide fluctuations in larval population.

Although the study was carried out in two very dry summers, it seems, however, that the observed high level of mortality of eggs and larvae is typical for England.

From the economic point of view, the high mortality suffered by eggs and young larvae, is very important as it will prevent a large number of caterpillars reaching the last two instars, notably the last one which is the most voracious, thus avoiding appreciable damage to the crop. In this respect any factor enhancing mortality during the early development should be encouraged and indeed taken into account in any integrated control programme for this pest.

SUMMARY

The research on Mamestra brassicae L. is divided into three sections covering aspects of the biology, effect of larval density on larval and pupal characters, and the study of mortality of egg and larval stages under field conditions.

SECTION 1

1. On brussels sprout plants the eggs are laid mainly in the intermediate region of the plant, on the underside of the leaf, and usually near the edges. After hatching the larvae remain in an aggregation and slowly, usually after the first moult, they disperse to the other leaves. The early instars are mainly located on that intermediate region but as they grow, they move up to the head of the plant; later instar may move to the ground underneath the plant.

2. Between 15 and 29°C the rate of growth of the immature stages was linear and the survival rate was very high.

3. An artificial diet was compared with Brussels sprout leaves for rearing larvae.

4. Males reared on brussels sprouts lived longer than did those reared on the artificial diet.

5. On both diets females showed large variations on fertility. High fertility type females (mean fertility 86.5%) were shorter-lived

than low fertility type (mean fertility 7.7%).

6. High fertility moth laid significantly more eggs than their counterparts. Diet did not have a significant effect on the fecundity of either types of females.

7. Preoviposition, oviposition and postoviposition periods were shorter in high fertility moths.

8. Multiple mating was observed in both types of females. On the basis of the number of spermatophores the average number of matings was significantly lower in the high fertility types.

SECTION 2

1. The habit of egg mass laying seems to be beneficial during the hatching and first instar. Hatching is very well synchronized within an egg mass which might provide the opportunity for aggregation of the hatchlings and consequently to early initiation of feeding. Compared with isolated larvae, first instar larvae perform better in groups; their mortality is less and they are heavier at the first moult. Overcrowding was harmful.

2. When reared in crowds, the larvae became darkened and increased their rate of development. The weight of pupae decreased significantly at high density whereas sex ratio, the rate of diapause and the length of the pupal period were not influenced. Compared with isolated individuals, crowded larvae were heavier during early instars but lighter during late instars.

3. Dark coloured individuals were more active and reacted readily to external disturbance. They also showed greater resistance to starvation and desiccation, and there was some evidence that they can tolerate some artificial stresses, for example D.D.T., better than their pale counterparts.

SECTION 3

1 Studies on the mortality of egg and larval stages carried out during 1975 and 1976, showed that the survivorship curves were concave in shape, corresponding to type C of Deevey (1947).

2. The average mortality during the two years study for the egg stage was of 45.5%

3. The main egg mortality factors in order of importance were disappearance, predation, dislodgement and parasitism. Disappearance varied from 7.7 to 24.8%. Predation was almost exclusively made by coccinellids and varied from 6.4 to 24.6%. Dislodgement ranged from 4.0 to 18.2 and seemed to have been caused by the changed in leaf turgidity. Parasitism was by Trichogramma and Telenomus, mainly the former, but never exceeded 6.8%.

4. Mortality during the larval stage was very high, in average 84.2 of this mortality occurred during the first instar and was primarily due to arthropods predators, notably Syrphids and Coccinellids. Late instar larvae suffered mortality caused by diseases, ground predators, and wasps.

5. Fully-grown larvae tended to stay near their original plants, and the average dispersal distance of 28 larvae with radioactive tags was 243 cm.

6. The high mortalities observed during egg and early larval stages prevent a large number from reaching the last two instars, especially the last one which is the most destructive, thus economic damage is small. Ploughing may play an important role in the control of M. brassicae.

ACKNOWLEDGEMENTS

I wish to express my gratitude to my supervisor Dr. G. Murdie for his guidance, patience and helpful advice throughout the work and his criticisms of the manuscript.

For determinations of insect material I thank Messrs. W. R. Dolling (Hemiptera), P. C. Barnard (Chrysopidae), M. E. Bacchus (Staphylinidae), K. G. V. Smith (Syrphidae), D. J. Carter (*Agrotis* species, *Discestra trifolii* and *Amphipyra tragopoginis*), P. O. Hillyard (Arachnida).

I would like to express my thanks to the following:
Dr. D. J. Galley for his help and interest with the experiments with radioactive material.

Mr. G. S. Gill for his help and guidance with the serological test.

Mr. L. Warner for the construction of the penetrometer.

Mr. H. Deviit for the photographs of the different stages of *M.* brassicae, and

Mrs. J. A. Kent and Miss C. Collins for typing the thesis.

My appreciation is due to Drs. F. Fernandez Yepez and C. J. Rosales for their encouragement throughout.

I am thankful to the technical staff, librarian and gardening staff of the field station, and especially to my friends who helped me in many different ways.

My sincere thanks go to my wife Heidy for her encouragement and unfailing support.

Finally, the financial assistance by the Consejo de Desarrollo Cientifico y Humanistico de la Universidad central de Venezuela is gratefully acknowledged.

REFERENCES

ABDINBEKOVA, A. A.; AKHMEDOV, R. M. & KULIEVA, KH. Z. (1976). Effect of temperature and photoperiod on the development of the noctuid *Barathra brassicae* L. in Azerbaidzhan. *Zoologischeskii Zhurnal.* 55: 378-386 (In Russian).

* ADASHKEVICH, B. P. (1975). Integrated protection of cabbage. Experiment and problems. *Zashchita Rastenii* 5: 27-28 (In Russian).

AFONSKAYA, N. A. (1966). The bionomics of the cabbage moth (*Barathra brassicae* L.) in the Omsk region. *Nauch. Trudy omsk. sel'. -Khoz. Inst.* 1: 25-34 (In Russian).

ANKERSMIT, G. W. & VAN DER MEER, F. Th. M. (1973). Studies on the sterile male technique as a means of control of *Adoxophyes orana* (Lepidopt., Tortricidae). 1. Problems of mass rearing (crowding effects). *Neth. J. Pl. Path.* 79: 54-61.

ASHBY, J. W. (1974). A study of arthrop predation of *Pieris rapae* L. using serological and exclusion techniques. *J. Anim. Ecol.* 43: 419-425.

AUDCENT, H. (1942). A preliminary list of the host of some British tachinidae (Dipt.). *Trans. Soc. Brit. Ent.* 8: 1-42.

BALACHOWSKY, A. (1972). Entomologie Appliquee a l'Agriculture. Tome II. Lepidopteres. Massen et Cie, Editeurs, Paris.

BALACHOWSKY, A. & MESNIL, L. (1936). Les insectes nuisibles aux plantes cultivees. Vol. II. Paris.

BALDWIN, W. F. & COWPER, G. (1969). The use of radioactive Platinum - Iridium wire (IR-192) as an internal tag for tracing insects. *Can. Ent.* 101: 151-152.

* BIROVA, H. (1973). On knowledge of the natural enemies (Hymenoptera and Diptera) of some injurious Noctuids. *Biologicke Prace* 19: 79-81 (In Slovakian).

BOBINSKAYA, S. G. (1971). Physiological differences in the state of *Hadena sordida* Bkh. populations (Lepidoptera, Noctuidae) at different levels of abundance of the species. *Ent. Rev. Washington D.C.* 50(3): 285-289.

BONNEMAISON, L. (1959). Remarques sur la diapause de la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). *Bull. Soc. ent. France* 64: 142-151.

BONNEMAISON, L. (1960a). Elimination de la diapausa chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). *Bull. Soc. ent. France* 65: 73-78.

BONNEMAISON, L. (1960b). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). I. Action de la temperature. *Bull. Soc. ent. France* 65: 196-206.

BONNEMAISON, L. (1961a). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). II. Influence de la lumiere sur les images et sur l'accouplement. *Bull. Soc. ent. France* 66: 62-70.

BONNEMAISON, L. (1961b). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). III. Influence de la diapause. *Bull. Soc. ent. France* 66: 128-133.

BONNEMAISON, L. (1961c). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). IV. Influence de l'age de la femelle sur la proportion de diapause dan sa descendance. *Bull. Soc. ent. France* 66: 134-137.

BONNEMAISON, L. (1961d). Influence de la temperature et de la photo-periode appliguees aux chrysalides, aux chenilles, aux oeufs et aux imagos de *Mamestra brassicae* (L.) sur la croissance et la diapause. *Bull. Soc. ent. France* 66: 226-232.

BONNEMAISON, L. (1962a). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). V. Influence de l'alimentation et de l'effet de groupe. *Bull. Soc. ent. France* 67: 15-24.

BONNEMAISON, L. (1962b). Etude de quelques facteurs de la fecondite et de la fertilite chez la noctuelle du chou (*Mamestra brassicae* L.) (Lep.). VI. Reserarches sur 'l'effet de groupe' chez les femelles. *Bull. Soc. ent. France* 67: 146-154.

BOREHAM, P. F. L. & GILL, G. S. (1973). Serological identification of reptile feeds of *Glossina*. *Acta trop.* 30(4): 356-365.

BOWDEN, J. (1977). Rept. Rothamsted Exp. Stn. for 1976. pt. 1 : 124.

BROWN, E. S. (1962). The African army worm *Spodoptera exempta* (Walker) (Lep. Noct.), a review of the literature. *Commonw. Inst. Ent., Lond.* : 1-57.

BROWN, E. S. & SWAINE, G. (1966). New evidence on the migration of moths of the African army worm, *Spodoptera exempta* (Walker) (Lepidoptera, Noctuidae). *Bull. ent. Res.* 56: 671-684.

BUROV, V. N. & MOKROUSOVA, Y. P. (1970). The regulatory role of insect population density as exemplified by the cabbage moth, *Barathra brassicae* L. (Lepidoptera, Noctuidae). *Ent. Review, Wash.* 49: 147-150.

BUTOVSKII, A. (1965). Control of the cabbage moth. *Zashch. Rast. Vredit. Bolez.* 6: 29-30 (In Russian).

CALCAGNOLO, G. & SAUER, H. F. G. (1955). O fe nomeno de diversidade de coloracao em lagartas do curuquere (*Alabama argillacea* Hubner). *O Biologico.* 21: 77-86.

CAMERON, A. E. (1939). Insect and other pests of 1938. *Trans. Higl. Agric. Soc. Scot.* 51: 136-174.

CAMPRAG, D. (1970). The occurrence and injuriousness of larvae of the genus *Mamestra* (Noctuidae, Lepidoptera) on sugar-beet in some districts of the Vojvodina. In: *Proc. 3th Int. Symposium Sugar beet protection. Novisad, Yugoslavia* Sept. 1969.

CAYROL, R. M. (1957). L'effet de groupe sur le developpement des larvae de *Plusia gamma* (Lepidoptera, Noctuidae) en correlation avec differents facteurs du milieu. *C. r. hebd. Seanc. Acad. Sci., Paris* 245: 580-581.

CHAUVIN, R. (1952). L'effet de groupe. In "*Structure et physiologie des societes animales*". Colloq. Intern. C.N.R.S., Paris, No. 34: 81-90.

CHAUVIN, R. (1967). *The world of an insect.* World Univ. Libr. London.

DANILEVSKII, A. S. (1965). *Photoperiodism and seasonal development of insects.* Oliver & Boyd, Edinburgh.

DANTHANARAYANA, W. (1975a). The bionomics, distribution and host range of the light Brown Apple Moth, *Epiphyas postvittana* (Walk.) (Tortricidae). *Aust. J. Zool.* 23: 419-437.

DANTHANARAYANA, W. (1975b). Factors determining variation in fecundity of the light Brown Apple Moth, *Epiphyas postvittana* (Walk.) (Tortricidae). *Aust. J. Zool.* 23: 439-451.

DAVID, W. A. L. & GARDINER, B. O. C. (1962). Observations on the larvae and pupae of *Pieris brassicae* (L.) in a laboratory culture. *Bull. Ent. Res.*, 53: 417-436.

DAVID, W. A. L. & GARDINER, B. O. C. (1966). Rearing *Mamestra brassicae* (L.) on semi-synthetic diets. *Bull. Ent. Res.*, 57: 137-142.

DEEVEY, E. S. (1947). Life tables for natural population of animals. *Quart. Rev. Biol.* 22: 283-314.

* DEGTYAREV, A. G. & SHARUDA, G. I. (1970). *Trichogramma* and the cabbage moth. *Zaschchita Ratenii.* 15: 13-14.

DEMPSTER, J. P. (1967). The control of *Pieris rapae* with D.D.T. I. The natural mortality of the young stages of *Pieris*. *J. appl. Ecol.* 4: 485-500.

DEMPSTER, J. P. (1971). The population ecology of the Cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera, Arctiidae). *Oecologia* 7: 26-67.

* DOCHKOVA, B. (1969). The cabbage moth on sugar beet and chemicals for its control. *Rastitelna Zashchita.* 17: 30-33 (In Bulgarian).

* DOCHKOVA, B. (1971). Noctuids - dangerous pest of plants. The cabbage moth and the gamma moth. *Rastitelna Zashchita.* 19: 9-10 (In Bulgarian).

DOCHKOVA, B. (1972). Some ecological studies on *Mamestra brassicae* L. (Lepidoptera, Noctuidae). *Gradinarska i Lozarska Nauka.* 9: 77-86 (In Bulgarian).

DOLIDZE, G. V. (1957). The study of problems of the ecology of the cabbage moth (*Barathra brassicae* L.) in Georgia. *Trud. Inst. Zashch. Rast.,* 12: 79-100 (In Georgian).

DOULL, K. M. (1953). Phase coloration in Lepidopterous larvae. *Nature, Lond.* 172: 813-814.

DROOZ, A. T. (1965). Colour studies of reared elm spanworm larvae and pupae. *Ann. Ent. Soc. Amer.* 59(3): 568-573.

DROOZ, A. T. (1966). Some effects of rearing density on the biology of the elm spanworm. *Can. Ent.,* 98(1): 83-87.

DRUZHELYUBOVA, T. S. (1976). Temperature and light as factors affecting development and behaviour in geographic populations of *Agrotis ypsilon* Rott. (Lepidoptera, Noctuidae). *Ent. Rev., Wash.,* 55: 9-14.

DUSAUSSOY, G. (1964). L'Elevage permanent de *Mamestra (Barathra) brassicae* L. comme insecte test de preparations pathogenes ou insecticides. *Ann. Epiphyties.* 15(2): 171-192.

EVANS, H. F. (1976). The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. *Ecol. Ent.* 1: 163-169.

FAST, P. G. (1964). Insect lipids: A review. *Memoirs Ent. Soc. Can.* No. 37.

FAURE, J. C. (1943a). The phases of the lesser army worm, *Laphygma exigua* Hübn. *Fmg. S.Afr.* 18: 69-78.

FAURE, J. C. (1943b). Phase variation in the army worm, *Laphygma exempta* Walk. *Sci. Bull. Dep. Agric. For. Un. S. Afr.* 234.

FERRO, D. N. & HARWOOD, R. (1973). Intraspecific larval competition by the codling moth, *Laspeyresia pomonella*. *Environ. Ent.* 2(5): 783-789.

* GARNAGA, N. G. (1975). Integrated control of cabbage pests. *Zashchita Rastenii.* 7: 24 (In Russian).

GAST, R. T. (1961). Factors involved in differential susceptibility of Corn Earworm larvae to DDT. *J. econ. Ent.* 54: 1203-1206.

GEHRING, R. D. & MADSEN, H. F. (1963). Some aspects of the mating and oviposition behavior of the Codling Moth, *Carpocapsa pomonella*. *J. Econ. Ent.* 56: 140-143.

GHENT, A. W. (1960). A study of the group-feeding behaviour of larvae of the Jack pine sawfly, *Neodiprion pratti banksianae* Roh. *Behaviour* 16: 110-148.

GRASSE, P. (1946). Societes animales et effet de groupe. *Experientia.* 2: 77-116.

GRISON, P. (1948). Effet du groupement sur la croissance des Chenilles du Bombyx Cul-brun (*Euproctis phaeorrhaea* Don., Lep. Liparidae). *C. r. Seans. Soc. Biol.*, 142: 610-612.

GRUYS, P. (1970). Growth in *Bupalus piniarius* (Lepidoptera; Geometridae) in relation to larval population density. *Verh. 1 of Res. Inst. Nature Management.* 1-127.

GUPPY, J. C. (1969). Some effects of temperature on the immature stages of the armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), under controlled conditions. *Can. Ent.* 101: 1320-1327.

* GYORY, J. & REICHART, G. (1964-65). Investigations on the food of birds during mass occurrence of major pests of forestry and agriculture. *Aquila*, 71-72: 67-98 (In Hungarian).

HAMMOND, H. E. & SMITH, K. G. V. (1953). On some parasitic Diptera and Hymenoptera bred from lepidopterous hosts; pt. 1. *Entomologist's Gazette* 4: 273-279.

HANNA, H. M. & AZAB, S. G. (1973a). Effects of larval population density on weights and components of *Spodoptera exigua* (Hb.) (Lepidoptera, Noctuidae). *Bull. Soc. ent. Egypte.* 57: 55-65.

HANNA, H. M. & AZAB, S. G. (1973b). Effects of larval crowding on the biology of *Spodoptera exigua* (Hb.) and *Nadiasa acaciae* Klug. (Lepidoptera). *Bull. Soc. ent. Egypte.* 57: 325-334.

HARCOURT, D. G. (1963a). Major mortality factors in the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). *Mem. ent. Soc. Can.* 32: 55-66.

HARCOURT, D. G. (1963b). Biology of cabbage caterpillars in eastern Ontario. *Proc. ent. Soc. Ont.*, 93: 61-75.

HARCOURT, D. G. (1966). Major factors in survival of the immature stages of *Pieris rapae* (L.). *Can. Ent.* 98: 653-662.

HIRATA, S. (1954). The phase variation observed in the army worm, *Barathra brassicae* L. I. The relations between the rearing density, and the variation of body colour of sixth-instar larva, weight of pupae, and rate of diapause. *Oyo-Dobuts. Zasshi.* 19: 41-46 (In Japanese).

HIRATA, S. (1956). On the phase variation of the Cabbage Armyworm, *Barathra brassicae* L. II. Influence of larval density upon the variations observed in the adult stage. *Res. Popul. Ecol.* 3: 79-92.

HIRATA, S. (1957). On the phase variation of the Cabbage Armyworm, *Barathra brassicae* L. III. Influence of larval density on body color of the 4th and 5th instar larvae. *Bull. educ. Fac. Hirosaki Univ.* 3: 50-56 (In Japanese).

HIRATA, S. (1957). On the phase variation of the Cabbage Armyworm, *Barathra brassicae* L. IV. Some regulating mechanisms of development in the crowded population. *Jap. J. appl. Ent. Zool.* 1: 204-208 (In Japanese).

HIRATA, S. (1960). On the phase variation of the Cabbage Armyworm, *Barathra brassicae* L. V. The effect of food plant on the density dependent variations in the larval and pupal stages. *Op. cit.* 4: 102-110.

HIRATA, S. (1962a). On the phase variation of the Cabbage Armyworm, *Barathra brassicae* L. VI. Phase variation in larval characters under different conditions of density and temperature. *Jap. J. Ecol.* 12: 223-228 (In Japanese).

HIRATA, S. (1962b). Comparative studies on the population dynamics of important lepidopterous pests on cabbage. I. Seasonal fluctuations in the numbers of eggs of the common cabbage butterfly, *Pieris rapae crucivora* (Boisduval), the asiatic common looper, *Plusia nigrisigna* Walker, and the Cabbage Armyworm, *Barathra brassicae* Linne. *Jap. J. appl. Ent. Zool.* 6: 8-14 (In Japanese).

II. On the habits of oviposition of *Pieris rapae crucivora*, *Plusia nigrisigna* and *Mamestra (Barathra) brassicae* on cabbage plants. *Op. cit.* 6: 200-207 (In Japanese).

HIRATA, S. (1963a). On the phase variation of the Cabbage Armyworm, *Mamestra (Barathra) brassicae* (L.). VII. Effect of larval crowding on food consumption and body weight. *Jap. J. Ecol.*, 13: 125-128 (In Japanese).

HIRATA, S. (1963b). On the phase variation of the Cabbage Armyworm, *Mamestra brassicae* (L.). VIII. Effect of larval crowding on the development and body colour of larvae when food is changed. *Op. cit.* 13: 211-216 (In Japanese).

HIRATA, S. (1963c). Comparative studies on the population dynamics of the important lepidopterous pests on cabbage. III. Seasonal trends of age-structure in population of *Pieris rapae crucivora, Plusia nigrisigna* and *Mamestra brassicae*. *Jap. J. appl. Ent. Zool.* 7: 7-13 (In Japanese).

HIRATA, S. (1965). Comparative studies on population dynamics of the important lepidopterous pests on cabbage. IV. Some observations on egg population of *Mamestra brassicae* (L.) in cabbage fields. *Op. cit.* 9: 151-161 (In Japanese).

HIRATA, S. (1966a). On the phase variation of the cabbage Armyworm, *Mamestra (Barathra) brassicae* (L.). IX. Phase variations in field populations. *Jap. J. Ecol.* 16: 140-145 (In Japanese).

HIRATA, S. (1966b). Comparative studies on population dynamics of the important lepidopterous pests on cabbage. V. Fluctuation in population size of the second generation of *Mamestra brassicae* (L.) in a cabbage field. *Jap. J. appl. Ent. Zool.* 10: 17-23 (In Japanese).

HIRATA, S. (1967). Comparative studies on population dynamics of the important lepidopterous pests on cabbage. VII. Distribution of larvae and pupae of *Pieris rapae crucivora* Boisd., *Mamestra brassicae* (L.) and *Autographa nigrisigna* Walk. on each individual plant of cabbage. *Op. cit.* 11: 107-113.

HITCHCOCK, S. W. (1961). Egg parasitism and larval habits of the Orange-Striped Oakworm. *J. econ. Ent.* 54: 502-503.

HODJAT, S. H. (1970). Effects of crowding on colour, size and larval activity of *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Ent. exp. & appl.* 13: 97-106.

HOFMANN, C. (1934). Der Einflusz von Hunger und engem Lebensraum auf das Wachstum und die Fortpflanzung der Lepidopteren. *Z. angew. Ent.* 20: 51-84.

HOWE, R. W. (1967). Temperature effects on embryonic development in insects. *Ann. Rev. Ent.* 12: 15-42.

ICHINOSE, T. (1955). The toxic effect of DDT to the larval instars of the cabbage armyworm, *Barathra brassicae* L. *Appl. Ent. (Japan).* 11: 1-6.

IKEMOTO, H. (1971). On the black pigment of the larval integument of the armyworm, *Leucania separata*. *Botyu-Kagaku.* 36: 128-131.

IONESCU, M. (1966). Combaterea larvelor de buha verzei (*Mamestra brassicae* L.). *Anal. Sect. Prot. Pl. Inst. cent. Cerc. agric.* 2: 261-267 (In Rumanian).

ISAACSON, D. L. (1973). A life table for the cinnabar moth, *Tyria jacobaeae*, in Oregon. *Entomophaga,* 18(3): 291-303.

ISHIKURA, H. & OZAKI, K. (1958). Continuous mass rearing of the cabbage armyworm, *Barathra brassicae* Linnaeus and the studies on the resistance of the reared armyworm to certain insecticides. *Bull. natn. Inst. agric. Sci. Tokyo.* 10: 1-42.

ISLAM, B. N. & SARDAR, M. A. (1971). Studies on the phase variation in Jute Hairy caterpillar, *Diacrisia obligua* Walker (Lepidoptera: Arctiidae). *Pakistan J. Zool.,* 3(1): 101-121.

ITO, Y. (1959). A comparative study on survivorship curves for natural insect populations. *Jap. J. Ecol.* 9: 107-115.

ITO, Y. & MIYASHITA, K. (1955). Dispersion and mortality rate of fall brood population of cabbage armyworm in a chinese cabbage field. *Oyo-Kontyu.* 11: 144-149.

ITO, Y. & MIYASHITA, K. (1968). Biology of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) in Japan. V. Preliminary life tables and mortality data in urban areas. *Res. Popul. Ecol.* 10: 177-209.

ITO, Y.; MIYASHITA, K. & YAMADA, H. (1968). Biology of *Hyphantria cunea* Drury in Japan. V. Effect of temperature on development of immature stages. *Appl. Ent. Zool.* 3: 163-175.

IWAO, S. (1962). Studies on the phase variation and related phenomena in some lepidopterous insects. *Mem. Coll. Agric. Kyoto Univ.* 84: 1-80.

IWAO, S. (1967). Resistance to starvation of pale and black larvae of the armyworm, *Leucania separata* Walker (Lepidoptera: Noctuidae). *Botyu-Kagaku.* 32: 44-46.

IWAO, S. (1968). Some effects of grouping in Lepidopterous insects. In "*L'Effet de groupe chez les animaux*". Collog. Intern. C.N.R.S., Paris, No. 173: 185-212.

JACOBSON, L. A. (1970). Laboratory ecology of the red-backed cutworm, *Euxoa ochrogaster* (Lepidoptera: Noctuidae). *Can. Ent.* 102: 85-89.

JOLY, P. (1972). The hormonal mechanism of phase differentiation in locust. *Proc. Intern. Study Conf. Current and Further Problems of Acridiology, London.* pp. 79-84.

JOLY, P. & MEYER, A. S. (1970). Action de l'hormone Junenile sur *Locusta migratoria* (Orthoptere) en phase gregaire. *Arch. Zool. exp. gen.* 111: 51-63.

JOLY, L. & JOLY, P. (1974). Comparison de la phase gregaire et de la phase solitaire de *Locusta migratoria migratoides* (Orthoptere) du point de vue de la teneur de leur hemolymphe en hormone Junenile. *Compt. Rend. Acad. Sci. Paris* 279: 1007-1009.

JONES, F. G. W. & JONES, M. G. (1974). *Pests of field crops.* 2nd ed. Edward Arnold, London.

KANAMITSU, K. (1962). Survival curves of the population of *Dendrolaimus spectabilis* Butler (Lepidoptera: Lasiocampidae). *Res. Popul. Ecol.* 4: 60-64.

* KARADZHOV, S. (1970). Cabbage moths and the possibilities of their biological control. *Rastitelna Zashchita.* 18: 14-18 (In Bulgarian).

KEY, K. H. L. (1957). Kentromorphic phases in three species of Phasmatodea. *Aust. J. Zool.* 5(3): 247-284.

KING, A. B. S. (1968). Studies of the biology and diapause of *Pionea forficalis* L., and of some factors affecting its relative abundance on Brassica crops. Ph.D Thesis. London University.

KIRITANI, K. & DEMPSTER, J. P. (1972). Different approaches to the quantitative evaluation of natural enemies. *Proc. 14th int. Congr. Ent.* 323-329.

KLOMP, H. (1966). The dynamics of a field population of the pine looper, *Bupalus piriarius* L. (Lep., Geom.). *Adv. ecol. Res.* 3: 207-305.

KOKUBO, A. (1965). Population fluctuations and natural mortalities of the pine-moth *Dendrolimus spectabilis*. *Res. Popul. Ecol.* 7: 23-34.

LEGAY, J. M. & PASCAL, M. (1951). De L'effet de groupe chez le ver á soie. *C. r. hebd. Séanc. Acad. Sci., Paris* 233: 445-447.

LEONARD, D. E. (1968). Effects of density of larvae on the biology of the gypsy moth, *Porthetria dispar*. *Ent. exp. et appl.* 11: 291-304.

LONG, D. B. (1953). Effects of population density on larvae of Lepidoptera. *Trans. R. ent. Soc. Lond.* 104: 543-584.

LONG, D. B. (1955). Observations on sub-social behaviour in two species of Lepidopterous larvae, *Pieris brassicae* L. and *Plusia gamma* L. *Trans. R. Ent. Soc. Lond.* 106(11): 421-437.

LONG, D. B. (1959). Observations on adult weight and wing area in *Plusia gamma* L. and *Pieris brassicae* L. in relation to larval population density. *Ent. exp. et appl.* 2: 241-248.

LONG, D. B. & ZAHER, M. A. (1958). Effect of larval population density on the adult morphology of two species of Lepidoptera, *Plusia gamma* L. and *Pieris brassicae* L. *Ent. exp. et appl.* 1: 161-173.

LOUGHTON, B. C.; DERRY, C. & WEST, A. S. (1963). Spiders and the spruce budworm. Dynamics of epidemics spruce budworm populations. (ed. by R. F. Morris). *Mem. ent. Soc. Can.*, 31: 249-288.

* LUCHNIK, V. N. (1926). Note on the egg parasite of *Barathra brassicae* L. *Bull. Caucasian plant Prot. Sta.* 1: 17-18 (In Russian).

LYONS, L. A. (1962). The effect of aggregation on egg and larval survival in *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae). *Can. Ent.* 94: 49-58.

MALEKI-MILANI, H. (1971). Elevage de la noctuelle du chou, *Mamestra (Barathra) brassicae* L. sur milieu artificiel. *Ann. Soc. ent. Fr. (N.S.)* 7: 39-56 (In French).

MANSOUR, M. H. & DIMETRY, N. Z. (1972). Effect of crowding on larvae and pupae of the greasy cutworm *Agrotis ipsilon* Hfn. (Lepid: Noctuidae). *Z. ang. Ent.* 72: 220-223.

MASAITIS, A. I. (1925). A note on the biology of *Barathra (Mamestra) brassicae* L. *Zashch. Rast. Vredit.* 2: 311-312 & 321 (In Russian).

MASAKI, S. (1956a). The effect of temperature on the termination of pupal diapause in *Barathra brassicae* Linne (Lepidoptera: Noctuidae). *Jap. J. appl. Zool.* 21: 97-107.

MASAKI, S. (1956b). The local variation in the diapause pattern of the cabbage moth, *Barathra brassicae* Linne, with particular reference to the aestival diapause (Lepidoptera: Noctuidae). *Bull. Facul. Agric. Mie. Univ.*, 13: 29-46.

MASAKI, S. (1958). Geographic adaptation in the seasonal life cycle of *Mamestra brassicae* (Linne) (Lepidoptera: Noctuidae). *Bull. Fac. Agric. Hirosaki Univ.*, 14: 16-26.

MASAKI, S. & SAKAI, T. (1965). Summer daiapuse in the seasonal life cycle of *Mamestra brassicae* Linne (Lepidoptera: Noctuidae). *Jap. J. Appl. Ent. Zool.*, 9(3): 191-204.

MATSUMOTO, S.; SANTA, H. & OTUKA, M. (1953). Studies on the diapause in the cabbage Armyworm, *Barathra brassicae* L. II. The effect of temperature and photoperiod on the induction of diapause. *Oyo-Kontyu* 9: 45-51 (In Japanese).

MATTHEE, J. J. (1945). Biochemical differences between the solitary and gregarious phases of locusts and noctuids. *Bull. ent. Res.* 36: 343-371.

MATTHEE, J. J. (1946). A study of the phases of the army worm (*Laphygma exempta* Walk.). *J. ent. Soc. Sth. Afr.* 9: 60-77.

MATTHEE, J. J. (1947). Phase variation in the lawn caterpillar (*Spodoptera abyssinia* Guen). *J. ent. Soc. Sth. Afr.* 10: 16-23.

MELIS, A. (1936). Contributo alla conoscenza morpo-biologica della *Polia (Mamestra) pisi* L. *Redia.* 22: 1-35.

MICHELAKIS, S. (1973). A study of the laboratory interaction between *Coccinella septempunctata* L. larvae and its prey *Myzus persicae* Sulz. M.Sc. thesis. London University.

MIYASHITA, K. (1971). Effects of constant and alternating temperatures on the development of *Spodoptera litura* F. (Lepidoptera: Noctuidae). *Appl. Ent. Zool.* 6: 105-111.

MIZUTA, K. (1960). Effect of individual number on the development and survival of the larvae of two Lymantriid species in aggregation and in scattering. *Jap. J. appl. Ent. Zool.* 4: 146-152.

MIZUTA, K. (1968). The effect of larval aggregation upon survival, development, adult longevity and fecundity of a zygaenid moth, *Artona funeralis* Butler. *Bull. Hiroshima Agric. Coll.* 3: 97-107.

MOCHIZUKI, S. & AGUI, N. (1976). Formation of black pigment in the integument of the cabbage armyworm, *Mamestra brassicae* L. in vitro (Lepidoptera: Noctuidae). *Appl. Ent. Zool.* 11(3): 258-260.

MORIMOTO, N. (1960a). Influence of density of the larval population upon the development in the cabbage butterfly, *Pieris rapae crucivora*. *Jap. J. appl. Ent. Zool.* 4: 153-158.

MORIMOTO, N. (1960b). Effect of density of larval population on some characters of larva, pupa and adult in the Rice stem borer, *Chilo suppressalis*. *Jap. J. appl. Ent. Zool.* 4: 197-202.

MORIMOTO, N. & SATO, Y. (1962). Synchrony of hatching within an egg mass and its effects on the formation of larval group on the rice stem borer, *Chilo suppressalis*. *Jap. J. Appl. Ent. Zool.* 6: 190-195.

MORLEY, C. & RAIT-SMITH, W. (1933). The Hymenopterous parasites of the British Lepidoptera. *Trans. R. ent. Soc. Lond.* 81: 133-183.

MORRIS, R. F. (1972). Predation by wasps, birds, and mammals on *Hyphantria cunea*. *Can. Ent.* 104: 1581-1591.

MURDIE, G. (1965). Studies in the cases and consequences of intra-specific variation in size of aphids. Ph.D thesis. London University.

* NIKOLOVA, V. (1945). Cabbage Moth - *Mamestra (Barathra) brassicae* L. as a cabbage pest in Bulgaria and its control. *Agric. Sci. I. Plant Indust.* 1: 123-156 (In Bulgarian).

NOLL, J. (1963). Uber den Einflub der Temperatur auf die Lebensdauer der imagines, auf Begin, Verlauf und Dauer der Eiablage sowie auf die Eizahlen (Ei- producktion) bei der Kohleule (*Mamestra (Barathra) brassicae* L.) und seine Bedeutung fur den Massenwechsel des Schadlings. *Nachr Bl. dt. PflSchDienst (N.F.)* 17: 9-24.

NOYES, J. S. (1974). The biology of the leek moth, *Acrolepia assectella* (Zeller). Ph.D thesis, London University.

OGURA, N. (1975). Hormonal control of larval coloration in the armyworm, *Leucania separata*. *J. Insect Physiol.*, 21: 559-576.

OGURA, N. (1976). Role of oesophageal connectives in cuticular melanization in larvae of the armyworm, *Leucania separata* Walker (Lepidoptera: Noctuidae). *Appl. Ent. Zool.* 11(2): 70-74.

OKU, T. & KOBAYASHI, T. (1973a). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. I. Discrimination from allied forms at immature stages and estimation of duration of larval instars in the field, with notes on field sampling. *Bull. Tohoku Natn. agric. Exp. St.* 44: 97-108 (In Japanese).

OKU, T. & KOBAYASHI, T. (1973b). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. II. Mortalities during the progress and breakdown of an outbreak on the sugar beet. *Kontyu.* 41: 267-279.

OKU, T. & KOBAYASHI, T. (1974a). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. III. Mortality factors of the egg and earlier larval stages. *Bull. Tohoku Natn. agric. Exp. Stn.* 47: 133-144. (In Japanese).

OKU, T. & KOBAYASHI, T. (1974b). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. IV. Occurrence of the partial third generation in autumn and its mortality at Morioka. *Bull. Tohoku Natn. agric. Exp. Stn.* 47: 145-156 (In Japanese).

OKU, T. & KOBAYASHI, T. (1974c). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. V. Notes on the predatory effect of birds against the larvae. *Bull Tohoku Natn. agric. Exp. Stn.* 47: 157-164 (In Japanese).

OKU, T. & KOBAYASHI, T. (1974d). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. VI. Mortality factors of the later larval and pupal stages. *Bull Tohoku natn. agric. Exp. Stn.* 47: 165-179 (In Japanese).

OKU, T. & KOBAYASHI, T. (1974e). Some dynamic aspects of field populations of the cabbage armyworm, *Mamestra brassicae* Linne, in Tohoku District. VII. Results of continuous population survey in a sugar beet field during several years with general discussion. *Bull. Tohoku natn. Agric. Exp. Stn.* 47: 181-195 (In Japanese).

OMINO, T.; YOKOI, S. & HIDEAKIRA, T. (1973). Experimental studies on the daytime behaviour of noctuid larvae, the cabbage armyworm, *Mamestra brassicae*, the tobacco cutworm, *Spodoptera litura*, and the black cutworm, *Agrotis ipsilon*. *Jap. J. appl. Ent. Zool.* 17: 215-220 (In Japanese).

OTUKA, M. & SANTA, H. (1955). Studies on the diapause in the cabbage armyworm, *Barathra brassicae* L. III. The effect of the rhythm of light and darkness on the induction of diapause. *Bull. Nat. Inst. Agric. Sci., C.* 5: 49-56 . (In Japanese).

PAIVA, M. R. S. de. (1977). Biology and population ecology of the mustard beetle *Phaedon cochleariae*. Ph.D thesis. London University.

* PEIU, M. (1963). Contributii la studiul combaterii larvelor de buha verzei (*Mamestra brassicae* L.) pe mazare. *Probl. agric.* 15: 49-54 (In Rumanian).

PETRUKHA, O. I. & BUTOUSKII, A. P. (1967). The conditions of development of the cabbage moth and the effectiveness of measures for its control. *Zashchita Rastenii, Kiev.* 5: 107-114 (In Russian).

POITOUT, S. & BUES, R. (1973). Mise en évidence d'une diapause nymphale de type "estival" dans des populations europeennes de deux lepidopteres Noctuidae Hadeninae (*Mamestra oleracea* L. et *Mamestra brassicae* L.). Facteurs d'induction et apercusur la variabilite inter-population de ce caractere. *Compt. Rend. Acad. Sci. Paris* 276: 3367-3370.

REAY-JONES, N. S. (1971). Studies on the Blackening response to crowding in armyworms (Lepidoptera: Noctuidae). Ph.D thesis. Oxford University.

RIVNAY, E. & MEISNER, J. (1966). The effect of rearing conditions on the immature stages and adults of *Spodoptera littoralis* (Boisd.). *Bull. ent. Res.* 56: 623-634.

ROSE, D. J. W. (1975). Field development and quality changes in successive generations of *Spodoptera exempta* Wlk., the African armyworm. *J. appl. ecol.* 12: 727-739.

* RYGG, T. & KJOS, O. (1975). Cabbage moth (*Mamestra brassicae* (L.)). *GartneryiKet.* 65: 286, 288 & 290 (In Norwegian).

SALAMA, H. S. & SALEM, S. A. (1971). Biology of *Spodoptera littoralis* Bois as affected by larval density (Lep., Noctuidae). *Z. angew. Ent.* 67: 141-143.

SALINAS, P. (1972). Studies on the ecology and behaviour of the larvae of *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae). Ph.D thesis. London University.

SANTA, H. (1955). Studies on the diapause in hibernating pupae of the cabbage armyworm, *Barathra brassicae* L. *Jap. J. app. Zool.* 20: 211-216 (In Japanese).

SASAKAWA, M. (1967). Phase polymorphism of the larger pellucid hawk moth, *Cephonodes hylas* L. (Sphingidae). Effect of population density on the larval coloration and development. *Sci. Rep. Kyoto Pref. Univ. Agr.* 19: 29-36.

SASAKAWA, M. (1973). The influence of continuous contact on larval colour in the larger pellucid hawk moth, *Cephonodes hylas* L. (Lepidoptera: Sphingidae). *Appl. Ent. Zool.*, 8: 198.

SASAKAWA, M. & YAMAZAKI. S. (1967). Effect of population density on the larval coloration and development of larva and pupa in the larger pellucid hawk moth, *Cephonodes hylas* L. (Lepidoptera: Sphingidae). *Jap. J. appl. Ent. Zool.* 11: 157-163 (In Japanese).

SCHNEIDER, G. (1973). Über den einflub verschiedener umweltfaktoren auf den farbungspolyphanismus der raupen des tropisch-ameriKanischen schwarmers *Erinnys ello* L. (Lepidopt., Sphingid.). *Oecologia* 11: 351-370.

SEHNAL, F. (1976). Action of juvenoids on different groups of insects. *The Juvenile Hormones* (Ed. by L. Gilbert), pp. 301-322. Plenum Press, New York.

SEHNAL, F.; METWALLY, M. M. & GELBIC, I. (1976). Reactions of immature stages of noctuid moths to juvenoids. *Z. ang. Ent.* 81: 85-102.

* SEREBROVSKII, A. S.; TUPIKOV, V. & KHVOSTOVA, V. B. (1944). *Ernestia consolrina* Meig., a parasite of the larvae of Noctuids that attack vegetables, and measures furthering its activity. *Proc. Lenin Acad. agric. Sci. U.S.S.R.* 9: 16-19 (In Russian).

SIGIURA, T. (1961). On the relation between the hatching velocity of the eggs and their numbers, and the aggregation behaviour of the larva in the tea tussock-moth (*Euproctis pseudoconspersa* Strand). *Bull. Fac. Agric. Mie. University* 24: 45-54.

SMITH, J. M. (1958). Temperature and egg laying in *Drosophila*. *J. Exp. Biol.* 35: 832-842.

SMITH, K. M. (1931). *A textbook of Agricultural Entomology*. Cambridge University Press. Cambridge.

SMITH, S. D. (1969). The effects of crowding on larvae of the meal moth, *Ephestia kühniella*. *J. exp. Zool.* 170: 193-203.

SNYMAN, A. (1949). The influence of population densities on the development and oviposition of *Plodia interpunctella* Hübn. (Lepidoptera). *J. Ent. Soc. S. Africa.* 12: 137-171.

SOUTH, R. (1946). *The moths of the British Isles.* Frederick Warne & Co. Ltd., London.

STEPANOVA, L. A. (1962). Ecology of crucifer pests. *Ent. Rev., Wash.,* 41: 451-460.

SUGIMOTO, T. (1962). Influences of individuals in aggregation or isolation on the development and survival of the larvae of *Artona funeralis*. *Jap. J. appl. Ent. Zool.* 6: 196-199 (In Japanese).

TAKAHASHI, F. (1961). Studies on the fluctuation in the experimental population of the almond moth, *Ephestia cautella* Walker. *Jap. J. Ecol.* 11: 239-245.

TAYLOR, O. R. (1967). Relationship of multiple mating to fertility in *Atteva punctella*. *Ann. Ent. Soc. Am.* 60: 583-589.

THOMPSON, W. R. (1943). A catalogue of the parasites and predators of insect pests. *Imp. Parasite Service.* Ontario, Canada.

* TRENCHEV, G. & DOCHKOVA, B. (1975). Parasites and predators of *Mamestra brassicae* in Northern Bulgaria. *Rastitelna Zashchita.* 23: 30-31.

TSUJI, H. (1959). Studies on the diapause of the Indian-meal moth, *Plodia interpunctella* Hubner. II. The effect of population density on the induction of diapause. *Jap. J. appl. Ent. Zool.* 3: 34-40.

UCHIDA, T. & MASAKI, S. (1953). The effect of low temperature after high temperature treatment upon the induction of diapause in the cabbage moth, *Barathra brassicae* L. *Oyo-Kontyu.* 8: 129-134 (In Japanese).

UCHIDA, T. & MASAKI, S. (1954). The effect of photoperiod on the induction of diapause in the cabbage moth, *Barathra brassicae* L. *J. Fac. Agric. Hokkaido Univ.* 2: 85-95 (In Japanese).

ULLYETT, G. C. & MERWE, J. S. (1947). Some factors influencing population growth of *Ephestia kühniella* Zell. (Lep., Phycitid.). *J. Ent. Soc. S. Africa.* 10: 46-63.

UMEYA, K. & YAMADA, H. (1973). Threshold temperature and thermal constants for development of the diamond-back moth, *Plutella xylostella* L., with reference to their local differences. *Jap. J. appl. Ent. Zool.* 17: 19-24.

UVAROV, B. P. (1961). Quantity and quality in insect populations. *Proc. R. ent. Soc. Lond. (C)* 25: 52-59.

UVAROV, B. P. (1966). *Grasshoppers and Locusts.* Vol. I. Cambridge University Press, London.

* VALCH, B. S. (1913). Outbreak of *Barathra brassicae* L., in the district of Voltchansk, Govt. of Charkov. *Bull. Pests Agr. & Methods fighting them.* 2: 1-4 (In Russian).

* VALCH, B. S. (1914). *Barathra brassicae* in the district of Voltschansk in 1913. *Op. cit.* 2: 29-33 (In Russian).

* VOELKEL, H. (1925). On the practical importance of *Trichogramma evanescens* Westw. *Arb. Biol. Reichsanst. Land. Forstw.* 14: 97-108.

WAFA, A. K. & EID, M. A. A. (1967). Effect of population density on weights and chemical analysis of the silkworm, *Bombyx mori* L. *Bull. Soc. ent. Egypte*, 51: 269-272.

WARDZINSKI, K. (1938). Der Einflusz der Einzelhaft sowie der schwachen Vergesellschaftung auf die Entwicklung und das Washstum der Raupen von *Pieris brassicae* L. *Z. angew Ent.* 25: 478-486.

WATANABE, N. & UMEYA, K. (1968). Biology of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) in Japan. IV. Effect of group size on the survival and growth of larvae. *Res. Bull. Pl. Prot. Jap.* 6: 1-5.

WAY, M. J.; SMITH, P. M. & HOPKINS, B. (1951). The selection and rearing of leaf-eating insects for use as test subjects in the study of insecticides. *Bull. Ent. Res.* 42: 331-354.

WEITZ, B. (1957). An automatic dispenser for multiple serological titrations. *J. Clin. Path.*, 10: 200-207.

WIGGLESWORTH, V. B. (1972). *The principles of insect physiology.* 7th ed., London.

WHELLAN, J. A. (1954). The African army worm and its control. *Rhodesia agric. J.* 51: 415-427.

WILLIAMS, C. B. & LONG, D. B. (1950). Phase coloration in larvae of lepidoptera. *Nature, Lond.* 166: 1035.

WILLIAMS, L. H. (1954). The feeding habits and food preferences of Acrididae and the factors which determine them. *Trans. R. ent. Soc. Lond.* 105: 423-454.

YAGI, S. (1976). The role of juvenile hormone in diapause and phase variation in some lepidopterous insects. *The Juvenile Hormones* (Ed. by L. Gilbert), pp. 288-300. Plenum Press, New York.

YAGI, S. & KURAMOCHI, K. (1976). The role of juvenile hormone in larval duration and spermiogenesis in relation to phase variation in the tobacco cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae). *Appl. Ent. Zool.* 11: 133-138.

YOKOI, S. & TSUJI, H. (1975). Experimental studies on the movement behaviour of the final instar noctuid larvae of the cabbage armyworm and the tobacco cutworm. *Jap. J. appl. Ent. Zool.*, 19: 157-161 (In Japanese).

ZAHER, M. A. & LONG, D. B. (1959). Some effects on larval population density on the biology of *Pieris brassicae* L. and *Plusia gamma* L. *Proc. R. Ent. Soc. Lond. (A)* 34: 97-109

ZAHER, M. A. & MOUSSA, M. A. (1961). Effects of population density on *Prodenia litura* (Lepidoptera: Noctuidae). *Ann. Ent. Soc. Amer.* 54: 145-149.

ZAHER, M. A. & MOUSSA, M. A. (1962). Effect of larval crowding on the cutworm, *Agrotis ypsilon* Rott. (Lepidoptera: Agrotidae). *Bull. Soc. ent. Egypte* 46: 365-372.

* ZANGHERI, S. (1952). Contributi alla conoscenza dell'entomofauna delle leguminose da seme. I. Nota preventiva sull'entomofauna del pisello e della fava. *Boll. Ist. Ent. Bologna* 18: 93-116 (In Italian).

* ZORIN, P. V. (1936). The importance of the parasites of the cabbage noctuid in the Leningrad Province. *Bull. Sta. reg. Prot. Plantes Leningr.* 7: 18-20.

* Original not seen

APPENDIX 1 TABLE 1 Some effects of larval crowding among species that show no density-dependent colour changes

SPECIES	Eggs laid (in)	Habit of larvae	Habit of adult	EFFECT ON LARVAE: Rate of devel.	Instar number	Weight and/or size	Mortality	Activity	Colour darkening	EFFECT ON PUPAE: Duration	Weight and/or size	Mortality	Colour	EFFECT ON ADULTS: Weight and/or size	Wind loading	Preoviposition period	Longevity	Fecundity	REFERENCES
NOCTUIDAE																			
Leucania placida		solitary		-			+				-								Iwao, 1962
Naranja aenescens	singly pairs			-							-					+	-	-	Iwao, 1962
Maliatha signifera	singly	solitary		-			+				-								Iwao, 1962
Agrotis segetum				-			+				-								Bobinskaya, 1971
Hadena sordida	masses	aggreg. first solitary later		-			+				-							-	Bobinskaya, 1971
SPHINGIDAE																			
Dilina tibiae	singly or in pairs	solitary																	Long, 1957
Laothoe populi	singly or in pairs	solitary																	Long, 1953
ARCTIIDAE																			
Hyphantria cunea	masses	aggreg.		+			=					=		-					Watanabe & Umeya, 1968
Arctia caja				-		-	+							-					Hofmann, 1934
LYMANTRIIDAE																			
Euproctis pseudocompersa	masses	aggreg.		+	-		-				=							=	Mizuta, 1960
Euproctis chrysorrhoea	masses	<L2: aggr. >L2: solitary		+ =		+ =to+													Grison, 1948
Lymantria dispar	masses	solitary		-		-	+			+	-							-	Mizuta, 1960
				=		-	+											-	Hofmann, 1934
				+	+	-	+			-	-	+						-	Leonard, 1968
GEOMETRIDAE																			
Bupalus piniarius	groups	solitary		-	-	-	=	=		+	-	=		-	-		=	-	Klomp, 1966
				-	-	-	=	=		+	-	=		-	-		=	-	Gruys, 1970
BOMBICIDAE																			
Bombix mori	masses	aggreg.				+					+			+				+	Legay & Pascal, 1951
						+					+			+					Wafa and Eid, 1967
ZYGAENIDAE																			
Artona funeralis	masses	aggreg. later		-	+		-FI +LI												Sugimoto, 1962
				-	-		-EI +LI			=	-							-	Mizuta, 1968

APPENDIX 1 TABLE 1 — CONTINUED

SPECIES	Eggs laid (in)	Habit of larvae	Habit of adult	EFFECT ON LARVAE: Rate of devel.	Instar number	Weight and/or size	Mortality	Activity	Colour darkening	EFFECT ON PUPAE: Duration	Weight and/or size	Mortality	Colour	EFFECT ON ADULTS: Weight and/or size	Wind loading	Preoviposition period	Longevity	Fecundity	REFERENCES
CRAMBIDAE																			
Chilo suppressalis	masses	aggreg. later solitary		-		-	-EI +LI			=	-	+		-				-	Morimoto, 1960b
PHYCITIDAE																			
Ephestia cautella				-	+	-								-				-	Takahashi, 1961
Ephestia kuhniella				-										-				-	Ullyett et al., 1947
				-										-					Smith, 1969
Plodia interpunctella														-				-	Snyman, 1949
TORTRICIDAE																			
Adoxophyes orana	masses	solitary		-		-	+				-								Ankersmit et al., 1973
Epiphyas postvitana	mass	solitary									-							-	Danthanarayana, 1975
Laspeyresia pomonella		solitary		-			+				-							-	Ferro & Harwood, 1973
PIERIDAE																			
Pieris brassicae	groups	aggreg. later small groups or solitary	yes	+						-	-			-	-	+	+	-	Long, 1953, 1959; Long & Zaher, 1958; Zaher and Long, 1959
				+															David & Gardiner, 1962
				+							-								Wardzinski, 1959
Pieris rapae crucivora																			
intermediate density				+		+	-			=	+	-		+			+		Morimoto, 1960
high density						-	+			=	-	+		-			-		Morimoto, 1960

EI Early instars

LI Late instars

APPENDIX 1 TABLE 2 Some effects of larval crowding among species that show density-dependent darkening of larval colour

SPECIES	Eggs laid (in)	Habit of larvae	Mass migration of larvae	Habit of adult	EFFECT ON LARVAE: Rate of devel.	Instar number	Weight and/or size	Mortality	Activity	Colour darkening	EFFECT ON PUPAE: Duration	Weight and/or size	Mortality	Colour	EFFECT ON ADULTS: Weight and/or size	Wind loading	Preoviposition period	Longevity	Fecundity	REFERENCES
NOCTUIDAE																				
Leucania separata	rows	aggreg. later solitary	yes	M.	+	=	−	+	+	=	+	−		=	−	−	+	+	=	Iwao, 1962
Leucania loreyi	rows	solitary	no		−			+			+	−					=	=	=	Iwao, 1962
Lithacodia stygia	rows	solitary			+			+				−								Iwao, 1962
Plusia gamma	loose cluster	loose aggreg. solitary later		M.	+	−	−	+HD −MD	+	=	+	=		=	−	−	−	+ −	+	Williams & Long, 1950; Long, 1953, 1959; Long & Zaher, 1958; Zaher & Long, 1959
Spodoptera exempta	groups	solitary (aggreg.)	yes	M.		+			+		=			=	−					Mathee, 1946
					+	=			+					=	−					Faure, 1943
Spodoptera abyssinia	groups	solitary							+											Rose, 1975
					=															Faure, 1943
Spodoptera littoralis	masses	solitary			+				+		÷	−			−					Mathee, 1947
					=ID			+			=	−						+	−	Hodjat, 1970
					+HD															Salama & Salem, 1971
					−			+			=	−	=				−	−	−	Rivnay & Meisner, 1966
					+				+		=	−			−		=	+	=	Zaher & Moussa, 1961
Spodoptera litura	masses	solitary (aggreg.)			+			=			−	−								Iwao, 1962
					+						=									Yagi & Kuramochi, 1976
Spodoptera exigua	masses	solitary (aggreg.)	yes	?	−?				+		+?			+	=		+?			Faure, 1943a, b
					+	−			+		−						=	=	−	Hanna & Azab, 1973
Agrotis ypsilon					−						=	−		=			=		−	Zaher & Moussa, 1962
					+LD						=LD									Mauseur & Dimetry, 1972
					−HD			+			+HD	−	+							
Diataraeea oleracea	masses	loosely aggreg.		no	+	−		+HD −MD												Long, 1953
Orthosia cruda	masses	loosely aggreg.																		Long, 1953
Orthosia gothica	masses	loosely aggreg.																		Long, 1953
Orthosia incerta	masses	loosely aggreg.																		Long, 1953
Orthosia stabilis	masses	loosely aggreg.																		Long, 1953
Trachea atriplicis		solitary			+															Iwao, 1962
Alabama argillacea	singly				+				+											Calcagnolo & Sauer, 1955
Persectania ewingi																				Doull, 1953
Mamestra brassicae	masses	aggreg. later solitary or aggreg.	yes	no	+	=	−	+	+		+	−				−	−	=	+	Hirata, 1954, 1956
					+							−							−	Bonnemaison, 1962a
					−		−					−				÷				Burov & Mokrousova, 1970
					+	=		+	+	=	=	−	=							Montagne, 1977

APPENDIX 1 TABLE 2 - CONTINUED

SPECIES	Eggs laid (in)	Habit of larvae	Mass migration of larvae	Habit of adult	EFFECT ON LARVAE: Rate of devel.	Instar number	Weight and/or size	Mortality	Activity	Colour darkening	EFFECT ON PUPAE: Duration	Weight and/or size	Mortality	Colour	EFFECT ON ADULTS: Weight and/or size	Wind loading	Preoviposition Period	Longevity	Fecundity	REFERENCES
NOTODONTIDAE																				
Exaereta ulmi	1-5	solitary							+						-				+	Sharov cited by Long, 1955; Uvarov, 1961; Iwao, 1968; Gruys, 1970.
SPHINGIDAE																				
Cephonodes hylas					+			+		=	-	-		=						Sasakawa, 1967; Sasakawa & Yamasaki, 1967
Erynnis ello																				Schneider, 1973
ARCTIIDAE																				
Diacrisia obliqua	masses				+	-	-	+	+		+	-			-	-	+	+	-	Islam & Sardar, 1971
SATURNIDAE																				
Saturnia pavonia	groups	aggreg. later solitary			=															Long, 1953
GEOMETRIDAE																				
Ennomos subsignarius	masses	solitary			-			+		+	+	-							-	Drooz, 1966a, b
HESPERIIDAE																				
Parnara guttata	singly	solitary		M.	-			+				-						-	-	Iwao, 1962 Mitamura cited by Iwao, 1962

M. migrant
HD high densities
MD moderate densities
ID intermediate densities
LD low densities

Appendix 2.

The Precipitin Test

Preparation of the antigen

Antigen was prepared from laboratory cultures of *Mamestra brassicae*. The insects were starved for 25 hours to remove the food from their guts. All five instar larvae were used as well as eggs since it is known that some antisera prepared using a single instar does not nescessarily react with other instars (Loughton et al., 1963). The insects were sorted in the laboratory, anaesthetised with carbon dioxide and immediately transferred to a container with silica-gel which was stored in a deep-freeze at $-20^{o}C$. This material was freeze-dried and stored in a desiccator until sufficient material was available to carry out the extraction of proteins.

A total of 8.0 grs of dry weight of insect was obtained and was crushed in a pestle and mortar. Distilled water was added to the powder and the mixture was then stirred mechanically overnight at $4^{o}C$ and later centrifuged at 3000 g for 10 min. The supernatant was removed and a second extraction of the residue was made. The extracts were pooled and freeze dried. The solid material thus obtained was dissolved in 20 ml of distilled water and this constituted the antigen used.

Preparation of the antiserum

The method used by Boreham and Gill (1973) was adopted for preparing the antiserum.

An emulsion of 0.5 ml of Freunds complete adjuvant with 0.5 ml of *Mamestra* antigen extract was prepared. Aliquots were injected into each of the auxillary and popliteal lymph-nodes of an adult New Zealand white

rabbit, weighing 2.5 - 3.0 kg. A second injection was given 7 days later. After a further period of ten days, a 10 ml sample of blood was taken from the marginal ear vein of the rabbit. The serum, containing antibodies, was separated initially by placing the blood sample tube in a water bath at 37°C for 1 hour. The serum was then centrifuged at 3000 g per 5 min. After centrifuging it was filtered through a Hemmings filter and was then ready to be tested for titre to *Mamestra* antigen.

Titre of antiserum

The titre of the anti-*Mamestra* serum was determined by preparing several dilutions of the antigen. Twelve doubling dilutions were prepared ranging from $^{1}/10$ to $^{1}/20480$.

The dilutions were tested using a multiple automatic dispenser (Weitz, 1957). A sample of 0.05 ml of the twelve dilutions of the antigen was drawn up into each tube of the dispenser. This was followed by an equal volume of the anti-*Mamestra* serum so that the antigen and antiserum formed two distinct layers. When the antiserum reacts with the antigen a white ring of precipitate forms at the interface between the two liquids.

The tubes were allowed to stand at room temperature for 2 h. Positive reactions were detected up to 1:2560 dilution.

To improve the titre a further injection was given and the procedure just described was repeated. Since the titre did not improve the rabbit was bled by cardiac puncture and about 100 ml of blood obtained. Serum was prepared as described above and stored at -20°C until required.

Specificity of antiserum

The specificity of the anti-*Mamestra* serum was tested against a

range of Lepidoptera and also against the food plant.

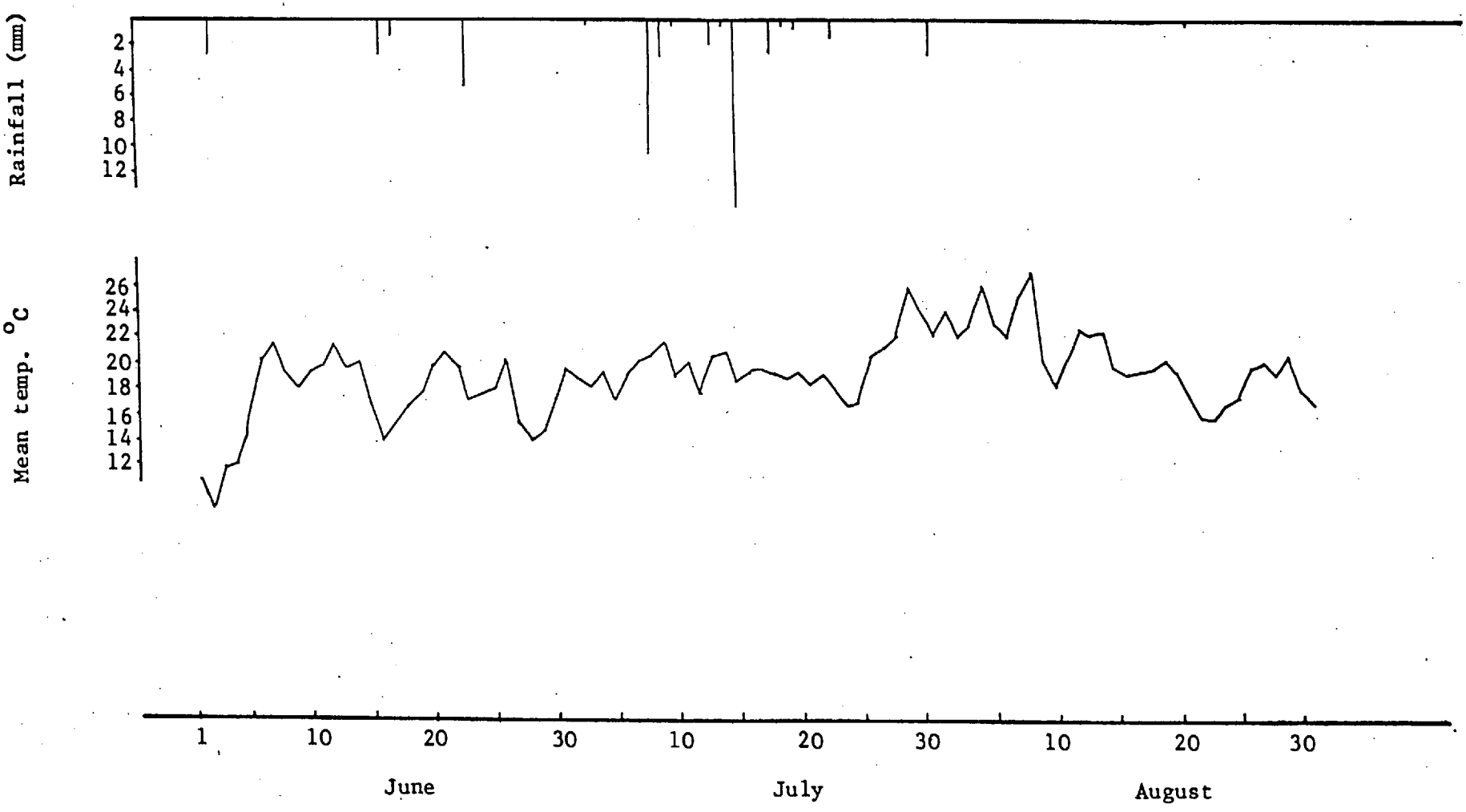
The serum gave no reaction with material from the sprout plant, nor with the following other Lepidoptera: *Pieris rapae, P. brassicae, Pionia forficalis* L., *Plutella xylostella*. It did, however, react strongly with *Noctua pronubra, Plusia gamma, Agrotis* spp. and an unidentified noctuid. *Plusia gamma* was rarely seen in the plot, however *N. pronubra* and three species of *Agrotis* were rather common. The cross-reaction with the noctuids was so strong that no absorption was attempted.

Tests on predators from the field

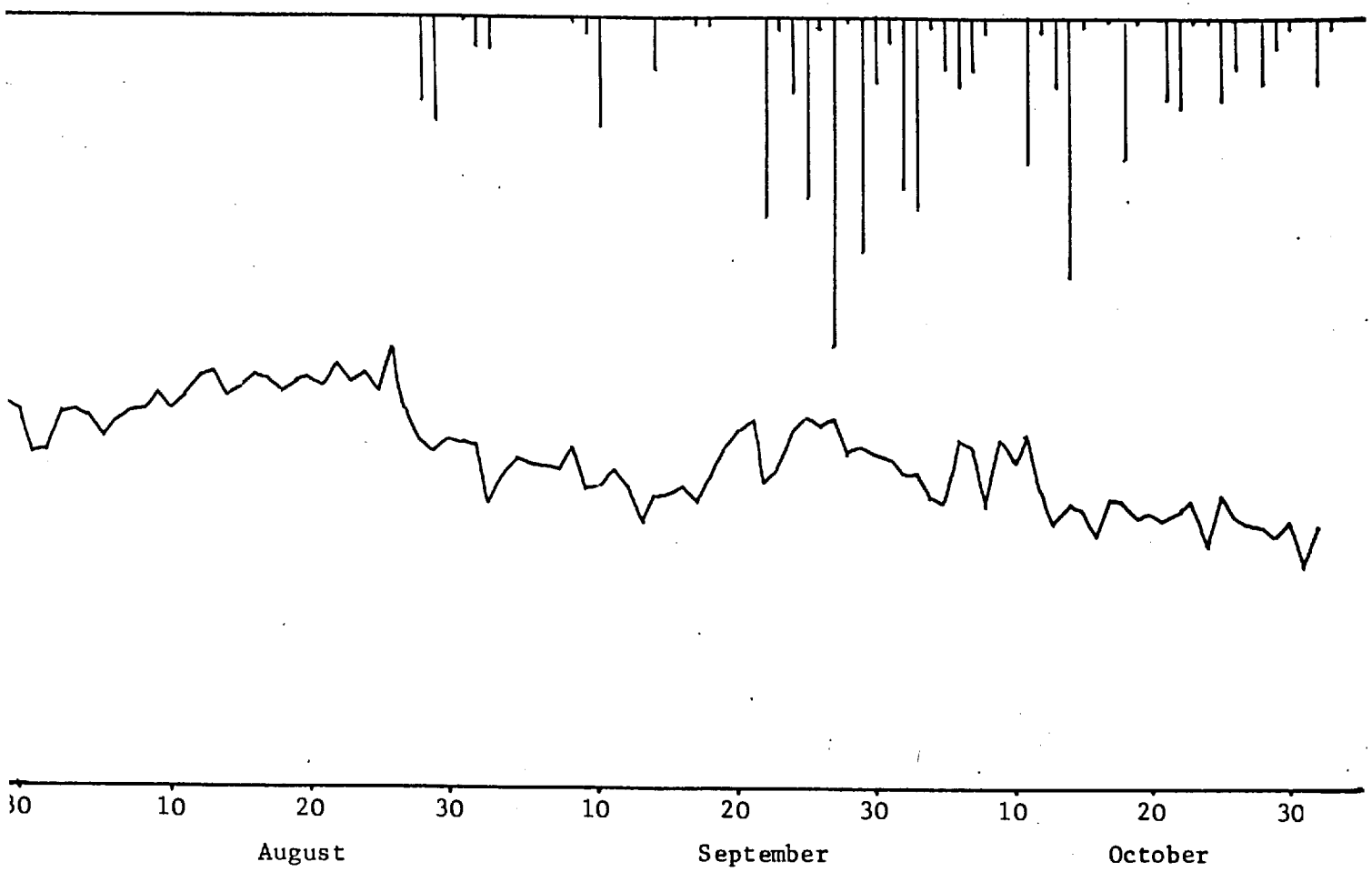
The potential predators collected in the Brussels plot were sorted, anaesthetised with carbon dioxide, and placed individually in small sample tubes; each tube was half-filled with silica-gel topped by a plug of non-absorbent cotton-wool. After introducing the insect the lid of the sample tube was fitted; the tube was numbered, and immediately placed in a deep-freezer at $-20^{o}C$.

After identification the whole insect (small species) or the gut (larger species) was crushed in individual tubes and allowed to soak in 0.2 ml of saline solution for a day and then centrifuged. A sample of 0.05 ml was drawn up into a serological tube with the dispenser and followed by an equivalent volume of the antiserum. The tubes were left at room temperature for 2 h. before being read by an indirect light against a black background. The presence of *Mamestra* was shown by the formation of the white ring at the interface between the two liquids.

Appendix 3, Figure 1. Total rainfall (mm) and mean temperature (^{o}C). 1975



ıperature (^{o}C). 1976



Appendix 4, Table 1. Analysis of variance for the 1975 field experiment.

Source of variation	SS	d.f.	MS	F-test
Treatments	27471.10	2	13735.55	60.84**
Days	6164.19	6	1027.36	4.55**
T x D	2855.65	12	237.97	1.05n.s.
Error	14221.15	63	225.73	
Total	50712.10			

Appendix 4, Table 2. Analysis of variance for the 1976 field experiment. Early summer.

Source of variation	SS	d.f.	MS	F-test
Treatments	85040.0125	3	28346.6709	567.27**
Days	21328.3646	8	2666.0456	53.35**
T x D	4285.5202	24	178.5633	3.57**
Error	5396.8020	108	49.9704	
Total	116050.6994	143		

Appendix 4, Table 3. Analysis of variance for the 1976 field experiment. Late summer.

Source of variation	SS	d.f.	MS	F-test
Treatments	90047.67	3	30015.89	574.77**
Days	29054.21	14	2075.30	39.74**
T x D	3906.89	42	93.02	1.78**
Error	7833.38	150	52.22	
Total	130842.15	209		

Appendix 5. Parasites of *M. brassicae* L. in Britain.

	Source (see below)
Hymenoptera	
Ichneumonidae	
Ichneumon deliratorius L.	3
Amblyteles armatorius Forst.	1, 3
Exetates cinctipes Ratz	1, 3
E. nigripes Grav.	1
Pimpla compunctor L.	1
Phygadenon fumator Grav.	1
Ophion scutellaris Thoms.	1
Astiphrommus mandibularis Thoms.	1
Eulophidae	
Eulophus sp.	1
Comedo opaculus Thoms.	4
Diptera	
Tachinidae	
Compsilura concinnata Mg.	2, 3
Siphona (=*Crocuta*) *cristata* F.	2, 3
S. geniculata DeG.	2
Phorocera assimilis Fall.	2
Exorista larvarum L.	2
Chaetotachina rustica Mg.	2
Eumea hortulana Mg.	2
Voria ruralis Fall.	2

Source : 1 Morley & Rait-Smith (1933

2 Audcent (1942)

3 Hammond & Smith (1953)

4 Thompson (1943)