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A CONTRIBUTION TO THE BIOLOGY OF CUTWORMS, AGROTIS SPP.

(LEPIDOPTERA, NOCTUIDAE), IN RHODESIA.

BY

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1. ABSTRACT

The systematic position of economically important cutworm species in Rhodesia has been clarified and, from literature and records, ^{and} the two most important species selected for study. These are Agrotis segetum (Denis & Schiffenmüller) and A. ipsilon (Häfnagel).

Developmental periods have been determined at seven constant temperatures and from the logistic curves thus obtained, close agreement between these and population cycles in the field was obtained.

A. segetum is tetravoltine and A. ipsilon quinvoltine in Rhodesia.

The seasonal abundance of moths was determined by light-trapping and peaks of moths were found to be associated with an increase in the convergence of airstreams; both species appear to be migrants. Factors affecting seasonal abundance have been discussed and the two most important appear to be immigration of moths and the availability of suitable larval food supplies. A method of forecasting the potential population after the cool, dry, season has been proposed involving rainfall data at the end of the rainy season.

Aspects of larval and adult biology of the two species have been investigated, and these provide data for formulating a pest management system. Larval phototactic responses showed that the first two and a half instars are photopositive while later instars were photonegative. Larval feeding behaviour was found to be closely related to their phototactic responses, that is, larvae in the first two and a half instars feed on the soil surface and older larvae shelter in the soil during daylight. Trichomal secretions of tobacco seedlings were found to be effective in trapping 1st instar larvae. Adult activity

capacity has been studied and it appears that the active and inactive characteristics are inheritable. The favoured oviposition site on agricultural lands is on crop debris.

~~Data on biology~~
Information on biology provides
data for formulation of a pest management
system

2. INTRODUCTION

Jack (1918) stated, "It would be difficult to estimate the average total amount of loss to agriculture in Southern Rhodesia each season through the agency of cutworms. Cutworms are as much a pest to the tobacco planter, the potato grower and the market gardener as they are to the maize grower, and it is probable that they constitute on the whole the most destructive plant pest that vexes this Territory."

Cutworms are the larval stage of several species of noctuid moths. They feed voraciously on almost any growing plant which is not too woody, and the seedlings of practically all annual and perennial crops are susceptible to attack by these pests. The cutworms derive their name from the habit of cutting plants at soil level and are, therefore, an economic problem in the spheres of agriculture and horticulture in Rhodesia.

There are many species of cutworms belonging to many genera throughout the world. The most important genera include Agrotis, Euxoa, Tryphaena, Anathes, Eupsilia, Abagrotis, Rhynchagrotis, Feltia, and Peridroma; all these are within the family Noctuidae.

In the literature (Jack, 1918; Smit, 1948; Rose, 1962) there is little detailed information on the biology of cutworm species in southern Africa, or elsewhere in the world with a climate comparable with that of Rhodesia, apart from a limited contribution to the biology of Agrotis segetum in Angola (Passos de Carvalho, 1968). There is a great deal of biological data on the many species of cutworms around the world, but the necessity to obtain such data under local conditions was shown by Druzhelyubova (1963) who distinguished three

geographical populations of A. segetum in the Soviet Union alone.
Each population had distinct reactions to climatic factors.

The purpose of this study was to obtain data on some aspects of the biology of cutworms under local conditions, which could be used for development of a pest management programme.

The approach has been first to select the most economically important species for study; namely Agrotis segetum and A. ipsilon.

3. ECONOMIC IMPORTANCE

The name 'cutworm' is given to the caterpillars of certain moths in the family Noctuidae that feed on plants at around soil level, frequently severing them from their roots. This form of attack destroys whole plants, and is excessively wasteful as the insect eats only a fraction of what it destroys. Sometimes cutworms feed on the leaves of plants, but more often on stems of young plants both above and below the ground level. Cutworms may burrow into larger roots such as turnips and swedes or into swollen stems (potato tubers) where they hollow out the interior. Hardier and woodier material may also be eaten, such as the bark of young trees and the germ of dry maize seed.

Jack (1918) recorded four species of cutworms in Rhodesia. These were Euxoa segetis Schiff., E. longidentifera Hamp., E. spinifera Hübner and Agrotis ypsilon Roths. Only E. segetis and A. ypsilon were considered to be of real importance, the former being rated as the most common species and the latter as being "the only rival to E. segetis in destructiveness." Rose (1962) rated A. segetum as the most common cutworm attacking main crops, the other important species being A. ipsilon which was recorded most frequently as the cause of outbreaks in early irrigated maize lands.

From the records of the Rhodesian Ministry of Agriculture it was found that the plants attacked by each species were:

Agrotis segetum (= E. segetis) - bean, cabbage, carrot, cotton, Delphinium, Gladiolus, groundnut, lawn grass, lucerne, maize, onion, pea, pine, potato, rape, rose, soya bean, strawberry, tobacco, tomato and wattle;

Agrotis ipsilon (= A. ypsilon) - cotton, maize, potato,
spinach, tobacco and tomato;

Pixoa longidentifera - coffee, daisy, lawn grass, maize,
spinach and swede;

A. spinifera (= E. spinifera) - grass, maize, pine, weeds;

A. muscosa - lawn grass, maize.

The records showed that larval attacks by A. segetum took place throughout the year with the exception of the month of April; by A. ipsilon in May, July, October and December; by E. longidentifera in March, May, June, September, October and November; by A. spinifera in July, October and November; and by A. muscosa in January, October and November.

The views of the two authors indicate that the most important species is A. segetum, and this is confirmed by the list of plants attacked and the months when attacks were recorded. The only other species considered by these authors as being of any importance was A. ipsilon and the plants attacked by it include three crops of major importance to Rhodesian agriculture (maize, cotton and tobacco), thus making this species second in importance. These species were accordingly singled out for study.

Both of the species are fairly cosmopolitan in distribution. A. ipsilon is known to occur in Europe (including the U.S.S.R.), Asia, Africa, Australasia and North and South America (Fig. 1), while A. segetum is found in Europe (including the U.S.S.R.), Asia, Africa, Australasia and South America (Fig. 2). Fig. 1 is taken from "Distribution Maps of Insect Pests" published by the Commonwealth

Institute of Entomology, London, with new areas included in southern Africa; Fig. 2 is drawn from a review of the literature (mainly from Review of Applied Entomology (series A) and Bulletin of Entomological Research) and as such the boundaries are not particularly accurate.

A. epsilon is commonly known in various parts of the world in the larval stage as the black, common, or greasy cutworm and in the adult stage as the dark swordgrass or the Y-moth; A. segetum is called either the turnip moth, dart moth, grain noctuid, melon-worm, common cutworm or winter noctuid.

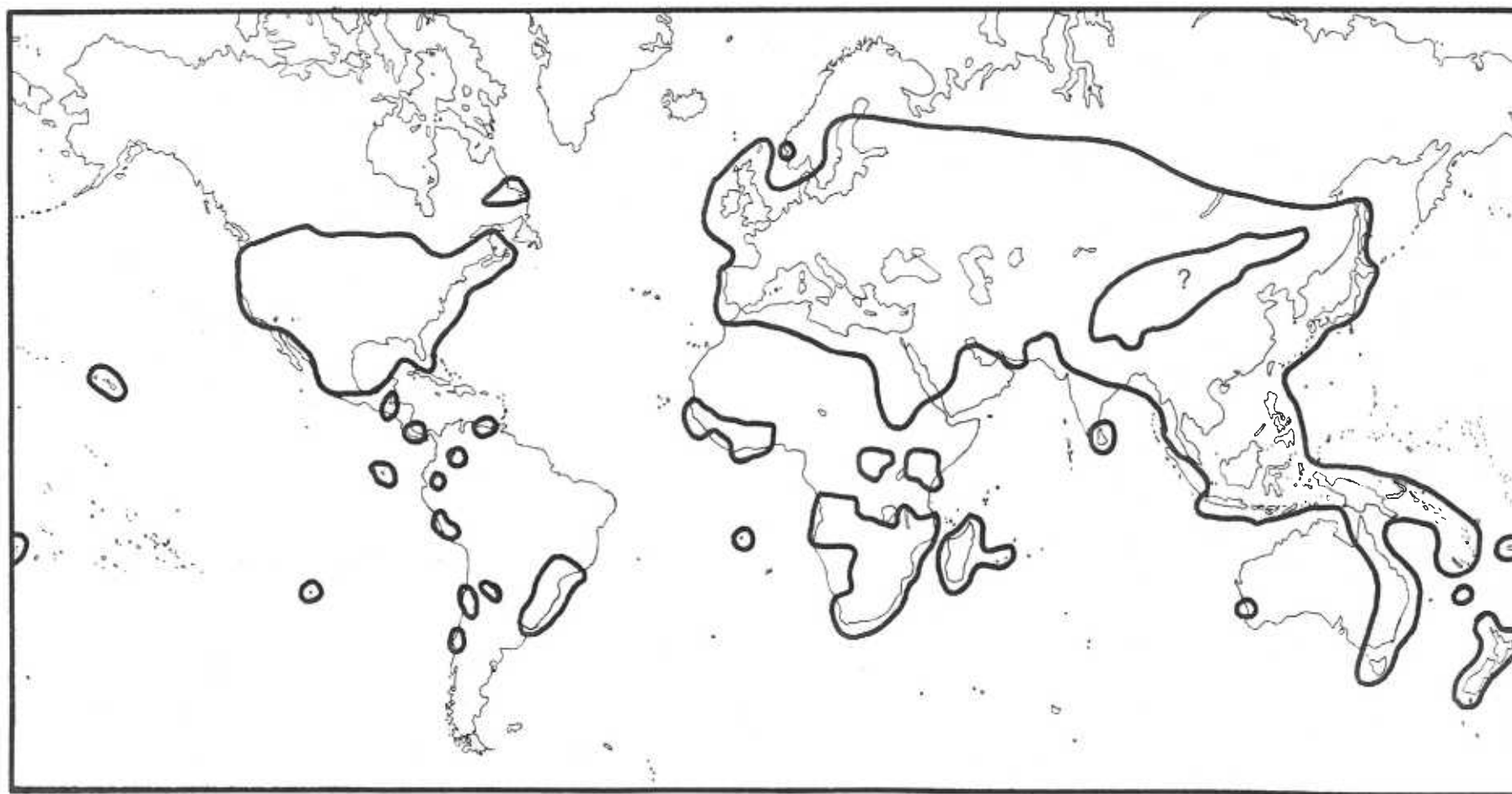


FIG 1. DISTRIBUTION OF *Agrotis ipsilon* (HÜFNAGEL)

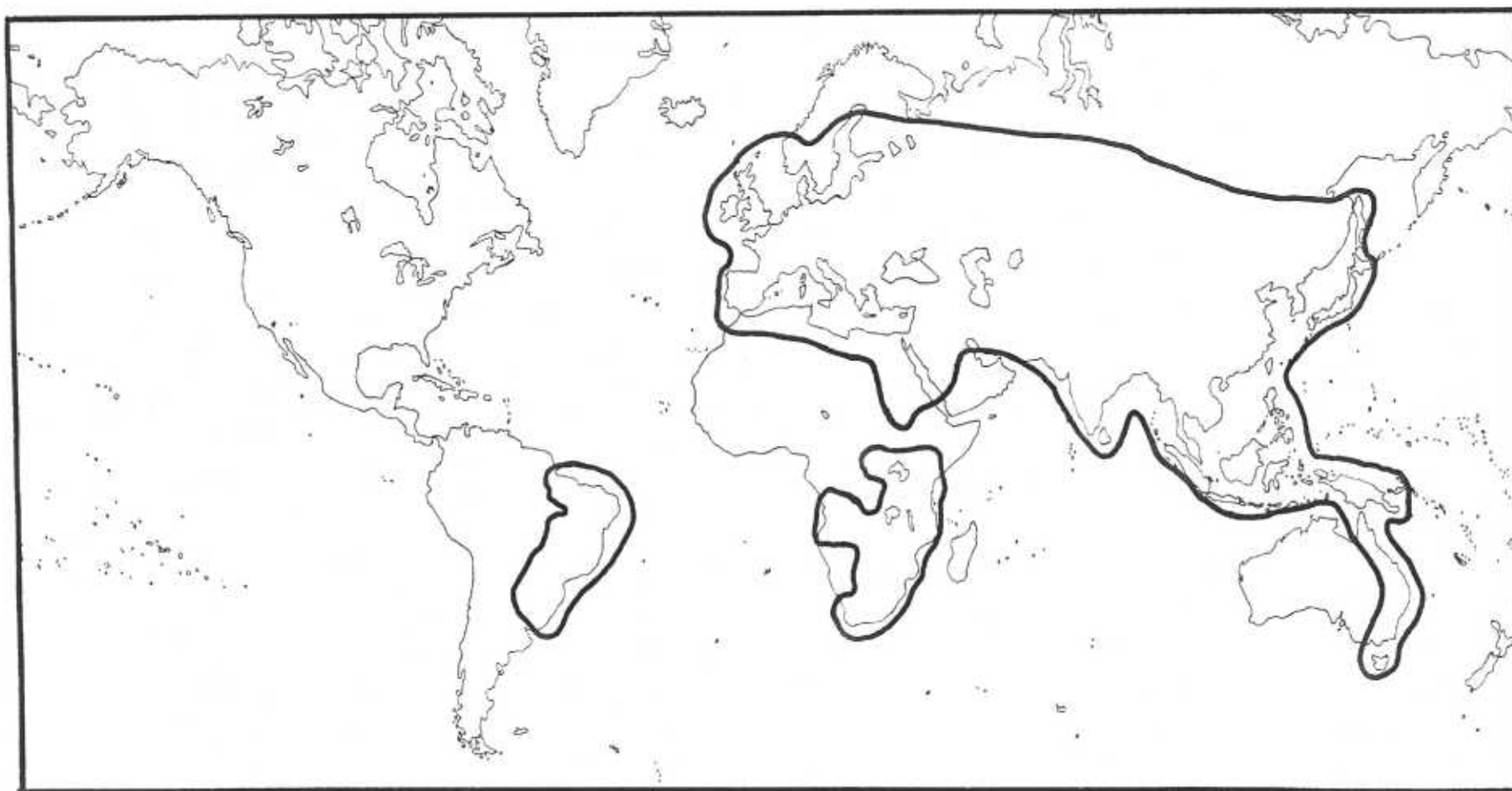


FIG 2. DISTRIBUTION OF *Agrotis segetum* (DENIS & SCHIFF.)

4. LOCALITY OF STUDY AND CLIMATE

All the detailed laboratory investigations have been carried out at the University of Rhodesia and the Salisbury Research Station, both located in Salisbury. The field work was carried out at Gwebi Agricultural College, about 24 km north-west of Salisbury. Salisbury is situated at an altitude of 1 500 m above sea level, latitude $17^{\circ}48' S$ and longitude $31^{\circ}03' E$, in Rhodesia.

The country is landlocked with the Indian Ocean being about 160 km from the eastern border. There is a plateau across Rhodesia in a north-east to south-west direction, forming a watershed on which Salisbury lies. On the eastern border there are highlands, rising up to 2 600 m above sea level, which follow a north to south direction. The altitude and distance from the sea give Rhodesia a remarkably temperatre climate, despite its being situated entirely within the trppics. It is only the low-lying areas, below 600 m, that experience the high temperatures usually associated with tropical regions.

The rainfall is concentrated into one season of about four months, and is considered with temperature when the year is divided into seasons (Patterson, 1970). On this basis the following seasons are distinguished:

Hot season	- mid-August to mid-November;
Main rainy season	- mid-November to mid-March;
Post-rainy season	- mid-March to mid-May;
Cool season	- mid-May to mid-August.

During the hot season the maximum temperatures sometimes exceed

32°C on the plateau and 40°C in the low-lying areas. There is a rapid rise in temperature from mid-August, and temperatures reach a peak in early October, then remaining fairly steady until the start of the main rains. The air is very dry at the beginning of the season, but the mean relative humidity subsequently rises to about 50 per cent.

The main rainy season usually begins between the middle and end of November. Temperatures then show little variation with maximum temperatures of about 26°C on the plateau and about 5°C higher in the lowveld. The diurnal range of temperature is, however, smaller than during the hot season. The main rains are closely linked with the presence of the Inter-Tropical Convergence Zone (ITCZ). Rainfall intensities are often high with falls of 75 to 100 mm over a 24 h period. The mean annual rainfall in Rhodesia decreases irregularly from the north to the south, from over 750 mm to 300 mm, though parts of the eastern border highlands average over 2 500 mm. The mean relative humidity during this season is about 75 per cent.

During the transitional post-rainy season there is often a temporary rise in temperatures, when the rains cease, followed by a downward trend. Showers may occur during the first few weeks of the season, but the air becomes very much drier by May.

During the cool season days are usually sunny and the mid-day temperatures are warm (± 21°C on the plateau), but from late afternoon there is a rapid fall in temperature. The air is usually very dry and heat escapes from the soil by radiation. With this rapid cooling and low dewpoint, temperatures sometimes drop below zero and

ground frosts may occur.

The monthly means of temperature and rainfall on the plateau and lowveld are shown in Figs. 3 and 4.

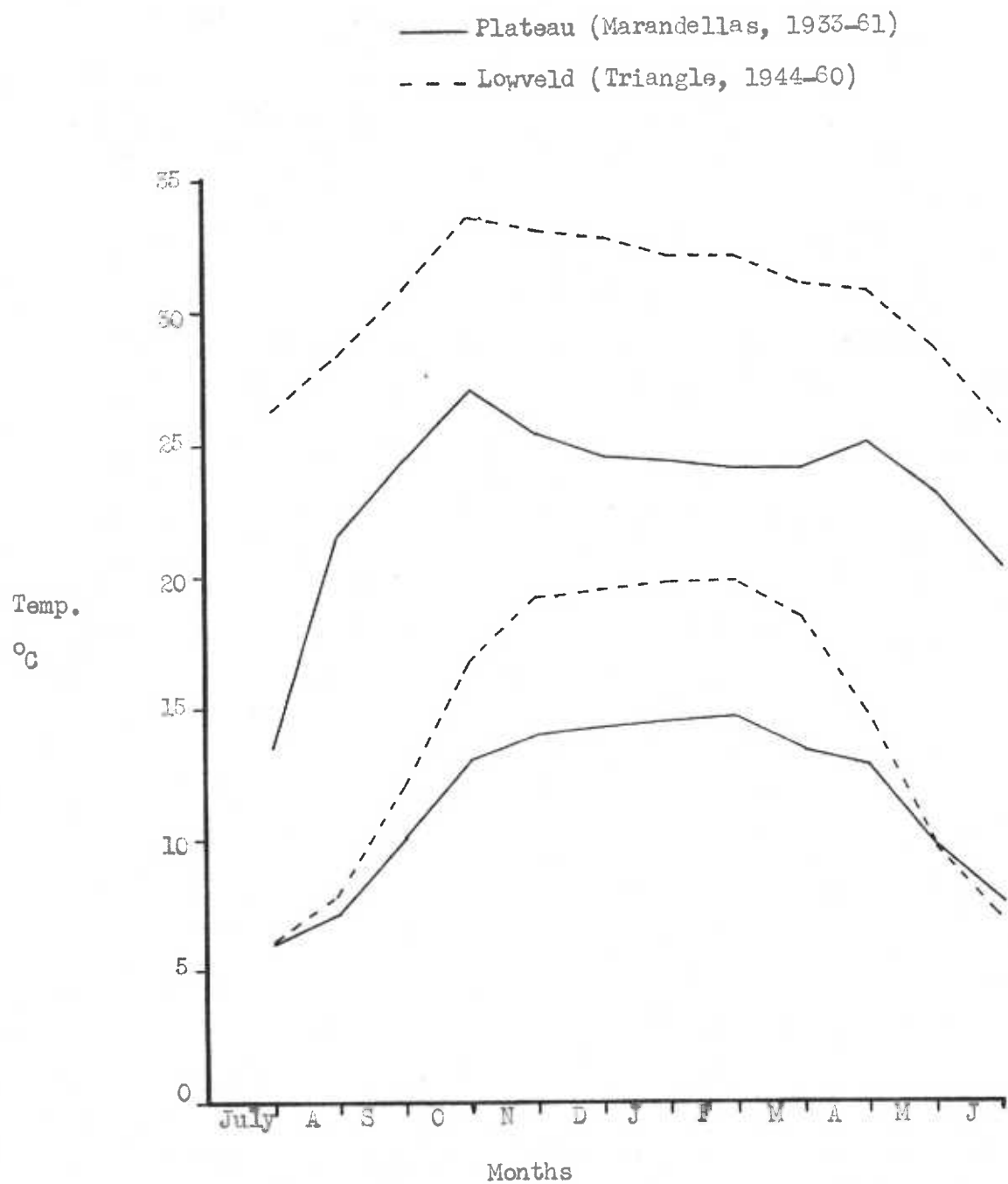


FIG. 3. MONTHLY MEAN MAXIMUM AND MEAN MINIMUM TEMPERATURES ON PLATEAU AND LOWVELD OF RHODESIA.

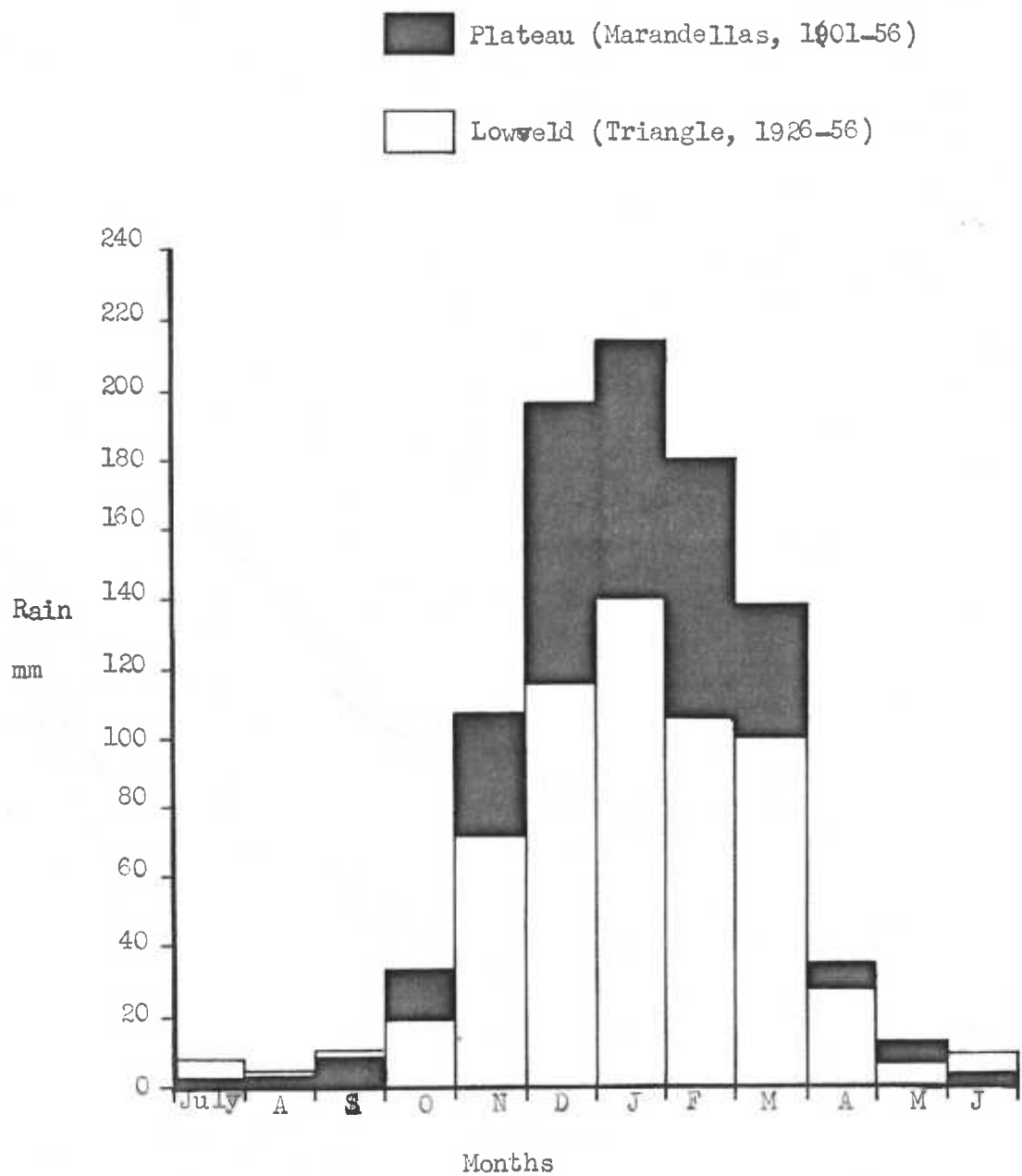


FIG. 4. MONTHLY MEAN RAINFALL ON PLATEAU AND LOWVELD OF RHODESIA.

5. INVESTIGATION OF THE SYSTEMATIC POSITION

5.1. Introduction

It was reported by Jack (1918) that there were four species of cutworms in Rhodesia, and these were named as *Euxoa segetis* Schiff., *E. longidentifera* Hamp., *E. spinifera* Hüb. and *Agrotis insilon* Roths. Rose (1962) also quotes four species in Rhodesia but names them as *Agrotis segetum* Schiff., *A. spinifera* Hüb., *A. insilon* Hüb. and *Euxoa longidentifera* Hamp. From the names attributed to the species by these two authors, with possible synonyms, problems in correct identification were apparent. Consultation of records revealed that another species, *Agrotis muscosa* Geyer, is also recorded as a cutworm in Rhodesia. The importance in clarifying the systematic position of these species became obvious, since correct identification provides a key to published information on life history, behaviour, ecology and other factors important in the management of a pest population.

5.2. Methods

Specimens of named moths in the reference collection of the Plant Protection Research Institute, Ministry of Agriculture, were examined to ascertain the status of the five species.

Live moths were obtained from a Robinson light-trap situated at Salisbury Research Station and each species was confined in glass preserve jars having a gauze lid. Quarter circles of filter paper were placed on the gauze as an oviposition site. Larvae hatching from eggs were placed on a semi-synthetic bean diet (Shorey and Hale, 1965), which will be described in more detail in section 6.2.1. Larval morphology was examined by means of a stereomicroscope having

a maximum magnification of x100, and characters that could be easily observed without dissection were used in constructing a larval key. Larvae in 2nd to 5th instars were used for this purpose and were preserved in Kahle's fluid prior to examination. It was found that Kahle's fluid did not seriously affect colouration of the larvae, its composition being:

95% ethyl alcohol	15 parts
40% formaldehyde	6 parts
glacial acetic acid	1 part
distilled water	30 parts.

Moth emerging from laboratory cultures were pinned and compared with specimens in the reference collection of the Plant Protection Research Institute. Pinned specimens were also submitted to Dr E. C.G. Pinhey of the National Museum of Rhodesia and to Dr I.W.B. Nye of the British Museum (Natural History) for confirmation of identification.

The external genitalia of the male moths were dissected from the species concerned and the right valvae were mounted in Canada Balsam on microscope slides and examined.

5.3. Results

An examination of the moths in the reference^e collection at the Plant Protection Research Institute, Salisbury, indicated that five species of cutworms occur in Rhodesia and all of these are in the genus *Agrotis*, namely *A. secretum*, *A. ipsilon*, *A. spinifera*, *A. long-identifera*, with the additional species being *A. muscosa*.

From examination of the external larval morphology a key was constructed to the five species of cutworm (Blair, 1968). The nomenclature of larval morphology is taken from Crumb (1956).

1. Setigerous tubercle I of abdominal segments distinctly smaller than setigerous tubercle II; skin granules coarse, strongly convex or slightly conical (Fig. 5) ..
..... 2
Setigerous tubercle I of abdominal segments much the same size as setigerous tubercle II; skin granules small, flat, or slightly convex (Fig. 6) segetum
2. Skin granules of posterior half of the sub-dorsal area of the abdominal segments distinctly paler than dorsal and supraspiracular areas 3
Skin granules of the posterior half of the sub-dorsal area of the abdominal segments not distinctly paler than dorsal and supraspiracular areas muscosa
3. Setigerous tubercle IV of abdominal segments at least twice as wide as the width of the spiracles; setigerous tubercle IV approximately the same height as the spiracle ..
..... longidentifera
Setigerous tubercle IV of abdominal segments at least three times the width of the spiracles; setigerous tubercle IV extends beyond the height of the spiracle .. 4
4. Frontal sutures terminating in the occipital angle or on the frons at a point approximately three-quarters its height spinifera
Frontal sutures terminating on the frons at a point approximately half its height ipsilon.

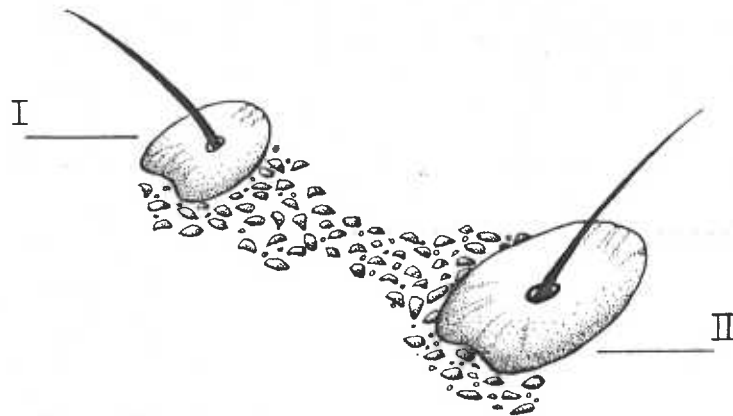


FIG 5. SKIN GRANULES OF *A. ipsilon*

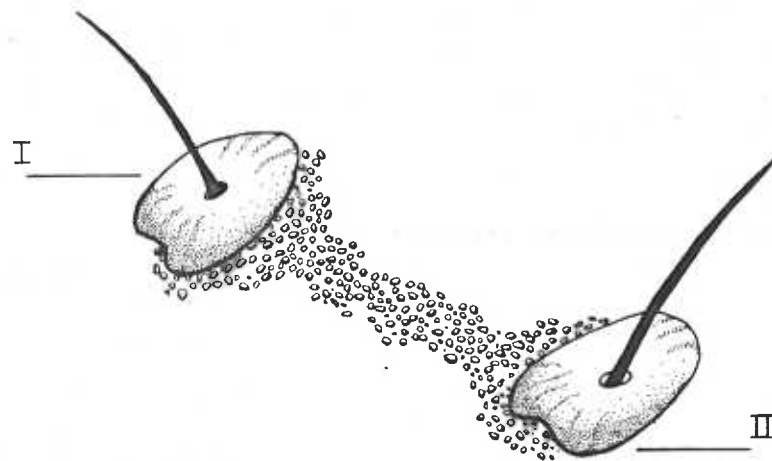


FIG 6. SKIN GRANULES OF *A. segetum*

During laboratory rearing of A. muscosa it was noticed that one culture of larvae had a different colouration and different fascies to the others. The female parent of this unusual culture, which had been collected in the light-trap, had colouration and markings very similar to those of other A. muscosa. The moth was submitted to Dr E.C.G. Pinhey for identification; it was named as Agrotis (Lycophotia) muscosa form amatura. Pinhey expressed the opinion that amatura might be a distinct species.

When the male genitalia were examined, it was seen that the valva of amatura and muscosa were of the same conformation but the harpe of the former was longer and more evenly pointed than the latter (Fig. 7). Also from Fig. 7 it is apparent that the genitalia of these two species was of a different overall conformation to those of A. segetum, A. insilon, A. longidentifera and A. spinifera. During observations on larval behaviour characteristics it was noticed that 1st instar larvae of amatura and muscosa spun silk, whereas none of the other species did so at any stage in their life cycle. External morphology of the moths showed that there is no antennal dimorphism in amatura and muscosa, whereas the males of the other species have plumose antennae and the females have filiform antennae.

From these observations on larval behaviour and adult morphology, it was speculated that amatura and muscosa were distinct species and that they did not belong to the same genus as the other species. Bayer (1964), in describing the valvae of the Agrotinae, places amatura and muscosa as separate species and also places them in the genus Lycophotia.

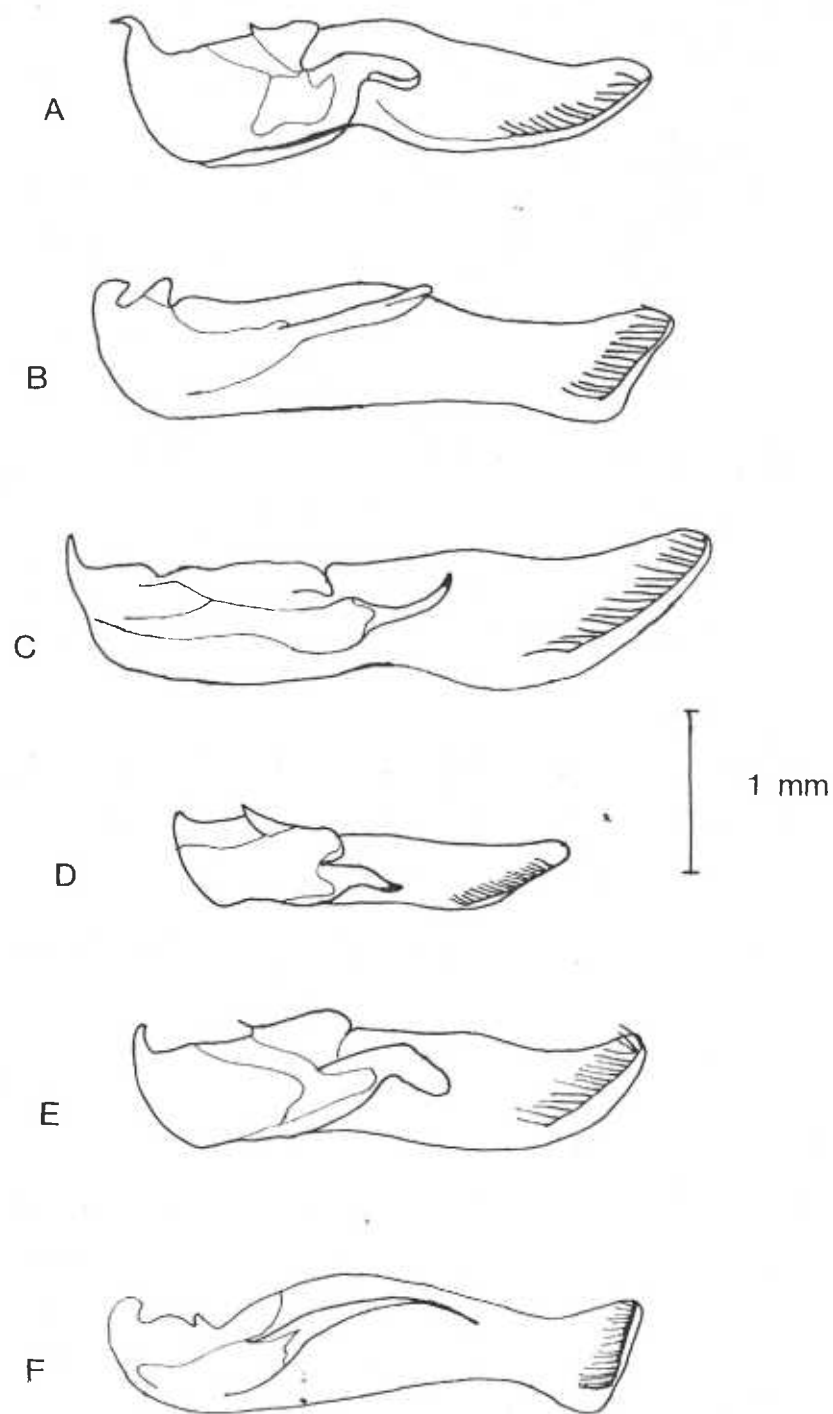


FIG 7. RIGHT VALVAE OF MALE GENITALIA

- A. Agrotis spinifera Hüb.; B. Mentaxya ignicollis Walk.;
 C. A. ipsilon Hüb.; D. A. longidentifera Hamp.; E. A. segetum
 (Denis & Schiff.); F. M. albifrons Geyer.

Dr I.W.B. Nye confirmed the identifications of the Agrotis spp. and also confirmed that anatura and muscosa were distinct species. However, the latter two species were placed within the genus Mentaxya and named as albifrons and ignicollis respectively. The following list summarises what is believed to be the present classification of the cutworms studied in this investigation.

Family : Noctuidae

Sub-family : Agrotinae

Genera : Agrotis Ochsenheimer, 1816, Schmett. Eur. 4: 66.

(Type species: Noctua segetum (Denis & Schiffermüller), 1775, by subsequent designation by Curtis, 1827, Br. Ent. 4: 165)

Mentaxya Geyer, 1837, in Hübner, Zuträge Samml. exot. Schmett. 5: 10.

(Type species: Mentaxya muscosa Geyer, 1837, by subsequent designation by Viette, 1958, Lambillionea 58: 41)

Species : Agrotis ipsilon Hüfnagel (Phalaena ipsilon Hüfnagel, 1766, Berl. Mag. 3: 146)
(original references in parentheses)

Agrotis longidentifera Hampson (Lixoa longidentifera Hampson, 1903, Cat. Lep. Phalaenae Br. Mus. 4: 166)

Agrotis segetum (Denis & Schiffermüller) (Noctua segetum (Denis & Schiffermüller), 1775, Ankündigung Syst. Werkes Schmett. Wienergegend: 81)

Agrotis spinifera Hübner (Noctua spinifera Hübner, 1808, Samml. eur. Schmett. 4: pl. 83, fig. 389)

Mentaxya albifrons Geyer (Eugraphe albifrons Geyer, 1833, in Hübner, Zuträge Samml. exot. Schmett. 5: pl. 148, figs. 859-860)

Mentaxya ignicollis Walker (Agrotis ignicollis
Walker, 1857, List Specimens Lepid. Insects
Colln. Br. Mus. 11: 740).

5.4. Discussion

The confusion of the Agrotis-Lycophotia-Mentaxya species has been clarified by Dr Nye who explains that amatura is a junior subjective synonym of albifrons: that muscosa is a good species but, in the past, both amatura and albifrons have been placed as junior subjective synonyms of it, so there has been a mixture of misidentification and synonymy.

As the relative economic importance of the species in the genus Mentaxya is low, and they do not feature in the literature of economic entomology, it is suggested that they should not be regarded as pests. Their ability to spin silk indicates that their biology is different. The genus Agrotis is the one of economic importance as cutworms in Rhodesia.

6. COMPARISON OF THE DEVELOPMENT OF AGROTIS SEGETUM AND A. IPSILON

6.1. Introduction

The life cycles of A. segetum and A. ipsilon have been documented in many parts of the world (for example Abdel-Gawaad and El-Shazli, 1971; Fiedler, 1937; Harris, Mazarek and White, 1962; Mangat, 1971; Nikoleavskii, 1930; Passos de Carvalho, 1968; Rivnay, 1964; Zimmerman, 1918). However, it was necessary to obtain data on the local 'races' of these two species as Druzhelyubova (1963) found three distinct geographical populations of A. segetum in the Soviet Union, with each population having distinct reactions to climatic factors. Literature on the cutworms of southern Africa (Jack, 1918; Smit, 1948; Rose, 1962) did not reveal much detailed information on the development of the two species, though an attempt was made by Passos de Carvalho (1968) in Angola on A. segetum which she reared at three constant temperatures. A knowledge of the developmental rates of the local 'races' would enable a better understanding of population cycles in the field; consequently the two species were reared in the laboratory under constant conditions.

It was also necessary to be able to identify the different stages in the cycle of the two species, so that development of field populations could be studied; larval head capsules were used to determine the stage of growth (instar).

The problem of defining instars and stages of insects has been a topic of recent controversy (Hinton, 1971; Wigglesworth, 1973; Hinton, 1973). Snodgrass (1935) stated that the beginning of an instar should be reckoned from the time the old cuticle is loosened

from the epidermis. Jenkin and Hinton (1966) introduced the term apolysis for the detachment of the epidermal cells from the cuticle; this was regarded as the crisis of moulting and not ecdysis (when the cuticle is shed). Wigglesworth (1973) points out that apolysis is a gradual process and is, therefore, not a convenient criterion for separating the instars. Hinton (1973) agrees that for many aspects of physiology, behaviour, and ecology of the insect, ecdysis is of much greater significance than apolysis. This is particularly true of the dramatic change in Behaviour at the pupal-adult ecdysis of an endopterygote insect. Since this study is not of a biochemical nature, where apolysis is more important than ecdysis, the classic system of defining instars and stages of insects has been used.

6.2. Methods

6.2.1. Developmental Periods at Constant Temperatures

Moths obtained from a mercury-vapour light-trap situated at the Salisbury Research Station were placed in glass preserve jars, measuring 90 mm in diameter and 170 mm high. The mouths of the jars were fitted with gauze, on top of which were placed quarters of filter paper circles (110 mm in diameter) which were held in position by sand-filled polythene bags. In the jars were placed small containers with cotton wool soaked in a 20 per cent glucose solution, to provide nourishment for the moths. The jars, with the moths, were placed at seven constant temperatures (15°, 18°, 21°, 24°, 27°, 30°, and 33°C) and the resulting eggs, larvae, and pupae were reared at these temperatures. Temperatures were checked by placing thermographs in each regime for seven days at each check. The variation in temperatures were found to be $15^{\circ} \pm 1^{\circ}\text{C}$, $18^{\circ} \pm 0.5^{\circ}\text{C}$, $21^{\circ} \pm 1^{\circ}\text{C}$, $24^{\circ} \pm 1^{\circ}\text{C}$, $27^{\circ} \pm 0.5^{\circ}\text{C}$,

$30^{\circ} \pm 1^{\circ}\text{C}$, $33^{\circ} \pm 1^{\circ}\text{C}$. The course of variation was found to be approximately equal above and below the stated temperatures, so that the latter can be said to be the mean temperatures.

Filter papers on which eggs had been laid were transferred daily to plastic pill boxes; eggs that had been deposited on the walls of the glass jars were transferred by means of a moistened, soft, camel-hair brush. On hatching, the larvae were placed in plastic pill boxes (50 mm in diameter, 22 mm high), having a fine-meshed gauze lid. Approximately 60 newly-hatched larvae were placed in each pill box and the number was decreased successively with their growth, until there were only three full-grown larvae per container. This successive reduction in numbers became necessary for, apart from increased space requirements, it was found that the larvae were cannibalistic. The larvae were provided with a semi-synthetic diet described by Shorey and Hale (1965). The diet consisted of the following ingredients:

Soaked beans	23.54 per cent by mass
Dried brewer's yeast	3.53
Ascorbic acid	0.35
Methyl p-hydroxybenzoate	0.22
Sorbic acid	0.11
Formaldehyde (40% solution)	0.22
Agar	1.41
Water	70.62
	100.00

The agar, as a warm solution, was added to the diet after it had been homogenised and the mixture was poured into trays 15 mm deep and allowed to gel. Once gelled, the diet was cut into 25 mm squares,

placed in polythene bags and stored in a refrigerator until required. Despite the three preservatives and mould inhibitors (methyl p-hydroxybenzoate, sorbic acid, and formaldehyde), included in the diet, it was found that the plastic pill boxes had to be disinfected in a 0.5 per cent solution of sodium hypochlorite to keep fungal and bacterial contamination to a minimum. Larvae were given fresh food at frequent intervals in order to reduce the incidence of contamination and to ensure that larval growth was not hindered.

When larvae had pupated, the pupae were removed from the diet, sexed (see section 6.3.2. (c)), and placed in disinfected pill boxes. Moths emerging from the laboratory cultures were used in further laboratory breeding, though moths obtained by light-trapping from 'wild' populations were continually introduced into the laboratory cultures. By this cross-breeding between the 'wild' and laboratory populations, the frequency of 'wild-type' genes was maintained in the gene pool.

Observations and records were made between 0800 h and 1200 h each day, so that individuals were observed at approximately 24 h intervals. The times taken for completion of each stage of development in the life cycle were noted for each temperature. From these results the mean periods of development were calculated together with their standard deviations and standard errors. Further treatment of the results was undertaken to compute the temperature-velocity and temperature-time curves of each stage over the range of temperatures used (Davidson, 1944). The mean developmental period in days and their reciprocals were plotted against temperature. A logistic curve of the form $\frac{1}{y} = \frac{K}{1 + e^{a - bx}}$ was fitted to the data. The fraction $\frac{1}{y}$ represents the reciprocal of the time required for complete

development to be achieved at a given temperature x ; and K , a and b are constants. The constant K was obtained from the formula

$$K = \frac{2P_1P_2P_3 - P_2^2(P_1 + P_3)}{P_1P_3 - P_2^2}, \text{ where } P_1, P_2 \text{ and } P_3 \text{ are values for } \frac{100}{y}$$

at three equally spaced temperatures. The value of K was substituted into the formula $\log_{10} \frac{K - P}{P}$ to obtain y^i which was then used in the formula for linear regression, $y^i = a + bx$. Thus values for a and b were calculated, and multiplied by 2.3026 to convert common to Napierian logarithms. The values of the constants K , a and b were then used in the equations for calculating development periods in days from known constant temperatures $\left\{ y = \frac{1 + e^{a - bx}}{K} \right\}$ and ~~for~~

for calculating percentage development in one day $\left\{ \frac{100}{y} = \frac{100 K}{1 + e^{a - bx}} \right\}$.

6.2.2. Description of Stages in Life Cycle of *A. segetum* and *A. ipsilon*

To provide a basis for the identification of species in the field, external morphological features of each stage in the life cycle were examined by means of a stereomicroscope having a maximum magnification of $\times 100$. Features that provided a means of distinguishing the two species were noted.

The larvae of both *A. ipsilon* and *A. segetum* undergo a series of moults during the growth process. Each stage of growth (instar) can be determined by the width of the head capsule, which is the least variable portion of the larva and the most durable part of the exuvium (Satterthwait, 1933). A population of each species was reared in the laboratory and the moulted head capsules were collected after each

moult. A total of 100 capsules from each instar were mounted on slides and measurements of width were made using a micrometer eyepiece in a stereomicroscope. The magnification used varied from x16 to x40, so that accurate results could be obtained.

6.3. Results

6.3.1. Development Periods at Constant Temperatures

(a) Incubation Periods of Eggs

The mean periods of incubation of eggs placed at seven constant temperatures are shown in Table I. The logistic curves for the two species are shown in Figs. 8 and 9, and the equations for determining the developmental periods in days (y) at known constant temperatures (x) are:

$$\text{A. ipsilon} \quad y = \frac{1 + e^{3.7834 - 0.1709 x}}{0.408737}$$

$$\text{A. segetum} \quad y = \frac{1 + e^{5.7653 - 0.3105 x}}{0.251320}$$

The equations for the average development per day are the reciprocals of the above x100 (temperature-time curve).

It can be seen from Table I that A. ipsilon is able to complete embryonic development in a shorter time than A. segetum at all the temperatures tested.

(b) Developmental Periods of the Larvae

The means periods of development of the larvae, fed on a semi-synthetic bean diet at seven constant temperatures, are shown in Table II. A groundnut diet, based on the bean diet,

TABLE I. DEVELOPMENTAL PERIODS OF EGGS OF A. IPSILON AND
A. SEGETUM AT SEVEN CONSTANT TEMPERATURES.

Species	Temp. °C	Mean period (days)	S.D.	S.E.	n
<u>A. epsilon</u>	15	12.9	1.08	0.03	1 289
	18	7.1	0.74	0.02	1 376
	21	4.9	0.80	0.02	1 585
	24	4.2	0.49	0.01	2 426
	27	3.4	0.68	0.02	1 149
	30	3.1	0.41	0.01	1 645
	33	2.9	0.22	0.01	502
<u>A. segetum</u>	15	14.5	1.21	0.04	914
	18	8.8	0.98	0.03	1 059
	21	5.7	0.76	0.02	1 434
	24	4.9	0.84	0.02	1 763
	27	4.3	0.78	0.03	675
	30	4.2	0.39	0.01	1 495
	33	4.0	0.47	0.02	555

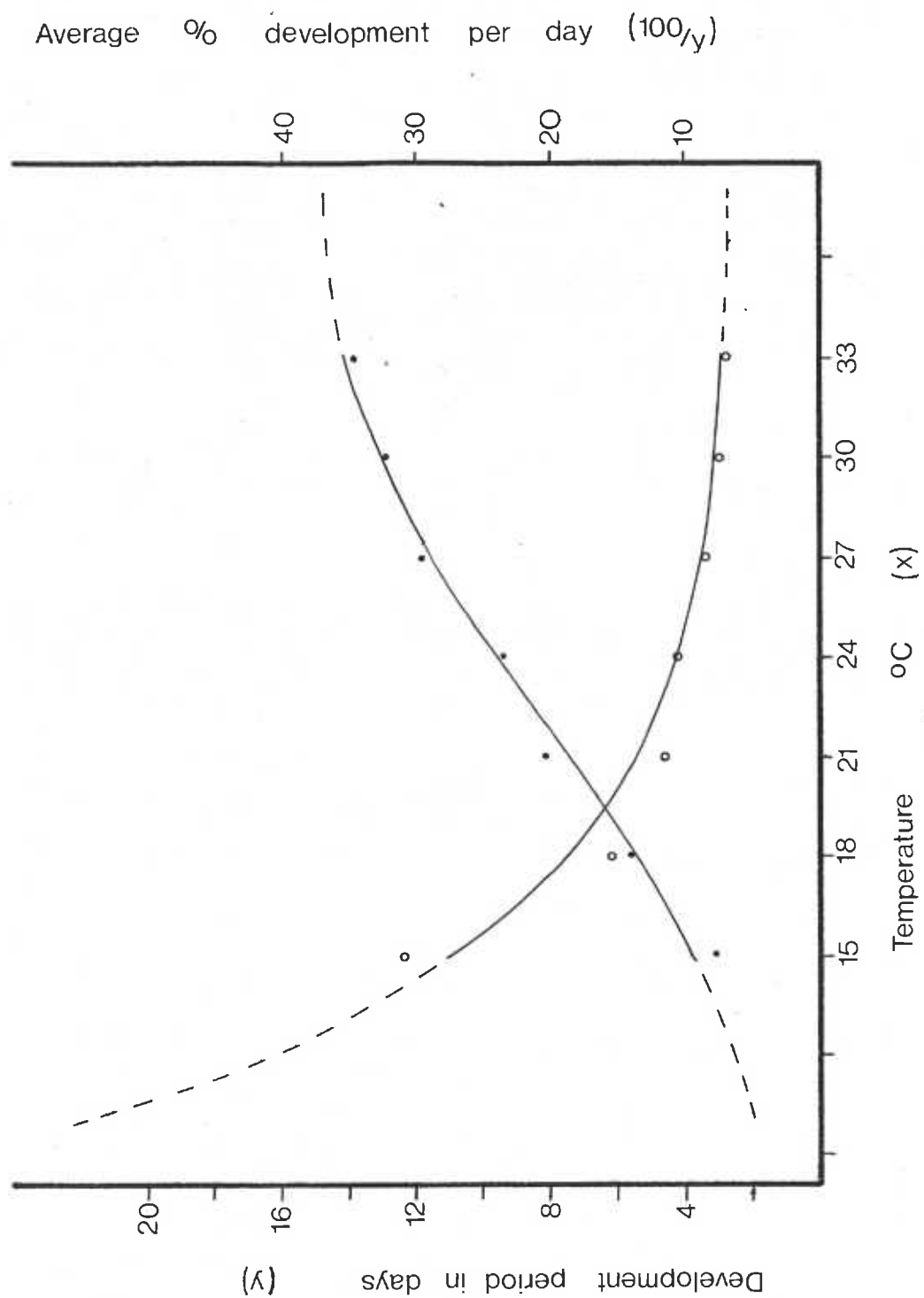


FIG 3. INCUBATION PERIODS OF *A. ipsilon* EGGS

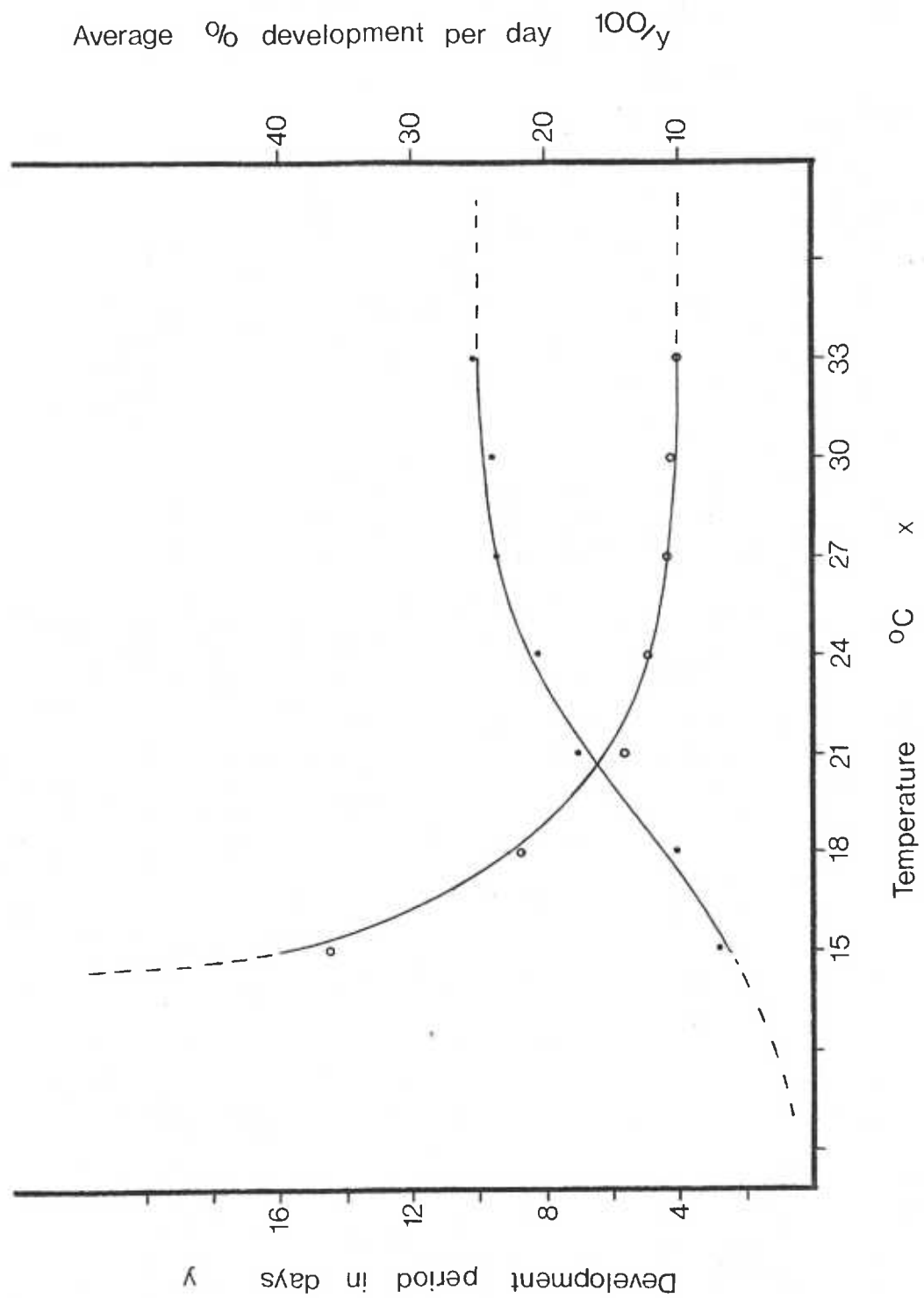


FIG 9. INCUBATION PERIODS OF *A. segetum* EGGS

TABLE II. DEVELOPMENTAL PERIODS OF LARVAE OF A. IPSILON
AND A. SEGETUM AT SEVEN CONSTANT TEMPERATURES AND REARED
ON BEAN DIET.

Species	Temp. °C	Mean period (days)	S.D.	S.E.	n
<u>A. ipsilon</u>	15	77.7	4.96	0.63	62
	18	41.3	17.25	2.44	50
	21	33.2	2.90	0.53	30
	24	28.9	2.59	0.24	116
	27	24.8	2.26	0.32	50
	30	21.4	1.21	0.40	27
	33	20.2	1.11	0.27	17
<u>A. segetum</u>	15	128.3	4.52	0.87	27
	18	62.8	1.61	0.18	80
	21	36.9	2.93	0.29	102
	24	33.2	5.82	0.56	108
	27	28.6	2.78	0.29	92
	30	31.1	4.74	0.45	111
	33	24.7	1.51	0.15	101

was offered to the larvae but it was found that a very high degree of mortality occurred. The few results that were obtained indicated that larval development was almost doubled. With the high mortality and the protracted developmental periods, the groundnut diet was discarded as being neither suitable nor reliable to obtain data that could be related to the field. The logistic curves for the larvae reared on the bean diet are shown in Figs. 10 and 11, and the equations used in calculating the periods in days (y) and the constant temperatures (x) are:

$$\underline{A. \text{ epsilon}} \quad y = \frac{1 + e^{3.0473 - 0.0978 x}}{0.098483}$$

$$\underline{A. \text{ segetum}} \quad y = \frac{1 + e^{7.0865 - 0.3825 x}}{0.036054}$$

Again it can be seen that A. epsilon develops at a faster rate than does A. segetum at all of the temperatures tested.

(c) Developmental Periods of the Pupae

The mean periods of development in the pupal stage at the temperatures used are shown in Table III. The developmental periods of both sexes have been tabulated separately, but the logistic curves (Figs. 12 and 13) have been calculated using the combined mean periods of both males and females. The equations used for the logistic curves are:

$$\underline{A. \text{ epsilon}} \quad y = \frac{1 + e^{3.2900 - 0.1125 x}}{0.188609}$$

$$\underline{A. \text{ segetum}} \quad y = \frac{1 + e^{3.9928 - 0.2108 x}}{0.082676}$$

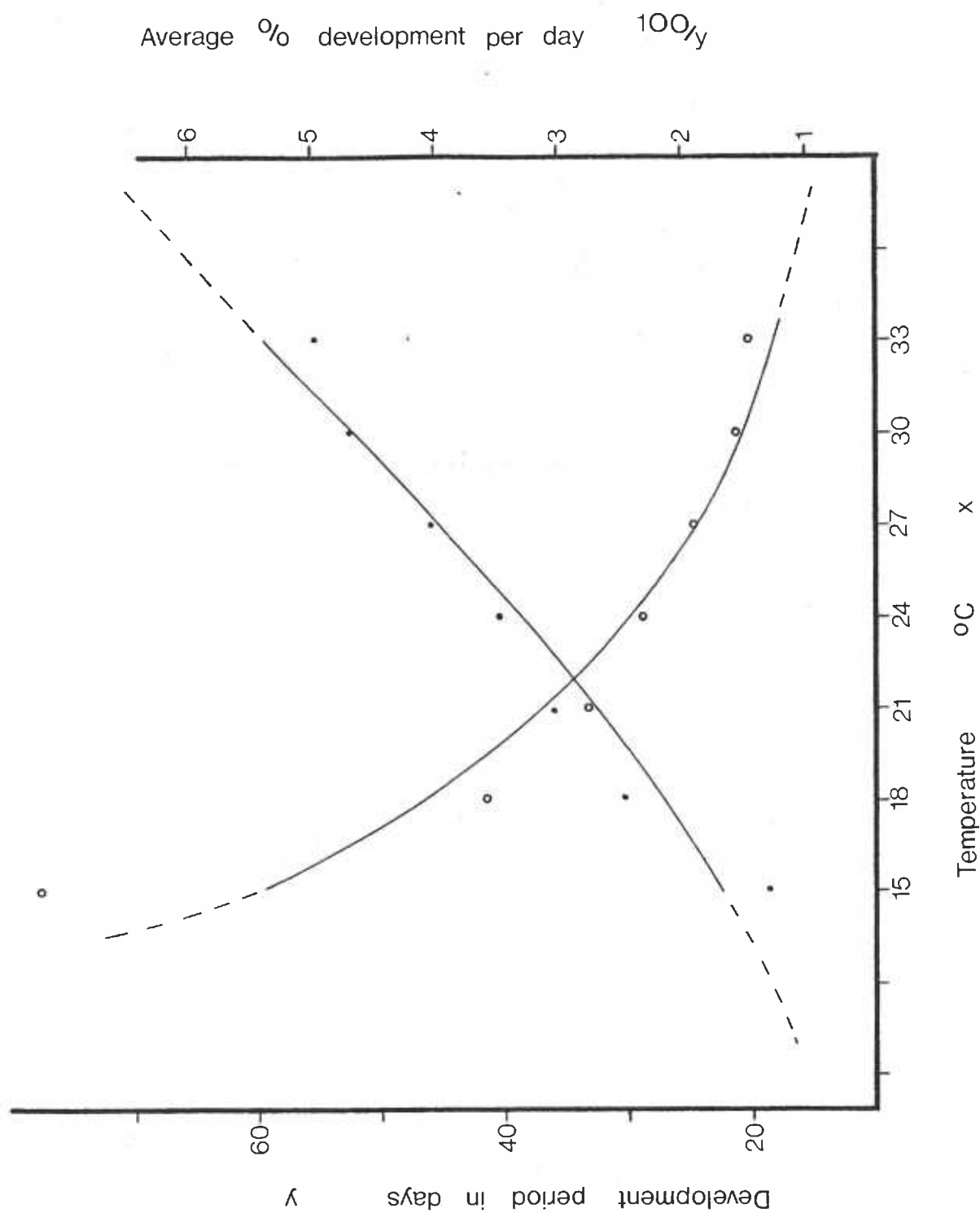


FIG 10. LARVAL PERIODS OF *A. ipsilon*

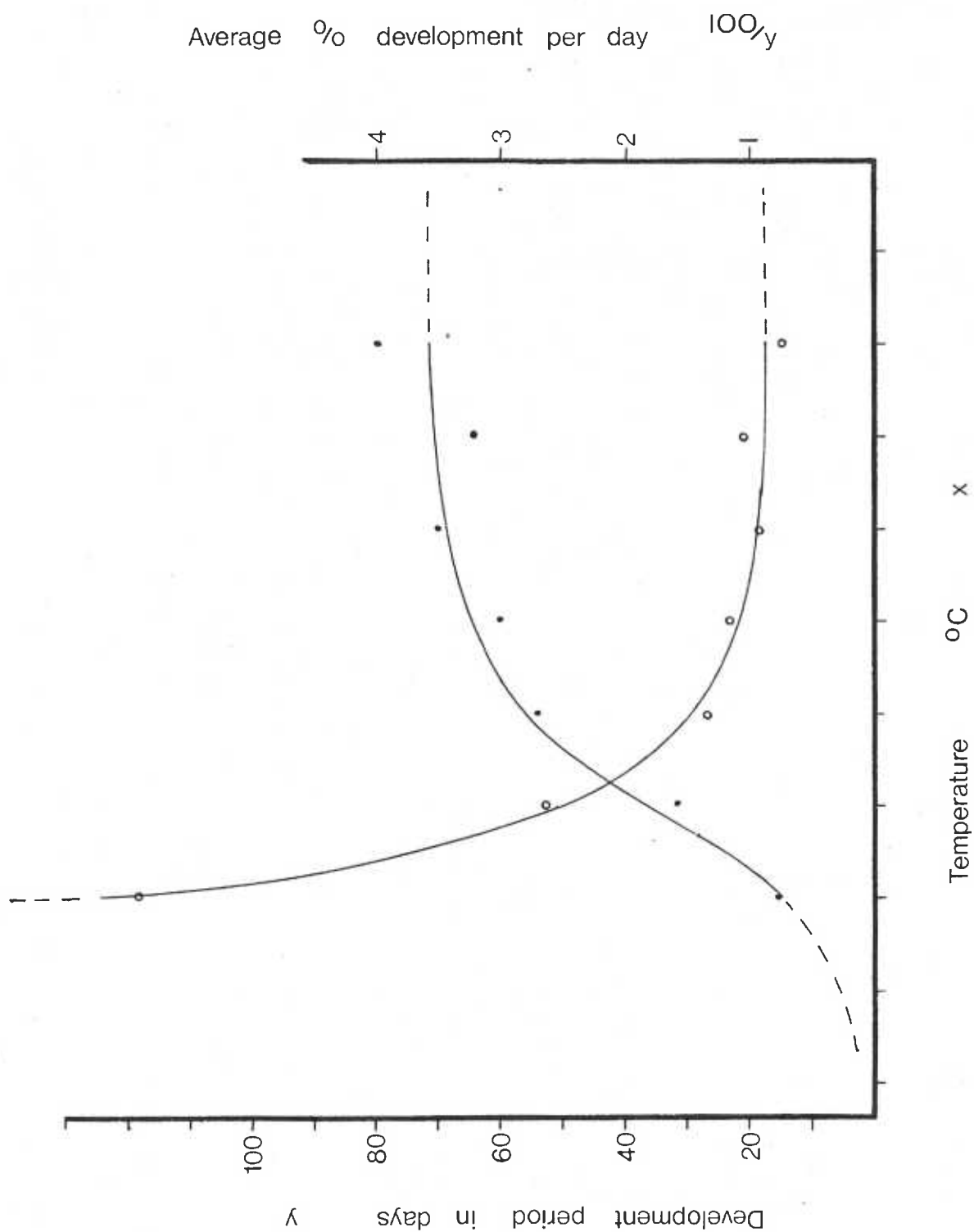


FIG 11. LARVAL PERIODS OF *A. segetum*

TABLE III. DEVELOPMENTAL PERIODS OF PUPAE OF A. IPSILON AND A. SEGUTUM
AT SEVEN CONSTANT TEMPERATURES.

Species	Temp. °C	Male pupae				Female pupae			
		Mean	S.D.	S.E.	n	Mean	S.D.	S.E.	n
<u>A. ipsilon</u>	15	39.9	1.83	0.46	17	38.5	1.50	0.42	14
	18	23.4	0.72	0.20	14	23.3	1.19	0.32	15
	21	16.3	0.75	0.23	12	16.0	1.06	0.43	7
	24	14.4	1.24	0.31	17	14.2	1.82	0.37	25
	27	12.1	1.13	0.38	10	11.1	0.90	0.28	11
	30	9.8	0.75	0.38	5	9.8	1.32	0.66	5
	33	9.0	-	-	1	10.0	-	-	3
<u>A. segutum</u>	15	44.5	1.92	0.61	11	44.0	2.65	1.00	8
	18	27.7	1.13	0.24	23	26.2	1.86	0.35	30
	21	18.8	1.32	0.26	28	17.7	1.21	0.22	30
	24	17.4	1.61	0.28	34	15.7	0.85	0.18	24
	27	14.7	2.24	0.52	20	13.3	1.35	0.29	22
	30	13.3	1.34	0.32	19	13.7	1.24	0.25	26
	33	12.2	0.95	0.25	16	11.6	0.62	0.18	13

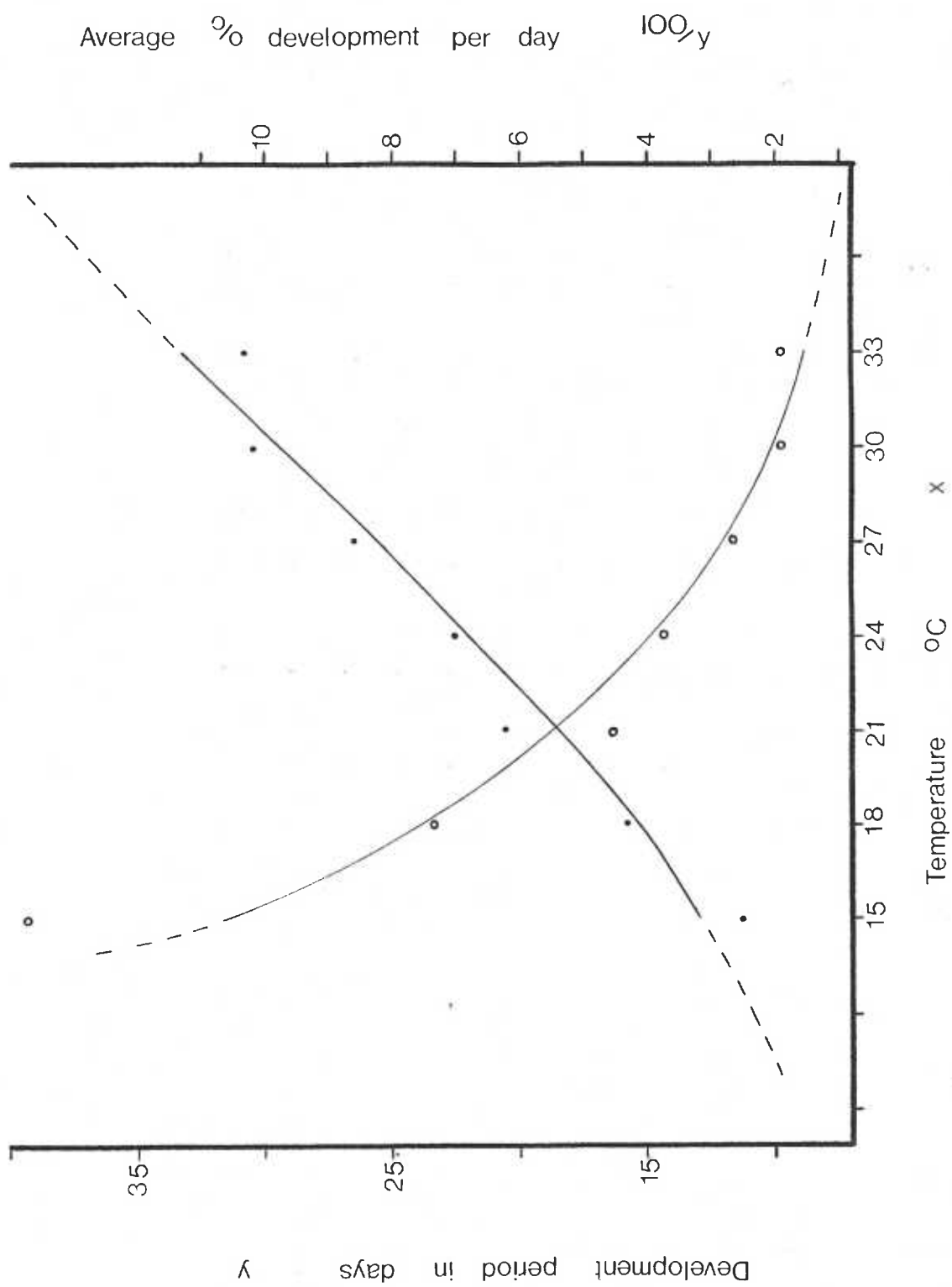


FIG 1. PUPAL PERIODS OF *A. epsilon*

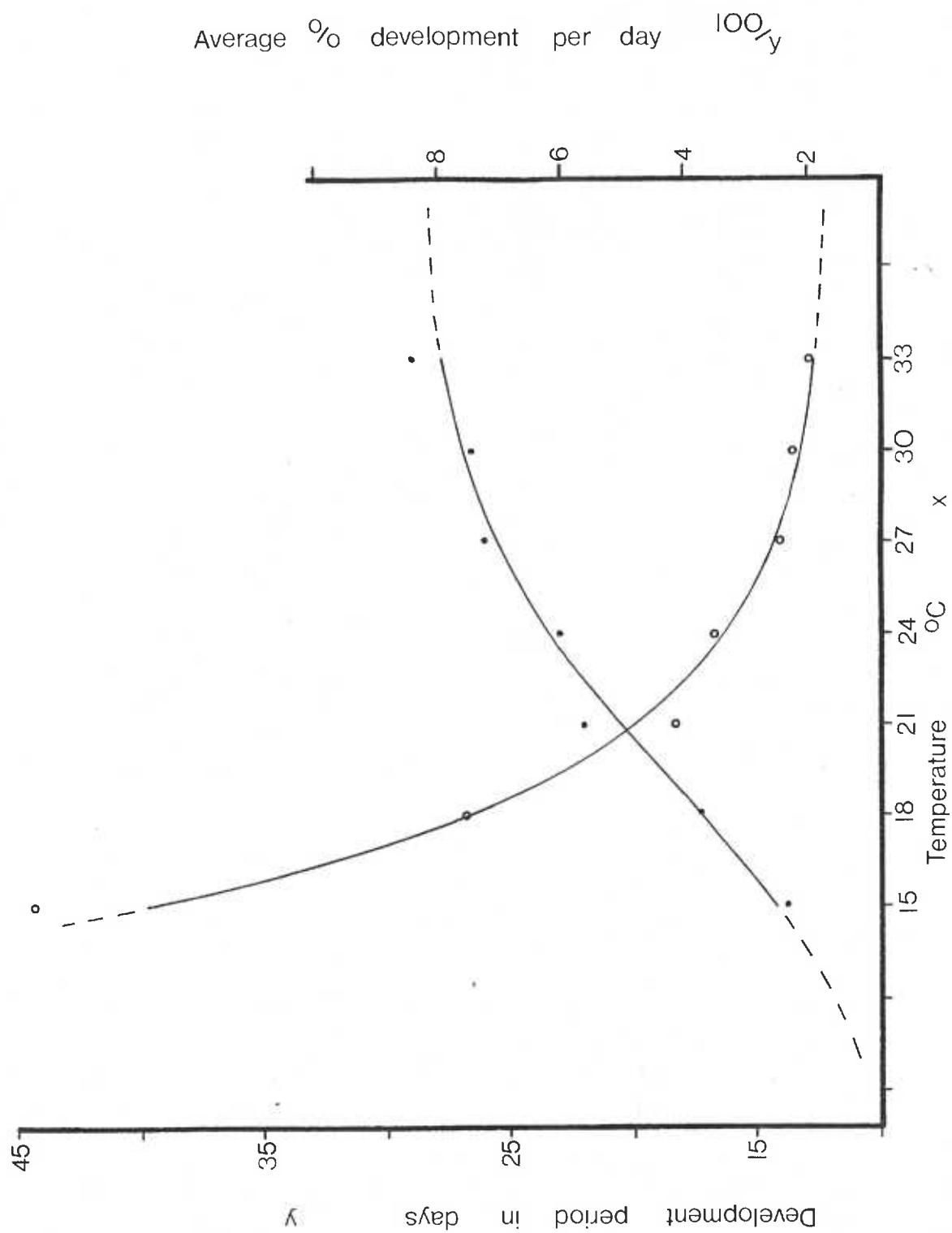


FIG 18. PUPAL PERIODS OF *A. segetum*

The more rapid development of A. ipsilon is again encountered in the pupal stage.

(d) Developmental Periods of Whole Cycle

The mean period for completion of the immature stages of both species at the temperatures used are tabulated in Table IV, and the logistic curves have been calculated from mean periods of development of egg, larva, and of both sexes of the pupae. As the size of sample of each stage was different, it was not possible to compute the standard deviations and standard errors for the whole cycle. The logistic curves have been calculated using the following equations and are shown in Figs. 14 and 15.

$$\text{A. ipsilon} \quad y = \frac{1 + e^{3.1227 - 0.1107 x}}{0.052174}$$

$$\text{A. segetum} \quad y = \frac{1 + e^{5.0244 - 0.2754 x}}{0.02192}$$

Taking the times for completion of the whole cycle from the deposition of eggs to the emergence of adults from pupae, it can be clearly seen that A. ipsilon is capable of faster development than A. segetum at all temperatures.

6.3.2. Description of Stages in Life Cycle of A. segetum and A. ipsilon

(a) Eggs (Plate 1)

The freshly-deposited eggs of Agrotis ipsilon and A. segetum are pure white, though there may be tinges of brown from scales of the female's abdomen, and in shape are ovoid but compressed at the base (anal pole). From the elevated micropylar field (cephalic pole), ridges radiate like meridians to the points of adhesion with the substrate. The radiating ridges give the eggs a sculptured appearance, and it is on this basis that the eggs of

TABLE IV. DEVELOPMENTAL PERIODS OF THE IMMATURE STAGES OF
A. IPSILON AND A. SEGETUM AT SEVEN CONSTANT TEMPERATURES.

Species	Temp. °C	Mean period (days)
<u>A. ipsilon</u>	15	128.9
	18	71.8
	21	54.3
	24	47.4
	27	39.8
	30	34.3
	33	32.6
<u>A. segetum</u>	15	187.1
	18	98.6
	21	60.9
	24	54.7
	27	46.9
	30	48.8
	33	40.6

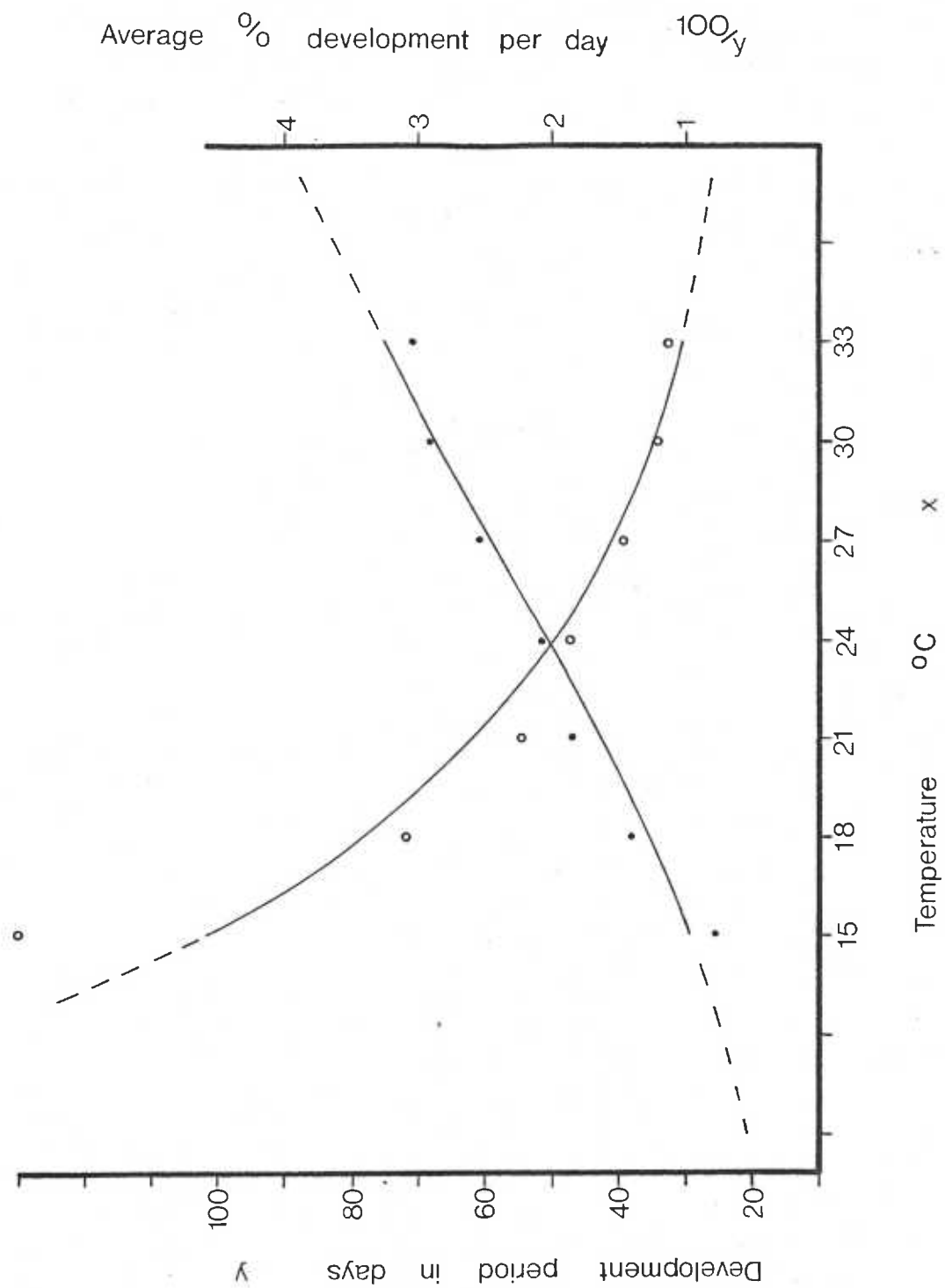


FIG 14. TOTAL IMMATURE PERIODS OF *A. ipsilon*

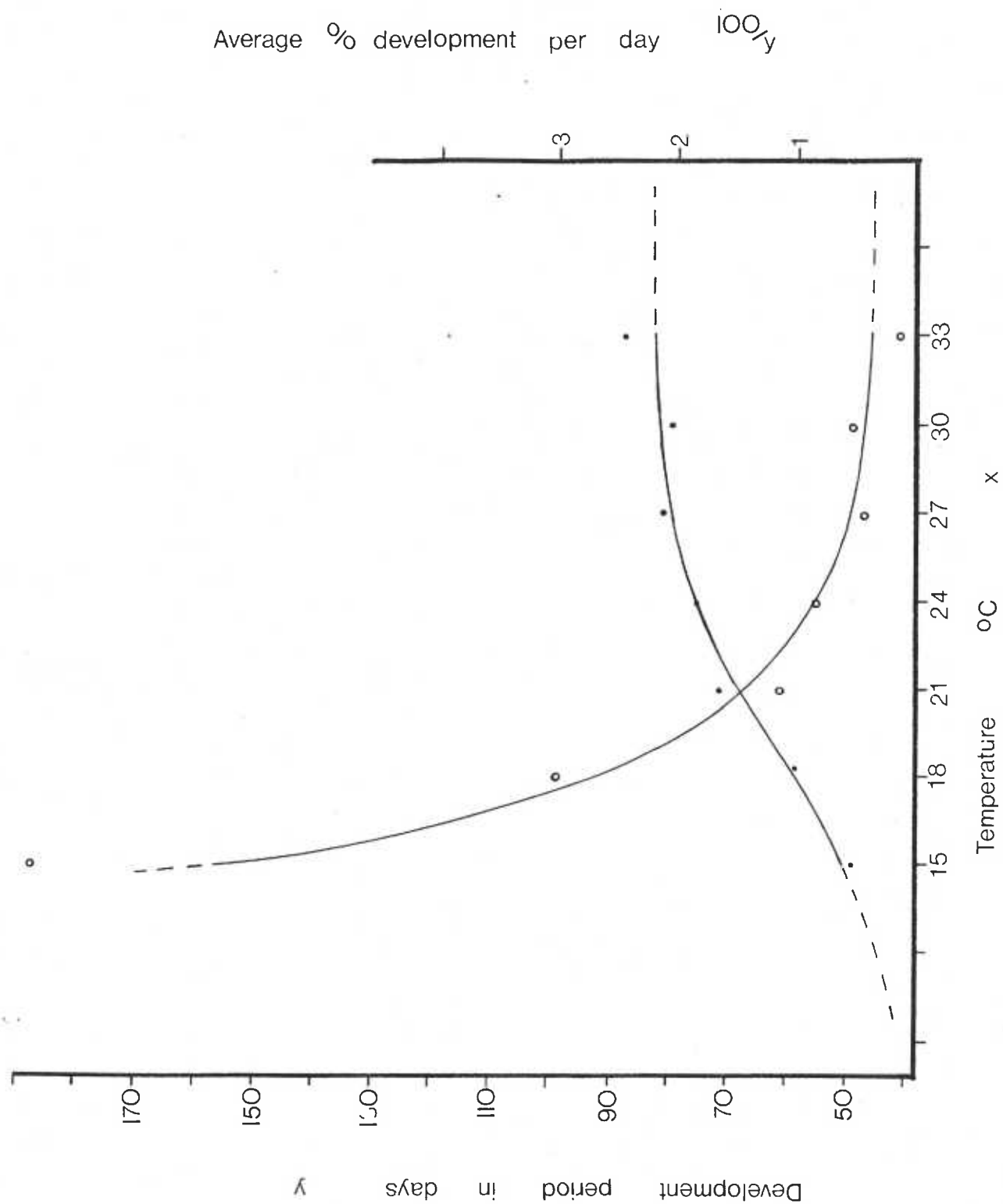


FIG 15. TOTAL IMMATURE PERIODS OF *A. segetum*



PLATE 1. EGGS OF AGROTIS SPP.

the two species can be readily distinguished. The troughs between the ridges of A. segetum are generally smooth at the micropylar end with a few pits towards the base, whereas cross-connecting ridges occur in the troughs of A. epsilon giving a distinctly pitted appearance.

About 24 h after being deposited, the eggs lose the white colour. A red-brown spot, of irregular shape and size, appears around the micropylar field and an irregular band of the same colour appears around the 'equator' of the egg. The rest of the egg darkens in colour to a light-grey. Later the egg becomes a uniform dark-grey colour and the embryo becomes visible within the chorion. The darkly pigmented head capsule of the embryo can be distinguished shortly before it is due to hatch.

Fiedler (1936) found that hatching of the young larvae takes place mainly at night. As the embryo lies in a spiral within the chorion, the exit hole that is chewed by the larva is found to the side of the micropylar field. After hatching the larvae feed on the chorion, starting at the exit hole, and continue until about half is consumed. The empty egg sac is the first food source of the newly-hatched larvae (Fiedler, 1936).

(b) Larvae (Plate 2)

From the measurements of larval head capsules, the mean and range of widths of each larval instar were determined, as shown in Table V and in Fig. 16.

From Table V and Fig. 16 it can be seen that A. segetum

TABLE V. MEAN WIDTH AND RANGE OF WIDTHS OF LARVAL HEAD CAPSULES

Species	Instar	Mean width (mm)	S.D.	Range of width (mm)
<u>A. ipsilon</u>	1	0.30	0.01	0.25 - 0.33
	2	0.49	0.03	0.44 - 0.54
	3	0.80	0.05	0.68 - 0.90
	4	1.35	0.09	1.10 - 1.68
	5	2.08	0.14	1.84 - 2.40
	6	3.07	0.22	2.50 - 3.63
	7	3.43	0.16	3.19 - 3.63
<u>A. segetum</u>	1	0.32	0.01	0.26 - 0.36
	2	0.54	0.03	0.48 - 0.59
	3	0.82	0.04	0.72 - 0.92
	4	1.34	0.09	1.04 - 1.68
	5	2.00	0.11	1.76 - 2.44
	6	2.91	0.21	2.32 - 3.36

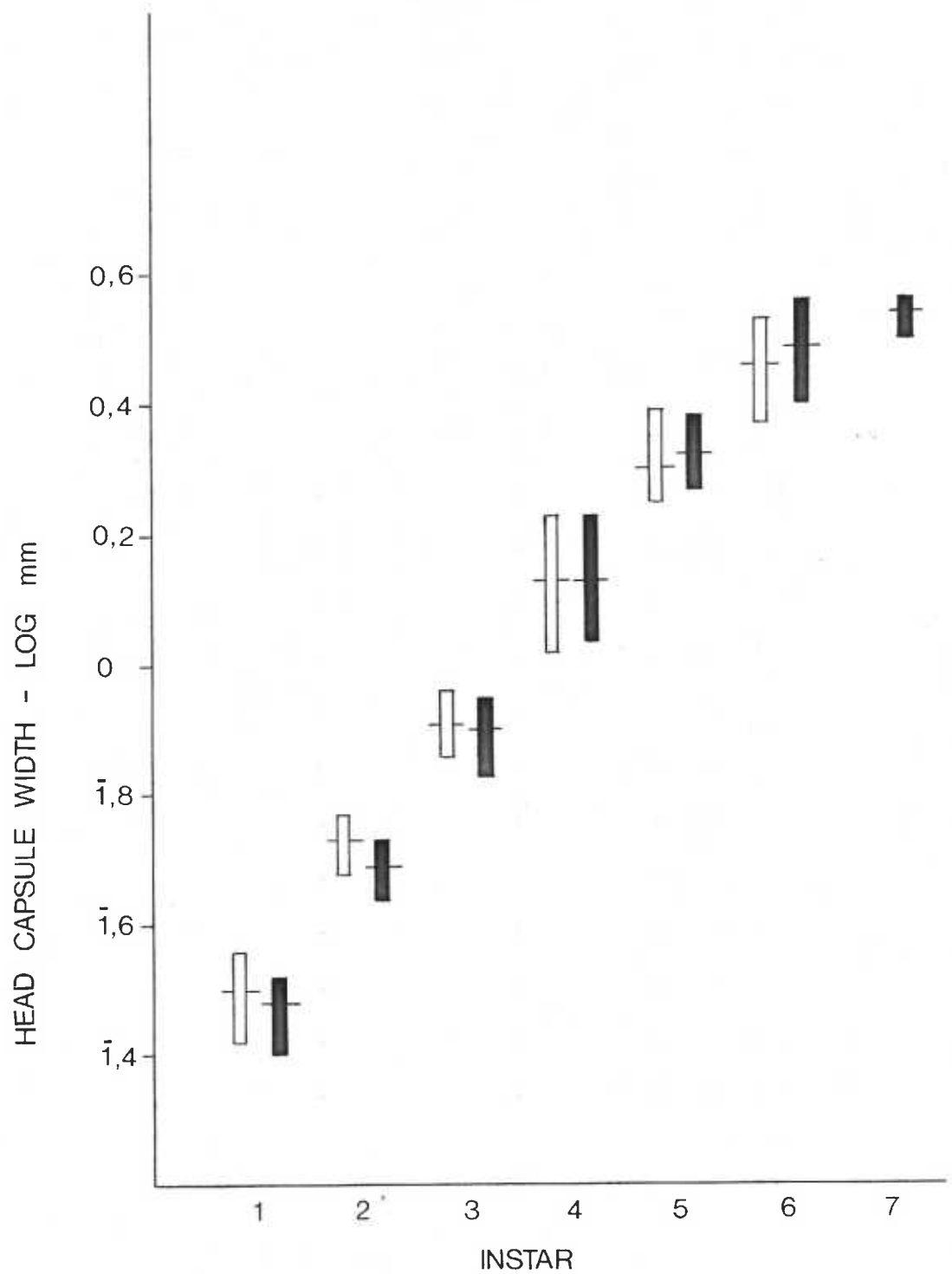


FIG 16. MEANS AND RANGES OF LARVAL HEAD CAPSULE WIDTHS

 A. epsilon
 A. segetum



PLATE 2. LARVA (left), PREPUPA (centre), AND PUPA (right)
OF AGROTIS SPP.

passed through six larval instars while seven are listed for A. ipsilon. However, of the population of A. ipsilon under observation only 6.6 per cent underwent the extra moult; the head capsules were no wider than those of 6th instar, so that despite an extra moult there appeared to be no appreciable growth.

First instar larvae are about 1.5 mm in length after hatching and grow to about 4 mm before the first moult takes place. Only two pairs (on abdominal segments V and VI) of the full complement of four pairs of abdominal pseudopods are functional during the 1st instar, so that the larvae have a semi-looping gait at this stage.

In the 2nd instar the third pair of pseudopods on abdominal segment IV become functional, so that the gait is somewhat looping. The length of the larvae varies from about 4 mm to 6 mm when in 2nd instar. During the 3rd instar all the abdominal pseudopods become functional, though the anterior pair on abdominal segment III may be reduced, and the gait is nearly normal. The larvae range in length from about 6 mm to 11 mm at this stage. By the 4th instar, when they vary in length from 11 mm to 19 mm, the gait is completely normal with all pseudopods completely developed. Fifth instar varies from about 19 mm to 26 mm, while 6th instar ranges from about 26 mm to 38 mm though A. ipsilon usually reaches a length of about 43 mm.

The larvae of A. segetum vary somewhat in colour, but are mostly a uniform dull-grey or lead coloured and frequently there is a suggestion of a reddish broad median dorsal stripe.

A. epsilon larvae are usually darker in colour than those of A. secretum, greasier in appearance, and rather more constricted between the segments. However, the two species are more easily distinguished in the larval stage by the skin granules, and the larval key (Blair, 1938) has been found useful for larvae in 2nd instar upwards (see section 5.3.).

When the larvae become fully grown, they cease feeding and prepare an earthen cocoon in which to pupate. Fiedler (1936) found that a fluid is secreted from the salivary glands and is mixed into the soil surrounding the larva by rolling and turning movements. These movements also enlarge and smoothe the cell in which the larva is located. Once the pupal cell is constructed, the larva becomes inactive and shrinks along its longitudinal axis undergoing a change in colouration from light- or dark-grey to a cream or yellow. This stage is known as the pre-pupa (Plate 2), a transition phase during which the full-grown larva prepares for the transformation to pupa. The pre-pupa in Lepidoptera does not, however, constitute a distinct instar (Imms, 1957), but includes the pharate pupal stage.

(c) Pupae (Plate 2)

When the larval skin of the pre-pupa is finally moulted within the earthen cell, the pupal cuticle is exposed. After a short time the cuticle hardens and darkens to a shiny chestnut-brown colour. The sexes may be distinguished at this stage by the morphology of the posterior abdominal segments (Blair and Read, 1969). In the female there is an apparent fusion of the aperture of the bursa copulatrix and the aperture of the oviduct to form a

longitudinal groove stretching between abdominal segments VIII and IX, while the male pupa has a genital aperture on segment IX. In both sexes there is an anal aperture on segment X. The sexes may be distinguished at a later stage when the moth is about to emerge by antennal characters, which can be discerned through the pupal cuticle. The females have filiform antennae and the males have plumose antennae. It was not possible to distinguish the two species in the pupal stage.

(d) Adults (Plates 3 and 4)

The moths of A. ipsilon have a wingspan of 40 to 50 mm and a length of 16 to 22 mm. The head, thorax and abdomen are a dull-grey at light brown in colour. The middle of the forewings are marked with a transverse brownish band, bordered by the antemedial and postmedial lines, and a reniform spot near the fore-margin; orbicular and claviform spots lie nearby towards the base of the wing (terminology according to Janse, 1932). Other parts of the fore-wing are greyish brown ^{with} dark-brown to blackish markings. The hind wings are white with dark veins and brown margins. The above description is made clearer when read in conjunction with Plate 3.

The moths of A. segetum have a wingspan of 35 to 40 mm and a length (head, thorax and abdomen) of 15 to 20 mm. The head, thorax and abdomen are greyish-brown to reddish brown as are the fore-wings, though the lateral and fore-margins of the latter are usually darker. A broad transverse central band of the fore-wing, demarcated by dark undulatory antemedial and postmedial lines, has a fairly large dark brown or grey reniform spot towards the outer

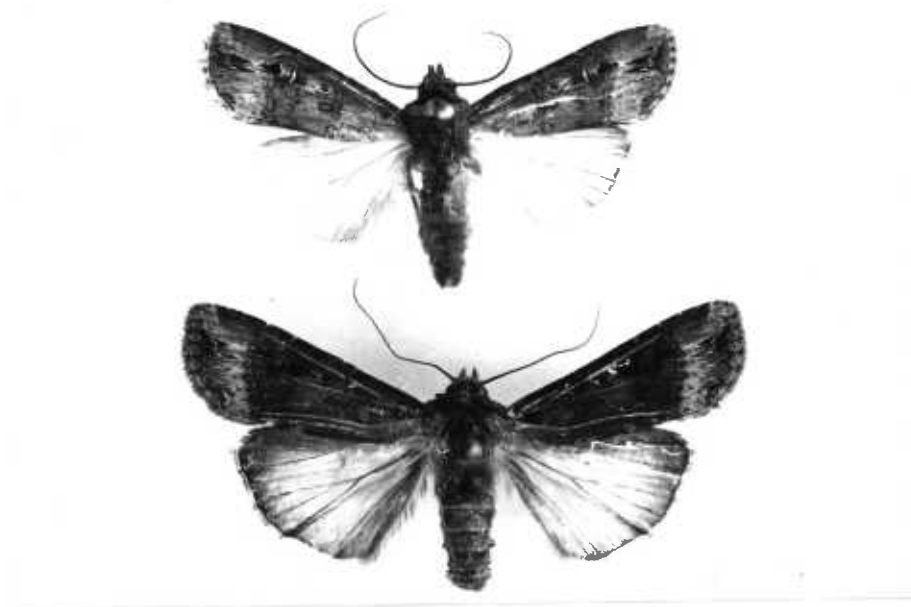


PLATE 3. MOTHS OF AGROTIS IPSILON HUFNAGEL.

(Top - male; Botton - female)



PLATE 4. MOTHS OF AGROTIS SEGETUM (DENIS & SCHIFFERMULLER).

(Top - male; Bottom - female)

margin and a smaller, lighter coloured orbicular spot towards the base (terminology according to Janse, 1932). The hind wings are pearly white with the veins becoming dark at the outer margins (see Plate 4).

6.4. Discussion

The results obtained from the rearing of A. segetum and A. ipsilon at constant temperatures show that for all immature stages in the cycle and at all temperatures used, there is more rapid development by A. ipsilon than by A. segetum. This phenomenon is confirmed in Bulgaria where the developmental rates from egg to adult for A. ipsilon (Nikolova, 1961) and A. segetum (Genchev, 1968) at about 25°C is 40.7 days and 45 days respectively. From this it would be expected that A. ipsilon, having the capability of completing more generations per year, to be the more opportunist of the two species. However, as was shown in the chapter on economic importance, A. segetum is the commonest and most destructive species in Rhodesia.

Comparison of the developmental rates of the two species in various parts of the world with those obtained in Rhodesia reveal interesting differences. In all cases of comparison, the relative logistic curves of each species have been used to compute the developmental rates in Rhodesia. If the data from countries with warm climates (like Rhodesia) are compared, it is seen that the development rates are similar. For example, the period required from egg to adult of A. ipsilon at 22°C in Egypt is 55.8 days (Abdel-Gawaad and El-Shazli, 1971) and in Rhodesia it is 56.0 days; and the same species in Alabama (Mangat, 1971) also develops at a similar rate to the Rhodesian population from egg to adult, that is, 67.5 and 66.5 days

respectively at 20°C, 41.2 and 43 days respectively at 26°C and 32.5 and 33.7 days respectively at 30°C. The development of the Angolan population of A. segetum (Passos de Carvalho, 1968) from egg to adult at 25°C takes 47 days and 39 days at 30°C and are comparable with the results of the local population, which takes 50 days at 25°C and 45 days at 30°C. However, if comparison of developmental rates is made with countries having cold climates it is apparent that the populations in these countries are better adapted to low temperatures than the Rhodesian population. Data given by Nikolova (1961) on the biology of A. ipsilon in Bulgaria shows that larval development at 18°C takes 24 days, whereas the local population takes 47 days at this temperature. Similarly with A. segetum, larval development at 13°C in Bulgaria (Genchev, 1968) takes 132 days and, by extrapolation of the temperature-time curve of the local population, it would take infinitely long in Rhodesia. Druzhelyubova (1963) found differences in responses to temperature by populations of A. segetum in the north and south of Russia. At 30°C the immature stages of the southern population lasted 45 days, while the northern population lasted 60 days at the same temperature.

The Rhodesian populations of A. segetum and A. ipsilon would seem to be adapted to the warmer temperatures, and no development takes place at temperatures below about 10°C.

It is also apparent from the results that female pupae develop at a faster rate than the male counterparts. This phenomenon has been noted in papers on cutworms of both species (Nasr and Naguib, 1963 a; Passos de Carvalho, 1968).

Davidson (1944) in his paper on the relationship between temperature and the rate of development of insects at constant temperatures, discussed various methods of handling data of these relationships. Of the various methods he found that the logistic curve best represented the trend of speed of development of insects for 85 to 90 per cent of the complete range of temperature at which development can continue. As can be seen from the results, the calculated logistic curves follow the trend of the observed means, and it is only at the lower limit of the experimental ranges of temperatures that appreciable discrepancies occur.

In obtaining measurements on widths of larval head capsules, it was noted that a small percentage of A. ipsilon underwent an extra moult. This phenomenon of extra moults in A. ipsilon has been documented by Satterthwait (1933), who found that there could be a 7th instar as well as an 8th instar in north America. He found that of those larvae reaching the adult stage, 57.4 per cent passed through six larval instars, 38.9 per cent required seven larval instars and 3.7 per cent required eight instars. He was unable to explain the reason for the extra moults and he found that the increase in head capsule width was reduced for stages after the 6th instar, as was found in this study.

From the capsule measurements it would appear that there is little overlap in width at least up to 5th instar and that this measurement can, therefore, be used with confidence to determine the stage of growth up to 5th instar. Some doubt may attach to a few specimens in the zone of overlap between 5th and 6th instars of A. serotum and slightly more doubt may apply in the case of A. ipsilon where the head

capsules of the larvae show overlapping widths in the 6th and 7th instars. However, since only 6.6 per cent exhibited the additional instar, the head capsule width can be used to determine the stage of larval growth of both species. Comparison of the mean capsule widths of A. segetum in Rhodesia with Angolan data (Passos de Carvalho, 1968) indicates that the Angolan population is slightly smaller up to the 5th instar, but that the final instar is the same size in both countries.

Fiedler (1936) maintains that prior to the emergence of the moth, the pupa leaves the earthen cell and, by drilling movements of the abdomen, moves to just below the soil surface to facilitate escape of the moth. However, all evacuated cells that have been examined in Rhodesia contain remains of the pupal cuticle, indicating that the pupa (pharate adult of Hinton, 1973) does not leave the cell. Nasr and Naguib (1963 b), working on A. epsilon, recorded that the moth has the strength to enable it to work its way through the soil to the surface.

7. EFFECTS OF TEMPERATURE ON FERTILITY OF AGROTIS SEGETUM AND A. IPSILON.

7.1. Introduction

During laboratory rearing of Agrotis segetum and A. ipsilon, it was noticed that female moths emerging from immature stages reared at 30° and 33°C very rarely produced fertile eggs. This occurred despite the females being confined with at least one male moth of the same species. It was of interest to determine which sex was sterile. Raichoudhury (1936) has shown that high temperatures retard spermatogenesis and reduce the motility of sperm in the moth Eobestia kothniella.

7.2. Methods

Male and female moths that had been reared at constant temperatures during their immature life were confined together in glass preserve jars (as described in section 6.2.1.), and placed at room temperature. The female moths were dissected, after eggs had been laid for two days, to determine whether they had been paired; using the presence or absence of spermatophores in the bursa copulatrix as the criterion of copulation by the male moth. The state of maturity of the female gonads were also noted during dissection. Fertility was measured by the eclosion of larvae from eggs.

7.3. ^{Results} ~~Methods~~

The fertility of moths that had been reared at various temperatures during their immature life and mated with moths of the opposite sex, which were also reared at various temperatures are shown in Table VI.

TABLE VI. FERTILITY OF EGGS LAID BY FEMALE MOTHS REARED AT
VARIOUS TEMPERATURES AND MATED WITH MALES REARED AT
VARIOUS TEMPERATURES.

Species	Rearing temp. °C		Mean eggs laid/ ♀	Mean sperm- atophores/ ♀	Mean eggs fertile %	Number matings
	Male	Female				
<u>A. sagatum</u>	33	33	79.6	0.11	0.00	9
	33	30	76.7	0.00	0.00	10
	33	27	81.2	0.20	0.00	10
	33	24	85.0	0.08	0.00	12
	30	33	126.9	0.23	0.00	13
	30	30	39.7	0.70	2.80	10
	30	27	63.7	0.20	0.00	10
	30	24	67.4	0.00	0.00	10
	27	33	129.1	0.40	0.00	10
	27	30	191.9	0.78	35.01	9
	27	27	220.9	0.40	33.00	10
	27	24	201.7	0.44	28.32	9
	24	33	94.1	0.00	0.00	10
	24	30	121.0	0.36	18.20	11
	24	27	141.9	0.22	18.40	9
	24	24	195.9	0.60	47.60	9
<u>A. ipsilon</u>						

During laboratory rearing at 30°C a gynandromorph of A. segetum emerged from a pupa that had been sexed as male, using the morphological features on the terminal abdominal segments. The moth (Plate 5) exhibited dimorphism in the antennae, compound eyes and wings; the left side being female and the right side male. However, the abdomen did not show any dimorphism as both the external and internal genitalia were typically those of a male. The head and thorax were the only two regions where dimorphism was manifested in a lateral plane.

7.4. Discussion



PLATE 5. GYNANDROMORPH MOTH OF AGROTIS SEGETUM.

(Left - male; Right - female)

8. ASPECTS OF BEHAVIOUR AFFECTING LARVAL BIOLOGY OF AGROTIS SEGETUM AND A. IPSILON.

8.1. Introduction

As it is the larvae of A. segetum and A. ipsilon that cause damage to plants, their behaviour is an important aspect in biological studies where vulnerable features are being sought to implement control methods. From the literature it is apparent that very little detailed behavioural work has been done on the larvae of Agrotis.

Jack (1918) observed that young cutworms fed considerably during the day on prostrate foliage. Fiedler (1936) records that Agrotis larvae were repelled by light a few days after hatching, and that by the 3rd instar they were completely photonegative. The light reactions of the cutworm Tryphaena prionba were investigated by Madge (1964), and of the spotted cutworm Amathes c-nigrum by Olson and Rings (1969). It appeared that the phototactic reactions of A. ipsilon and A. segetum have not been investigated in any detail, and since the observations and results of the above workers show that young larvae are photopositive, it seemed that a knowledge of this aspect of larval behaviour could be of great value in population management.

Other aspects of larval behaviour investigated were their feeding behaviour, their ability to survive on crop debris and weeds, depth of pupation in the soil and their patterns of emergence from, and entry into, soil. Observations by myself and other entomologists in Rhodesia (Jack, 1918; Rose, 1962) indicated that crop residues on agricultural lands encouraged cutworm attack on the next crop; the larvae attacking seedlings are usually in 4th instar onwards, and the

only food available for these larvae to have developed to this stage of growth is crop residues and growing weeds. It was, therefore, decided to investigate the survival ability of larvae on crop residues. The reason for attempting to find the patterns of emergence from, and entry into, soil was that a previously recommended control method of using insecticidal baits was found to be ineffective in many cases. It was necessary to know whether larvae in the later instars came to the soil surface.

8.2. Methods

8.2.1. Phototactic Responses

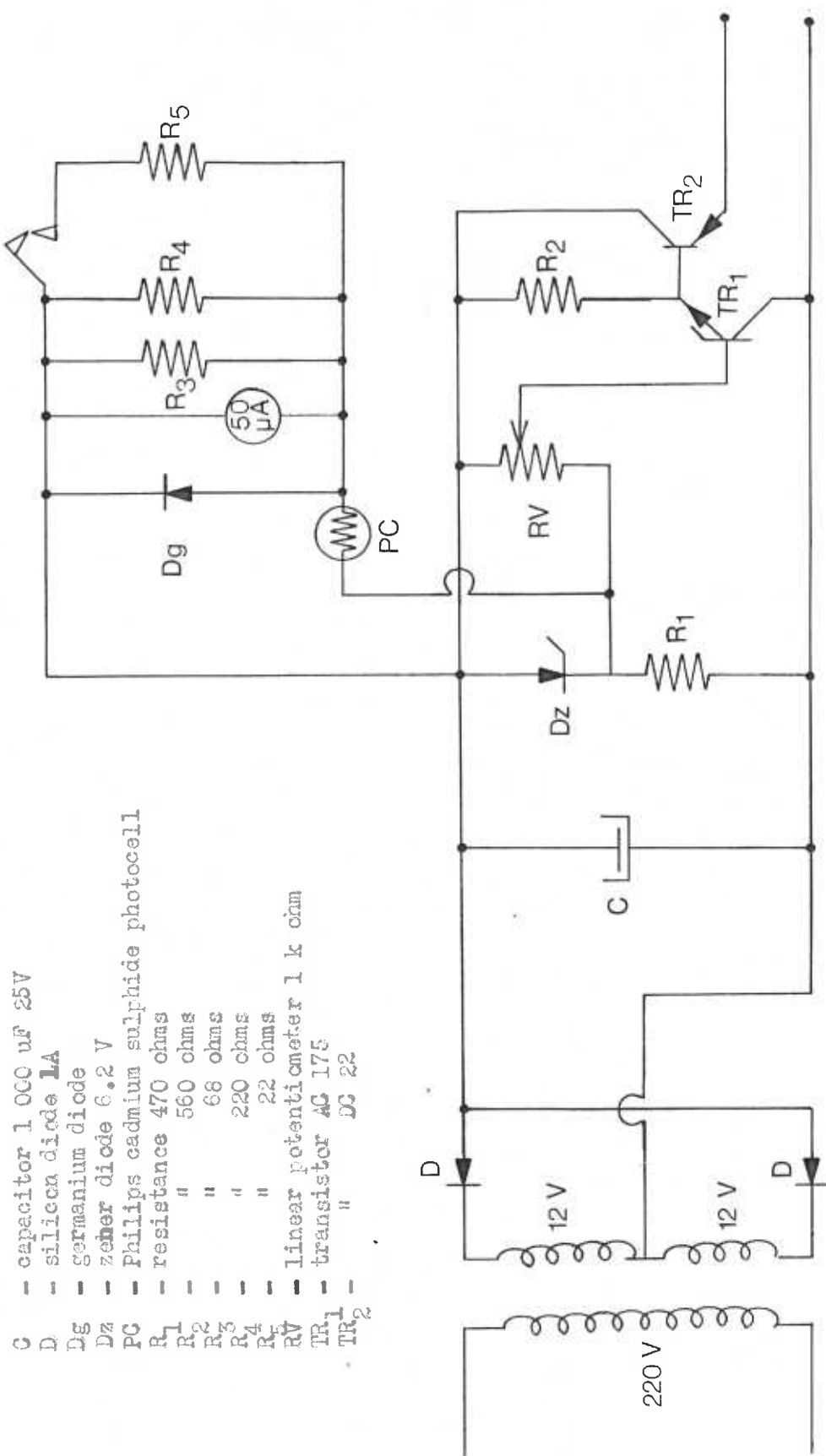
A wooden, light-proof, rectangular box (565 mm high and 145 mm²) was constructed, on the lines of the apparatus used by Olson and Rings (1969), to test the photic reactions of the two species of cutworms under study. The interior of the apparatus was coated with matt black paint to reduce reflection of light. The front of the box was removable and an opening at the top of the box allowed a 10 W incandescent lamp, with a condenser, to be housed. Two glass plates, which aided in eliminating most ultra-violet radiation, were situated at different levels in the box. The first, situated 290 mm from the base, held a petri dish containing 30 ml of a 3 per cent solution of ferric ammonium sulphate which eliminated radiant heat. The second glass plate was situated 140 mm from the base. On either side of the box, 80 mm from the base, were two holes which allowed a thermometer and a photocell to be inserted.

The lamp was supplied from a variable (0 to 6 V at 1.5 A maximum) stabilised power supply. The stabilised voltage for the photocell measuring circuit was also taken from this supply. The illuminance in

the light-proof box was controlled by means of a linear potentiometer and the photocell. The latter was connected to a microammeter, having a toggle switch to give a high and a low range, and the readings obtained were calibrated against an Eel Photometer. The electronic circuit is shown in Fig 17.

The choice chambers consisted of petri dishes, one 60 mm in diameter and another 90 mm in diameter, with a layer of paraffin wax in the bottom. The smaller chamber was used to test the responses of larvae in 1st and 2nd instars, and the larger chamber for the last four instars. One half of each chamber, including the lid, was covered with a matt black paint. However, when light from the lamp struck the paraffin wax, it was noticed that there was reflection of light into the darkened half of the chamber. The degree of darkness in the darkened half was tested by placing circles of photographic bromide paper in the choice chambers and exposing them to ^{the} light source for 5 s. After developing the exposed papers, it was seen that the darkened half of the chambers were not dark enough to provide a satisfactory choice. The dishes were, therefore, blackened completely except for half the lid, and circles of bromide paper were again exposed. It was found that the reflection of light into the darkened half of the chambers was considerably reduced and provided a more distinct choice of light and dark.

Twenty larvae in 1st and 2nd instar were used in each test, 15 larvae in 3rd instar, 10 4th instar larvae and six larvae in 5th and 6th instars. The larvae were reared at 24°C and the tests were conducted at 20° to 25°C between 0800 h and 1400 h. Larvae of known age were randomly distributed in the choice chamber and the light



- C - capacitor 1 000 µF 25V
- D - silicon diode 1A
- Dg - germanium diode
- Dz - zener diode 50 V
- PC - Philips cadmium sulphide photocell
- R1 - resistance 470 ohms
- R2 - " 560 ohms
- R3 - " 68 ohms
- R4 - " 220 ohms
- R5 - " 22 ohms
- RV - linear potentiometer 1 k ohm
- TR1 - transistor AG 175
- TR2 - " DC 22

FIG 17. ELECTRONIC CIRCUIT OF LIGHT APPARATUS

intensity was determined at 713.5 lx. Each test was run for 10 min, after which time the number of larvae in the light and dark halves were noted. The tests were replicated five times for each day of age and the mean reaction index (RI) was calculated according to the formula:

$$RI = \frac{100(L - D)}{N}$$

where L is the number of larvae in the illuminated side, D is the number in the dark side and N is the total number of larvae in the test (Madge, 1964). A choice for the light side is thus shown as a positive value, and for the dark side as a negative one.

During field observations, the number of larvae observed above and below the soil surface between 0900 h and 1230 h were noted. Sampled individuals were brought into the laboratory and the width of the head capsules measured to determine the instar of the larvae.

5.2.2. Feeding Behaviour

(a) General Observations

Observations on the feeding behaviour of the larvae were carried out during field work at Gwebi Agricultural College. The larvae were confined within asbestos cylinders, measuring 0.6 m in diameter and 0.45 m high, over young maize plants growing in an agricultural land and tobacco seedlings growing in a seedbed.

(b) Feeding Behaviour of First Instar Larvae on Tobacco

Larvae hatching on tobacco seedlings were never observed feeding and they very soon died. Specimens of dead Agrotis larvae

were examined microscopically, and it was found that they were held fast in the droplets of secretion at the distal ends of the trichomes (Plate 6). The young larvae did not seem to have the ability to overcome the stickiness of the secretion and apparently died from starvation.

Experiments were carried out to investigate the cause of death of the 1st instar larvae. Newly-hatched larvae of both species were placed in plastic pill boxes containing discs of tobacco leaves, which were treated in four ways. The first treatment consisted of fresh tobacco leaves, the second of fresh leaves that were rubbed three times with a cheese-cloth to spread the secretion at the distal ends of the trichomes, the third consisted of leaves that had been under refrigeration and then rubbed, and the fourth of fresh leaves that were washed in running water (1 litre/min) for 15 min to remove the trichomal secretion. The food source was renewed each day after assessment of survival had been made.

A further experiment was carried out to ascertain whether there were differences in the amount of trichomal secretion produced by three varieties of tobacco. A Virginian tobacco (Kutsaga El), a burley tobacco (21) and a Turkish tobacco (Samson) were those tested. In each case fresh leaves were used, and the food source was renewed each day.

8.2.3. Survival of Larvae on Crop Debris and Weeds

Agrotis segetum larvae in 4th and 6th instars that had been reared on bean diet were given dry maize stalks, moistened dry maize stalks



PLATE 6. FIRST INSTAR AGROTIS LARVA IMMOBILISED BY
TRICHOMAL SECRETIONS ON TOBACCO LEAF.

and bean diet (control), and placed at a constant temperature of 24°C. Twenty-eight larvae in 6th instar were used in each of the three treatments, and 20 larvae in 4th instar were used in each treatment. Pupae that resulted from 6th instar larvae under the three treatments were weighed soon after pupation.

A land planted to maize at Guebi Agricultural College suffered a cutworm attack, and provided material for observations on the survival of larvae on weed growth. The land was irrigated in early August to bring it to field capacity, and was then ploughed. In early November the land was disc-harrowed and sown to maize a week later. Counts of larvae per length of row of maize were made in the areas with a poor plant stand and in areas with a good stand.

8.2.4. Depth of Pupation

Larvae that were about to enter the pre-pupal stage were placed in glass beakers containing a red-loam soil or a sand. The soils were at least 80 mm deep and were brought to varying moisture levels (10, 20, 28 and 35 per cent by mass in the case of the red-loam soil, and 0, 5, 10 and 18 per cent in the sand). Bean diet was placed on the surface of the soils and the beakers were covered with polythene sheeting, to maintain the moisture levels in the soils, and then placed in a dark room at a constant 26°C. Once the larvae had pupated, the depth of the pupae below the soil surface was measured.

8.2.5. Patterns of Emergence from and Entry into Soil

Before embarking on this study, it was necessary to establish whether photonegative larvae tunnelled through the soil in search of food, or only burrowed to take refuge during daylight. Photonegative

larvae were placed in pots containing moist soil and bean seedlings. Once burrows had been formed in the moist soil, a solution of warm gelatin was poured into each burrow mouth and allowed to gel by placing the pots in a refrigerator. In this way a caste of the burrow was obtained.

The study posed problems in recording when later-instar larvae in the field came to the soil surface and retreated into the soil, since the phototactic responses are negative at this stage of growth (see section 8.3.1.) and this activity is, therefore, likely to take place at night. Apparatus was developed to record these activity patterns in the laboratory.

The apparatus consisted of an artificial burrow with a spring loaded cage above. A tube, 60 mm long and 19 mm in diameter, was filled with Plaster-of-Paris, and then a hole 10 mm in diameter and 55 mm deep was bored to produce an artificial burrow. A clear plastic pill box, 50 mm in diameter and 22 mm high, with a fine-meshed gauze lid and an 18 mm hole bored through the floor, constituted the cage. Around the bored hole in the floor of the cage a rigid plastic collar, 20 mm in diameter, was attached to the ventral surface and a length of coil-sprung curtain wire was screwed into a hole in the side of the cage. The cage was suspended by means of the coil spring, so that the rigid plastic collar fitted over the tube of the artificial burrow (Fig. 18). The apparatus was electrically wired so that the cage and the burrow acted as a switch, and then connected to an electromagnetic marker. The mains power source was stabilised and rectified by means of the electronic circuit used in the light-dark choice chamber apparatus (Fig. 17). When a larva moved from the artificial

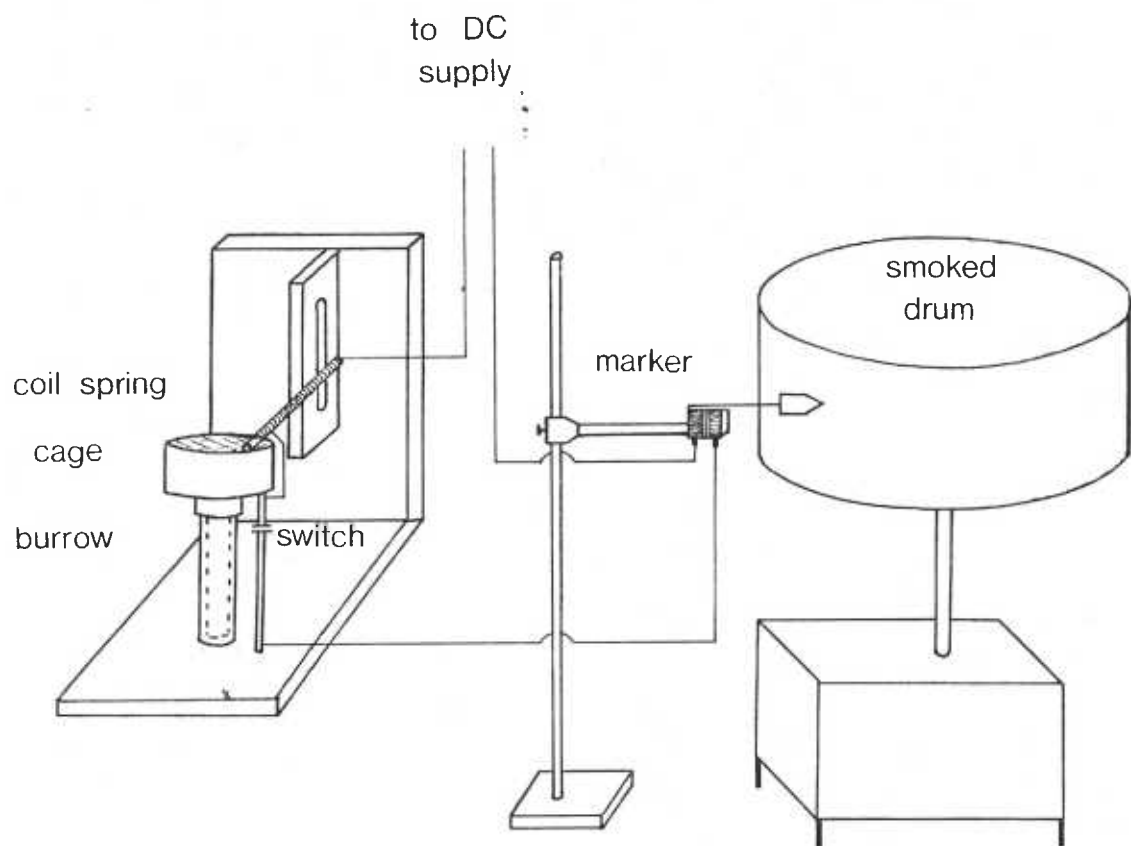


FIG. 18. APPARATUS TO MEASURE LARVAL ACTIVITY.

burrow into the cage, its mass caused the switch to be closed and the marker to be deflected. The marker was applied to a smoked drum revolving once every 48 h and the apparatus was placed in a room with a 12 h dark: 12 h light cycle, with a day temperature of 24°C and dropping at night to 16°C.

A larva in 6th instar was placed in the cage during daylight, and allowed to move into the burrow. Food, in the form of discs of fresh cabbage leaf, was placed in the cage and held fast by means of adhesive tape; this was found to be necessary as larvae were able to draw loose food into the burrow and produce a false result of the time that would be spent on the surface. In other cases, no food was placed in the cages. The larvae were allowed to remain in the apparatus for two nights, and the results are expressed as the mean per night.

8.3. Results

8.3.1. Phototactic Responses

Phototactic responses of A. ipsilon and A. segetum larvae at an illuminance of 713.5 lx are shown graphically in Figs. 19 and 20. It can be seen that in both species the larvae have a positive phototaxis in the first two instars, and that during the 3rd instar the taxis is reversed to become negative. In A. ipsilon the switch occurs between the first and second day during the 3rd instar and in A. segetum between the fourth and fifth day, also in the 3rd instar, at a temperature of 24°C. The fact that the change in reaction occurs in the middle of an instar and not at the moult, as might be expected, is one of interest. Another feature of the results is the drop in RI on the last day of each instar. This can be explained by the reduction in activity of the larvae as they prepare for the moult into the next

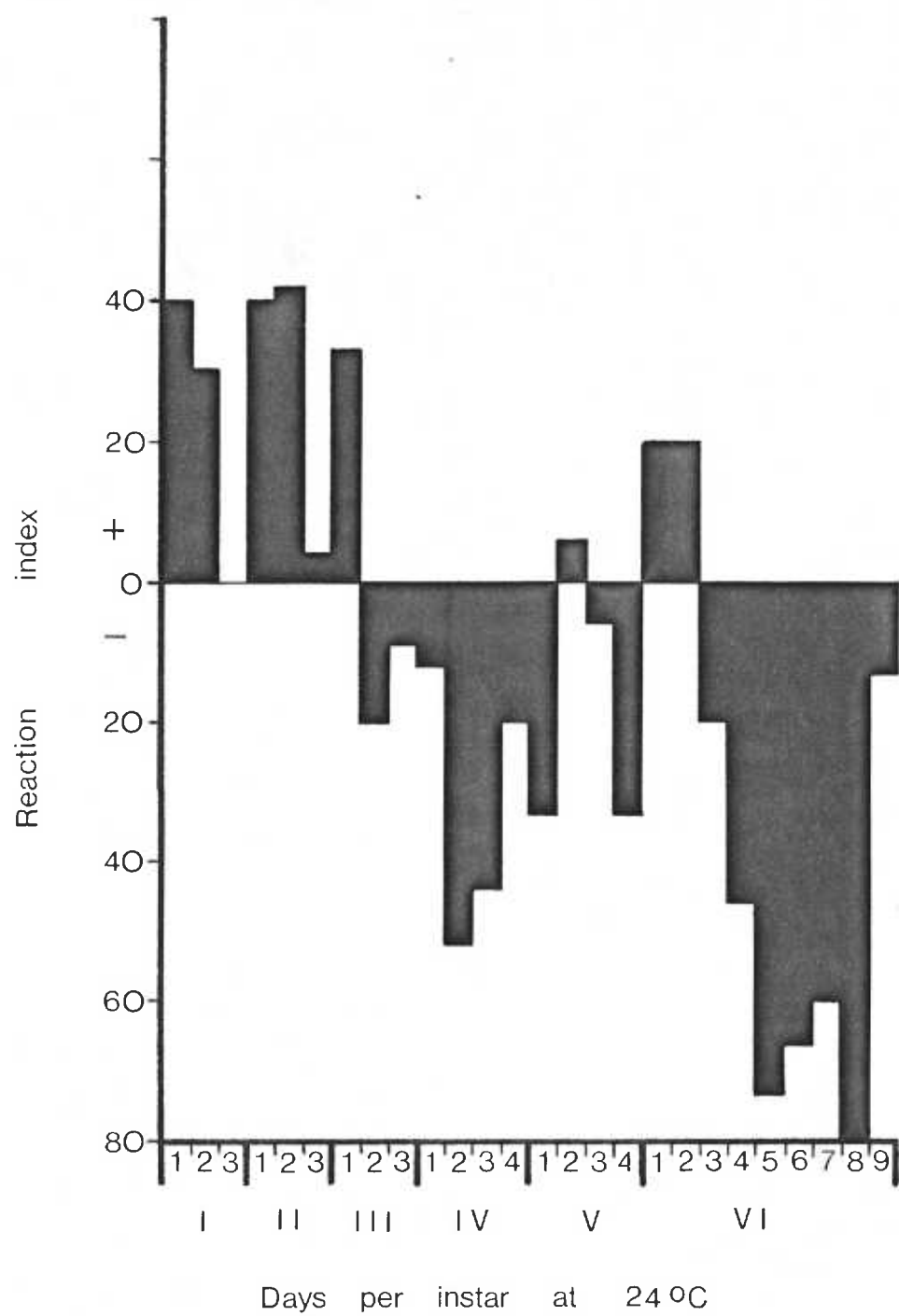


FIG 19, PHOTOTACTIC REACTIONS OF *A. ipsilon*
LARVAE AT 713,5 lx

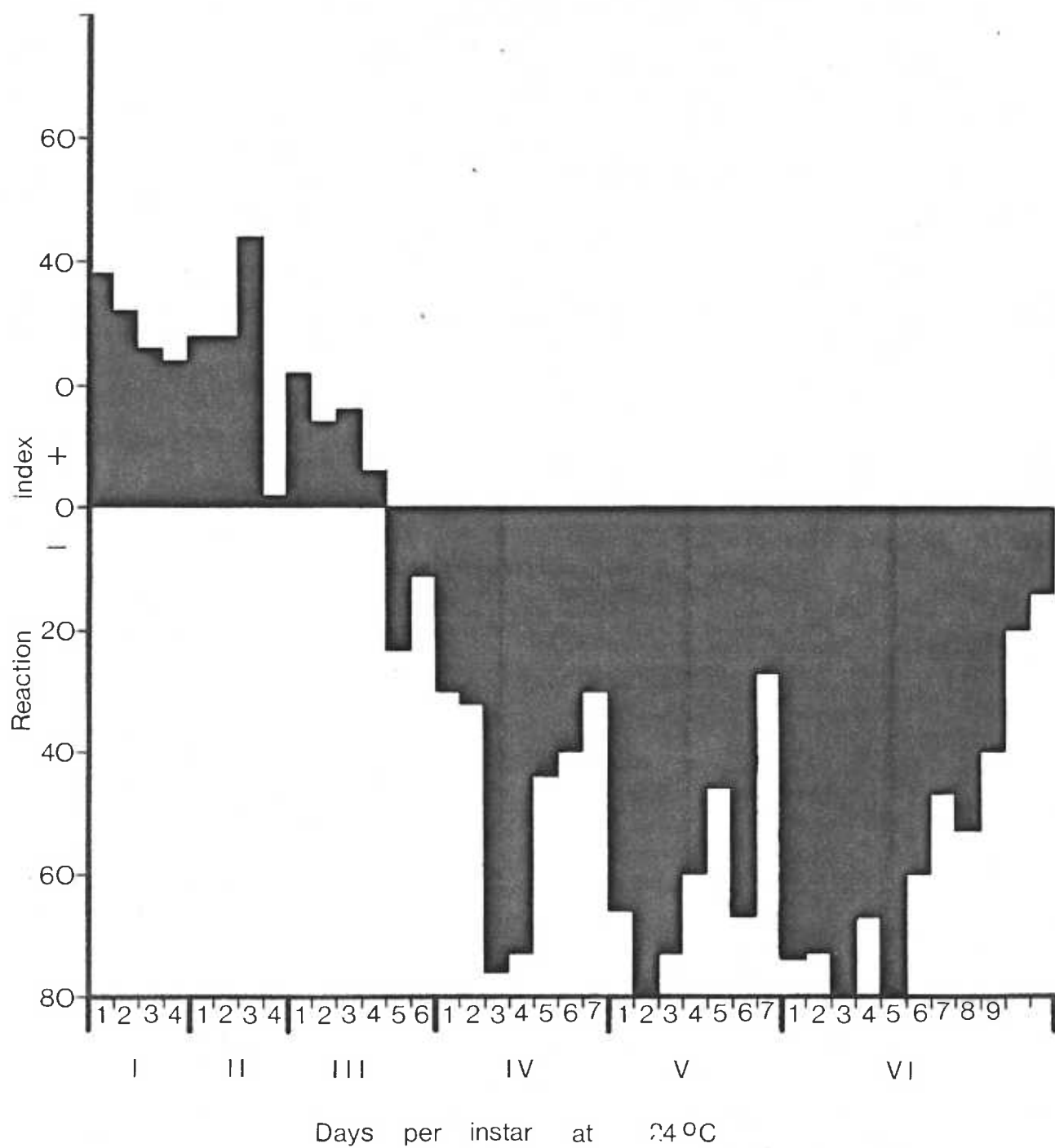


FIG 20. PHOTOTACTIC REACTIONS OF *A. segetum* LARVAE
AT 713,5 lx

instar. The reason for the change in phototaxis of A. epsilon from negative to positive on the second day in the 5th instar and on the first and second days in the 6th instar is not known. Larvae of these ages were re-tested, and the net reaction was always found to be positive. In interpreting the phototactic responses in Figs. 19 and 20, it can be said that the line representing zero RI is the soil surface, and that a positive response indicates that most of the larvae are above the soil surface and a negative response shows that most are below the soil surface during daylight.

Observations in the field have substantiated the results that were obtained in the laboratory. The results of these observations are shown in Table VII.

The larvae of both species are on or above the soil surface during the day when in 1st and 2nd instar, and during the 3rd instar this positive reaction was greatly reduced. When the larvae are in 4th, 5th and 6th instars, they are mostly in the soil during daylight hours. From the laboratory and field experiments, A. epsilon larvae could be expected to be on the surface of the soil during daylight for about seven days after hatching from eggs during summer (main rainy season) in Rhodesia. In the case of A. segetum larvae, these may be expected to be found on the surface for about 12 days after hatching during the same season.

Comparison of the RIs of the two species from the field and laboratory experiments are shown in Table VIII. As the field results are on a per instar basis, the per day laboratory results have been converted to means for each instar to allow a comparison to be made.

TABLE VII. TOTAL NUMBER OF LARVAE FOUND ABOVE AND BELOW THE
SOIL SURFACE IN THE FIELD AND THE PHOTOTACTIC REACTION INDEX (RI) DURING DAYLIGHT.

Instar	Above soil surface		Below soil surface		RI	
	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>
1	951	834	30	16	+ 93.88	+ 96.24
2	562	495	10	11	+ 96.50	+ 95.65
3	141	167	136	154	+ 1.81	+ 4.05
4	20	2	60	68	- 50.00	- 94.29
5	1	1	22	24	- 91.30	- 92.00
6	0	0	17	14	-100.00	-100.00

TABLE VIII. COMPARISON OF THE LARVAL PHOTOTACTIC REACTION
INDICES (RI_s) OF FIELD AND LABORATORY EXPERIMENTS.

Instar	<u>A. segetum</u>		<u>A. ipsilon</u>	
	Field RI	Lab. RI	Field RI	Lab. RI
1	+ 96.24	+ 30.00	+ 93.88	+ 23.33
2	+ 95.65	+ 25.50	+ 96.50	+ 28.66
3	+ 4.05	+ 4.00	+ 1.81	+ 1.33
4	- 94.29	- 46.42	- 50.00	- 32.00
5	- 92.00	- 59.86	- 91.30	- 16.50
6	-100.00	- 55.27	-100.00	- 35.33

In each case, except in the 3rd instar, the RIs of the field results are higher than the laboratory results. The reason for this is thought to be due to the lower illumination used in the laboratory experiments than that encountered in the field, resulting in a stronger field response.

8.3.2. Feeding Behaviour

(a) General Observations

Soon after hatching from eggs and until they reach the 3rd instar, the larvae have a positive phototaxis and it was shown that they were found on or above the soil surface during daylight (section 8.3.1.). The young larvae were observed feeding on tender foliage, particularly prostrate foliage, during the day. Young larvae were never seen feeding on parts of a plant higher than 200 mm from the soil surface; when they hatched from the few eggs deposited on parts of a plant higher than this level, they moved to the lower parts before feeding. They feed on either surface of a leaf, consuming the mesophyll and leaving the further epidermis intact. Their feeding, therefore, produced an appearance of 'windows' that were etched into the leaf surface. When veins were encountered by the larvae, these were not eaten so that a skeletonised appearance was also produced (Plate 7). Most plants encountered in the field were eaten with the exception of tobacco seedlings that had been hardened; the reasons for this are dealt with in section 8.3.2. (b). In this case it was found that larvae, after hatching, very soon died and feeding marks were never observed. It would appear therefore that an infestation of cutworms is not able to establish itself on tobacco, but must rely on other plants growing nearby for food.

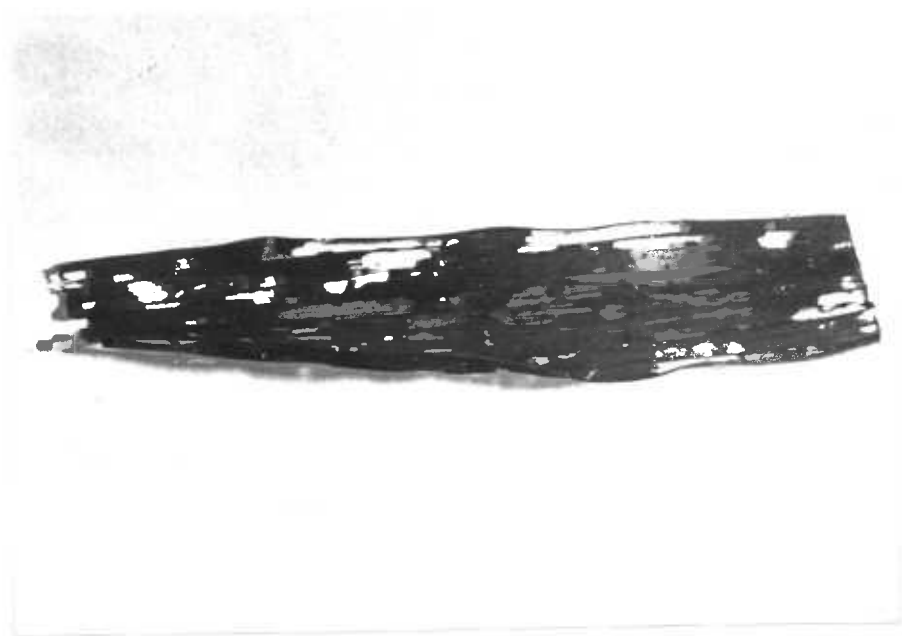


PLATE 7. FEEDING BY PHOTOPOSITIVE AGROTIS LARVAE
ON YOUNG MAIZE LEAF.

With the change in phototaxis, there is also a change in feeding behaviour. The larvae in 4th instar onwards shun light during the day and are found in concealed situations, usually below the soil surface, but when overcast conditions occur they may be found feeding under prostrate foliage. In this latter case all the tissues of the leaf are eaten, resulting in a holed or ragged-edge leaf, as opposed to the skeletonised appearance produced by the younger larvae. The more typical feeding of older larvae is the cutting of stems of seedlings at or near ground level (Plate 8), and it has been observed that the felled aerial parts may be pulled into the soil where they are consumed. It has also been observed that the prop roots of maize may be eaten and the base of the stalk may be bored; the larvae may be found in the cavity so formed during the day (Plate 9). The more developed larvae, having larger mandibles, are able to eat fairly woody material. It has also been found that the larger larvae are able to overcome the sticky trichomal secretions of tobacco leaves, and are able to feed on these.

(b) Feeding Behaviour of First Instar Larvae on Tobacco

The survival of larvae on tobacco leaves (Kutsaga El) treated in four ways are shown in Table IX. Binomial confidence limits at the 95 per cent level have been computed using the formula $\frac{\bar{m}}{n} \times \frac{n - \bar{a}}{n - \bar{b}} = \bar{p}'$ and obtaining the values for $\bar{m}$, $\bar{a}$ and $\bar{b}$ from tables given by Burstein (1971). When no overlap of these limits results between treatments, the latter can be said to be significantly different, that is, if two or more treatments have been designated with different letters they are significantly different.



PLATE 8. STEM-CUTTING BY PHOTONEGATIVE AGROTIS LARVAE.



PLATE 9. CAVITY IN MAIZE STEM CAUSED BY AGROTIS LARVAE.

TABLE IX. SURVIVAL OF FIRST INSTAR LARVAE ON VIRGINIA
TOBACCO (KITSAGA E1) LEAVES.

Species	Day	Per cent survival with leaf treatment			
		Fresh	Rubbed	Refrigerated and rubbed	Washed
<u>A. ipsilon</u>	1	40.4 (35-45) A	65.4 (60-70) B	71.7 (67-76) B	94.4 (90-98) D
	2	0.3 (0-2) A	2.1 (1-4) A	55.7 (51-61) C	93.9 (89-94) D
	3	0.0 (0-1) A	0.4 (0-2) A	30.0 (26-35) B	93.3 (89-98) D
	n	270	240	300	180
<u>A. segetum</u>	1	73.3 (70-80) A	98.7 (95-102) B	91.7 (86-96) B	96.7 (92-101) B
	2	14.2 (9-20) A	82.7 (78-87) C	28.9 (24-35) B	96.7 (92-101) D
	3	1.7 (0-5) A	71.3 (67-76) C	12.2 (8-17) B	95.0 (90-99) D
	n	120	300	180	180

(Numbers in parentheses are the 95 per cent confidence limits)

From Table IX it is seen that significant differences in the survival of A. ipsilon could be demonstrated after two days, and the same was evident for A. segetum. There were no significant differences in the survival rate of A. ipsilon larvae on fresh and rubbed leaves, but there were significantly different survival rates between these two treatments and the rubbed and refrigerated leaves and the washed leaves. Each leaf treatment was significantly different from each of the other in the case of A. segetum.

In Table X the survival of 1st instar larvae of A. segetum and A. ipsilon on fresh leaf discs of the three types of tobacco are given.

No significant differences in the survival of 1st instar larvae were found on the three types of tobacco, with the exception of A. segetum on the third day when survival on the Turkish was significantly different from the other two types. The possible reason for the lack of significance in this experiment is the small numbers of larvae used; with larger numbers of larvae, it is felt that differences would be obtained. It appears that there is better survival on the Turkish tobacco than on the Virginian and burley tobaccos, and from the previous experiment, that there is significantly higher survival on the washed Virginian leaves than on the other treatments.

Despite the apparent adverse effects of the trichome secretions, a few larvae were able to survive for three or four days without feeding. As mentioned in section 6.3.2. (a), Fiedler (1936) found that the egg sac provided the first food source of the newly

TABLE X. SURVIVAL OF FIRST INSTAR LARVAE OF AGROTIS SEGETUM
AND A. IPSILON ON THREE TYPES OF TOBACCO.

Species	Day	Per cent survival with tobacco variety		
		Burley (21)	Virginia (K El)	Turkish (Samson)
<u>A. ipsilon</u>	1	56 (38-73) A	72 (54-87) A	80 (62-93) A
	2	32 (17-51) A	40 (24-59) A	60 (42-76) A
	3	8 (1-23) A	16 (5-33) A	20 (8-37) A
	4	0 (0-11) A	12 (3-28) A	20 (8-37) A
	5	0 (0-11) A	8 (1-23) A	20 (8-37) A
	n	25	25	25
<u>A. segetum</u>	1	85 (65-97) A	95 (76-104) A	100 (82-107) A
	2	55 (35-74) A	70 (49-86) A	100 (82-107) A
	3	35 (17-56) A	55 (35-74) A	100 (82-107) B
	4	35 (17-56) A	50 (30-70) A	60 (36-79) A
	5	10 (2-29) A	25 (11-46) A	0 (0-14) A
	n	20	20	20

(Numbers in parentheses are 95 per cent confidence limits)

hatched larvae. The initial meal may allow a small number to survive for three or four days.

8.3.3. Survival of larvae on Crop Debris and Weeds

The survival of A. segetum larvae that were offered dry maize stalks, moistened dry maize stalks and bean diet (control) are shown in Fig. 21.

It is seen that 4th instar larvae are not able to survive for more than 10 days when the only food source is dry maize stalks, whether moistened or dry. These results are in agreement with those obtained by Jack (1918). However, the 6th instar larvae were able to pupate, and the level of survival was much the same as larvae in the control treatment. It would seem that once the larvae have reached the final instar, they are able to withstand adverse conditions but the resulting pupae are smaller than those resulting from larvae having a fresh food supply. The mean mass of pupae produced from larvae having dry maize stalks and moistened dry maize stalks was $0.229 \text{ g} \pm 0.0118 \text{ g}$ and $0.236 \text{ g} \pm 0.0126 \text{ g}$ respectively, while the mean mass of those produced from larvae given bean diet was $0.304 \text{ g} \pm 0.0075 \text{ g}$. When these means were subjected to a student's "t" test, it was found that the mean mass of pupae resulting from larvae fed dry maize stalks and moistened dry maize stalks were not significantly different ($P > 0.5$), while the latter two were significantly different from the pupae resulting from larvae fed on bean diet ($P < 0.01$).

From this it seems that unless larvae are in the final instar, they are unable to survive on crop debris, and so must be surviving on fresh food to be able to attack newly-emerged crop plants. An

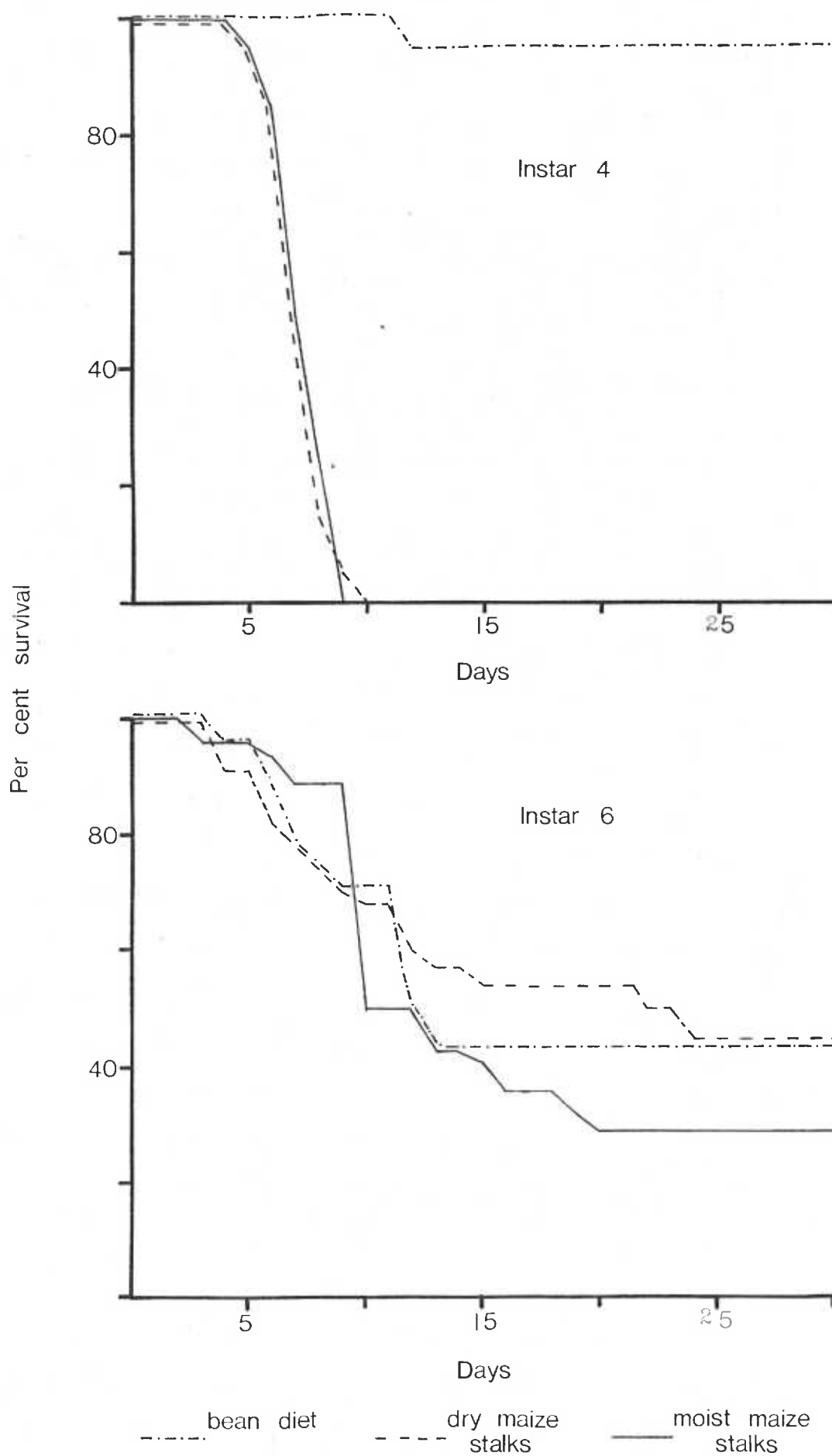


FIG. 21. SURVIVORSHIP CURVES OF A. SEGETUM LARVAE

observed example of weed growth in an agricultural land at Gwebi Agricultural College showed that this provided a food source, and allowed larvae to survive and attack newly-emerged maize plants. There were patches in a land which did not allow a fine tilth to be obtained, and also allowed weed growth to continue. The weeds were not greatly affected by disc-harrowing (due to the poor penetration of the harrow in these patches) and were able to continue growth. With the emergence of the maize seedlings, it was found that there was a marked reduction in plant stand on the weedy patches. Around the wilting seedlings were found up to three larvae in 4th and 5th instar per plant. The debilitating effects of larval feeding necessitated re-planting maize in these weedy patches. Counts of number of larvae per length of row showed that in the weedy patches there was a mean of 4.2 larvae per metre of row, while in the non-weedy patches there were practically no larvae present.

8.3.4. Depth of Pupation

The two different types of soils (sand and Loam) were found to have the following water-retention properties; the red-loam soil was saturated at a moisture of 39.5 per cent, while the sand was saturated at 19.8 per cent moisture. It was found that when a soil was saturated, larvae in their later instars were unable to burrow into the soil and none of 20 larvae under observation were able to pupate and succumbed. From this it would seem that the moisture content of the soil may influence the depth at which full-grown larvae are able to pupate. The results of the depth of pupation in soils of varying moisture contents are shown in Figs. 22 and 23.

It is seen from Figs. 22 and 23 that there is a trend of increasing

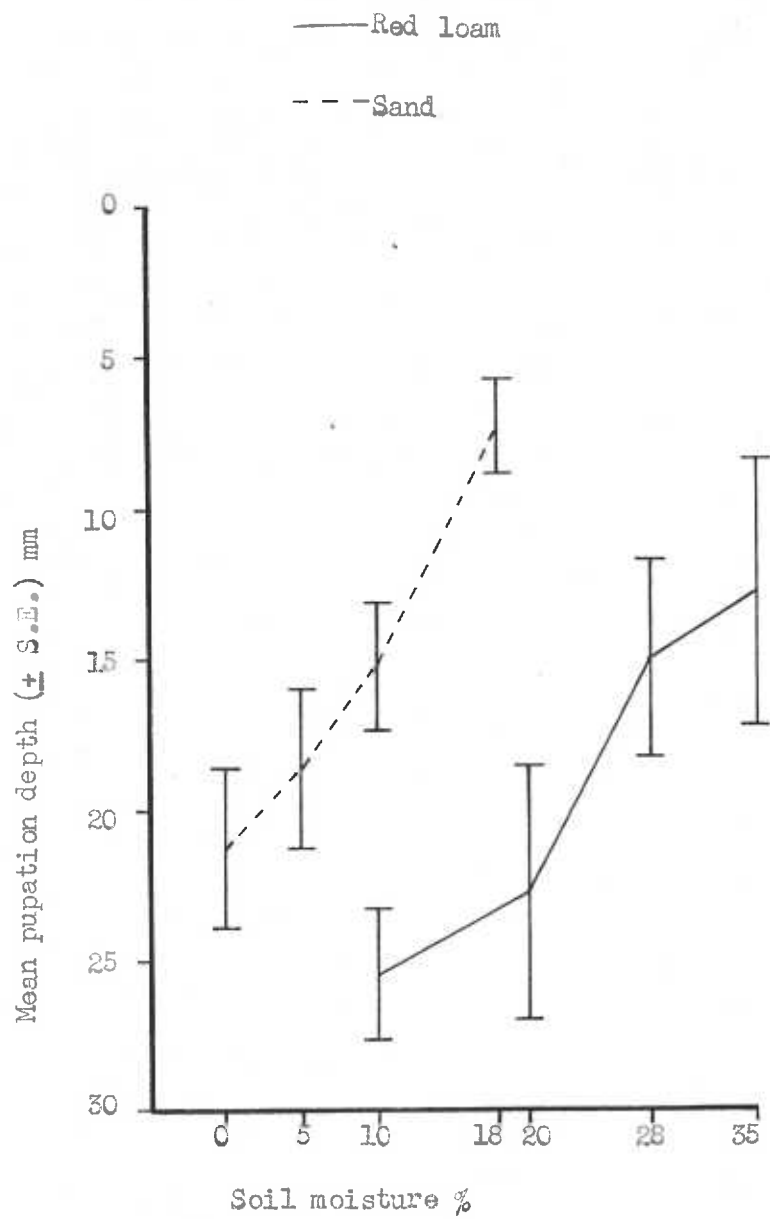


FIG. 22. MEAN DEPTHS OF PUPATION OF A. SEGETUM AT DIFFERENT SOIL MOISTURE CONTENTS.

larvae were placed in pots containing moist soil and bean seedlings. Once burrows had been formed in the moist soil, a solution of warm gelatin was poured into each burrow mouth and allowed to gel by placing the pots in a refrigerator. In this way a caste of the burrow was obtained.

The study posed problems in recording when later-instar larvae in the field came to the soil surface and retreated into the soil, since the phototactic responses are negative at this stage of growth (see section 8.3.1.) and this activity is, therefore, likely to take place at night. Apparatus was developed to record these activity patterns in the laboratory.

The apparatus consisted of an artificial burrow with a spring loaded cage above. A tube, 60 mm long and 19 mm in diameter, was filled with Plaster-of-Paris, and then a hole 10 mm in diameter and 55 mm deep was bored to produce an artificial burrow. A clear plastic pill box, 50 mm in diameter and 22 mm high, with a fine-meshed gauze lid and an 18 mm hole bored through the floor, constituted the cage. Around the bored hole in the floor of the cage a rigid plastic collar, 20 mm in diameter, was attached to the ventral surface and a length of coil-sprung curtain wire was screwed into a hole in the side of the cage. The cage was suspended by means of the coil spring, so that the rigid plastic collar fitted over the tube of the artificial burrow (Fig. 18). The apparatus was electrically wired so that the cage and the burrow acted as a switch, and then connected to an electromagnetic marker. The mains power source was stabilised and rectified by means of the electronic circuit used in the light-dark choice chamber apparatus (Fig. 17). When a larva moved from the artificial

depth of pupation with decreasing moisture content of the soil.

8.3.5. Patterns of Emergence from and Entry into Soil

It was established from casting larval burrows that no extensive tunnelling through the soil took place. The burrow (Fig. 24) seems to be a site of refuge, and larvae must come to the soil surface in search of food unless the burrow is positioned in a food source (such as in a potato tuber or large stem of a plant).

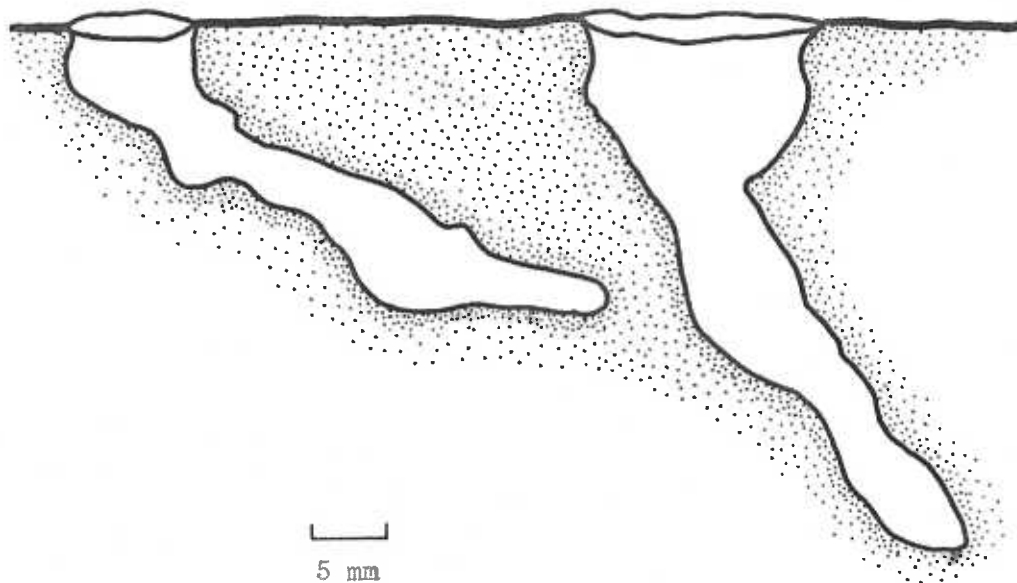


FIG. 24. TYPICAL BURROWS OF AGROTIS LARVAE

8.4. Discussion

The succession of experiments described in this section have helped to clarify much that was either not understood, or at least only vaguely realised, about the behaviour of cutworms in Rhodesia. Important points that seem to have emerged are that in the absence of growing vegetation only full-grown larvae are likely to survive and pupate, and young larvae certainly cannot develop on debris in the soil. The presence of larvae in a field before a crop is planted, therefore, is clearly associated with weed growth as was confirmed by the field records. Furthermore, young larvae developing on weeds or on young plants are confined to growing vegetation above ground before their behaviour changes at the 3rd instar, and they then live in burrows in the ground during the day. It is also evident that they usually only shelter in the burrows, so they are not soil insects in the sense that most of their active life is above ground level. Experiments to try to find conditions governing time spent by the larvae out of the burrows showed that more larvae come to the soil surface when there is no food present than when food is present. The implications of these findings on devising suitable management programmes is deferred for consideration later, with data from other sections.

The larval phototactic reactions of A. segetum and A. insilon in the laboratory show differences when compared with results obtained by Madge (1964) for Tryphaena pronuba, and by Olson and Rings (1969) for Anathes c-nigrum. In T. pronuba 1st instar larvae were photopositive, 2nd instar were intermediate and 3rd to 7th instars were photonegative. First to 3rd instars of Anathes c-nigrum were photopositive, 4th instar was intermediate and 5th to 7th instars were photonegative. The

photic reactions of T. promba and A. c-nigrum were only tested on an instar basis and not on each day of the larval period, so that the point of change in reaction of these species cannot be compared with the results obtained for A. segetum and A. ipsilon. The fact that A. segetum and A. ipsilon are photopositive for the first two and a half instars, both in the field and in the laboratory, represents a weak link in the life cycle from the viewpoint of control and will be discussed at a later stage.

Since larvae are unable to survive for any appreciable time on crop debris but were able to survive on growing weeds, the latter will allow the carry-over of larvae during the hot season. The presence of crop debris will act as a mulch, thereby conserving soil moisture resulting from light showers during the hot season, and provide suitable conditions for the germination of weed seeds that may be present. The germinating weeds will thus provide a food source for young larvae that may hatch from eggs laid by females during the hot season. The introduction of a bare fallow, with weeds being strictly controlled, for a period of say a month before a crop is due to be sown will ensure that there is no resident population of larvae present. Should 6th instar larvae be present prior to the introduction of the bare fallow, they would probably pupate. Since the pupal period varies from 14 to 19 days at the daily mean temperature prevailing during the hot season, the resulting moths will have emerged before the following crop is sown.

Work in Egypt on A. ipsilon by Willcocks and Bahgat (1937) indicates that full-grown larvae seek higher ground to pupate, and that many larvae pupated in ridges dividing fields into hods. Nasr

and Naguib (1963 a) showed that 42 per cent of A. ipsilon larvae selected a soil with a moisture content of 10 per cent as a pupation site. However, this figure of 10 per cent is of no value unless the soil type is known, since the different soil types have different water retention properties. Cook (1926) found that soil moisture was a factor of great importance in the ecology of the pale western cutworm, Perosagrotis orthogonia Morr. (now Agrotis orthogonia). The rate of increase or decrease of populations was found to be roughly proportional to the excess or deficiency of rainfall, and the relation was explained in three ways: too much moisture directly affecting the insect; moisture exposing the insect to attack by parasites; or moisture favoured the development of fungal and bacterial diseases. It was observed that larvae were unable to burrow into saturated soils (section 8.3.5.) and usually succumbed. Saturated soils would cause photonegative larvae to remain on the soil surface where they would be more susceptible to parasitism and predation. Ulliyett (1945), working in South Africa, has shown that cutworms in soils with a high moisture content were more susceptible to a bacterial disease known as streptococcal septicaemia.

Thurston, Smith and Cooper (1966) found that the major constituent of the trichome secretion in seven Nicotiana spp. was the alkaloid nicotine, with nornicotine and anabasine also being found in two of the species tested. The concentration of nicotine, or perhaps the physical and chemical condition of the nicotine, is postulated by the authors to be the cause of resistance or susceptibility in tobacco varieties to aphids. The same postulate could well be applied to 1st instar larvae of A. segetum and A. ipsilon, which were affected by the trichome secretion of the tobacco varieties tested. The alkaloid

secretion become obvious once the tobacco seedlings are 'hardened', so that from this stage of plant growth onwards it seems that 1st instar larvae are unable to establish on tobacco, and must rely on other plants (probably weeds) to undergo the first part of larval development. Once the larvae are in the 3rd or 4th instar, they are able to overcome the stickiness of the tobacco and feed without being trapped. This would indicate that it is the physical property that is causing mortality of the young larvae.

The fact that larvae do not tunnel extensively through the soil is understandable, since there is little morphological adaptation in Agrotis larvae for such activity. The only apparent adaptation to tunnelling or burrowing is a somewhat flattened frontal area of the head capsule; this part of the head has been observed in use as a shovel when a larva burrows into the soil.

9. ASPECTS OF BEHAVIOUR AFFECTING ADULT BIOLOGY
OF AGROTIS SEGETUM AND A. EPSILON.

9.1. Introduction

Three aspects of adult behaviour have been investigated. The first of these was the sites of oviposition, as eggs had not personally been observed in the field. Jack (1918) found that eggs were laid on the stems of plants, stones, clods of earth, sticks, tree trunks, or to any other stable object. The reason for investigating oviposition was to find the preferred site(s), so that an egg scouting technique could be developed, which could provide a warning system of imminent outbreaks. This technique has been used very successfully in timing insecticide applications for the control of cotton pests in Rhodesia (Tunstall, Matthews and Rhodes, 1962).

Secondly, an attempt was made to compare the relative activities of A. epsilon and A. segetum moths. The study has so far shown that there are differences between the two species. These differences are seen in the development periods (shorter in A. epsilon), the number of larval instars (variable in A. epsilon), and the phototactic reactions of the larvae (variable in A. epsilon). This would indicate that A. epsilon is more variable than A. segetum. Wellington (1957, 1964) states *inter alia* that, "populations are composed of individuals and individuals differ. Differences in activity and behaviour affect rates of development and survival after eclosion. They persist in modified form into the adult stage, when they appear as differences in responsiveness and in flight capacity. The level of adult activity in turn provides a clear indication of the kind of progeny a female may produce: inactive moths will give rise to predominantly inactive

larvae and active moths will give rise to predominantly active larvae. Inactive moths oviposit near their birthplace, while active moths will usually travel farther before they oviposit."

Thirdly, some preliminary work was carried out on the presence of a sex pheromone in virgin females of A. segetum, as this aspect could also provide a tool for the management of populations.

9.2. Methods

9.2.1. Oviposition Sites

Sites of oviposition were determined by placing asbestos cylinders, measuring 0.6 m in diameter and 0.45 m high, over young maize plants growing in an agricultural land and over tobacco seedlings growing in a seedbed. The tops of the cylinders were covered with mosquito netting and vials containing a 20 per cent solution of glucose, for the nourishment of the moths, were placed within the cylinders. A male and female moth of one species, that is, either A. ipsilon or A. segetum, were introduced into each caged area through an opening in the netting. The number of eggs laid on the various substrates that were available to the moths were recorded, though eggs deposited on the walls of the cylinders and the netting were ignored (amounted to 26.4 per cent of the total eggs deposited) as these substrates were considered to be unnatural.

An analysis of variance was carried out on the data, which were transformed to obtain homogeneity.

When moth numbers in the light-trap at Salisbury were at a reasonably high level, the area under crops in the vicinity of the trap was

scouted for eggs to obtain data on oviposition sites in the field. Once eggs were located on any substrate, an area of 2 m^2 around the oviposition site was carefully scouted for further eggs.

9.2.2. Capacity for Activity

An attempt was made to compare the relative activities of A. segetum and A. epsilon moths. Moths emerging from laboratory cultures reared at 24°C were placed in cages measuring $100 \times 80 \times 100\text{ mm}$ and consisting of a pith framework with mosquito netting sides. The cages were suspended on a length of wire 1 mm in diameter, and in the manner shown in Fig. 25. As a moth moved in the cage, so the balance of the system was upset and the pointer attached to the length of wire was deflected. The pointer was gently applied to a smoked drum revolving once every 24 h or once every 48 h. This method of measuring activity has advantages over flight mills since the moths are not handled, ensuring that no injury can occur and that activity is purely voluntary. The activity recorders were placed in a room having a constant temperature of 24°C and a day/night cycles of 12/12 h. Only one sex was used during a recording period so that no possible influence of the female sex pheromone (see section 9.3.2.) on activity of the males would result.

Moth activity was measured on the basis of periods of 30 min and 5 min continuous duration, the former providing a measure of sustained activity and the latter of discontinuous activity (Dingle, 1968). Each moth was confined in the activity recorder for a period of two nights, and the age of the moths under test varied from 0 to 2 days at the onset of the recording.

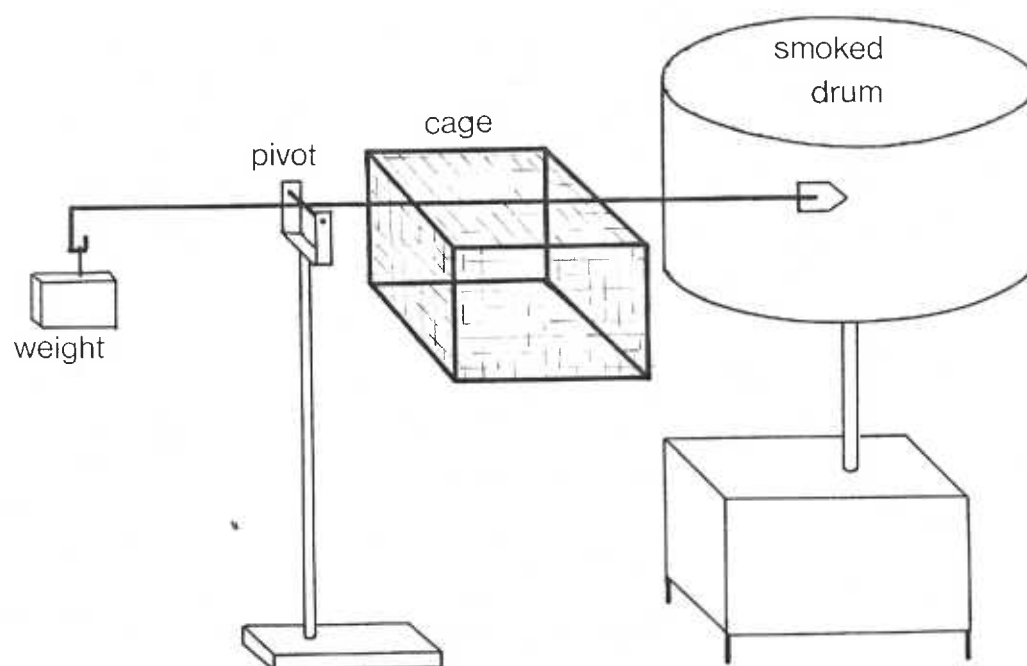


FIG. 25. APPARATUS TO MEASURE MOTH ACTIVITY.

The mean number of 30 min and 5 min activity periods recorded for each species and sex was partitioned into groups: the one group containing those individuals with a mean of 0.5 to 9 periods of 30 min activity or 0.5 to 54 periods of 5 min activity per night, and the other group containing individuals with a mean of over 9 periods of 30 min activity or over 54 periods of 5 min activity per night. The former group may be termed the inactive individuals and the latter the active moths. The individuals which showed no periods of activity were recorded separately.

Histograms of the frequency of activity periods were constructed and an attempt made to distinguish possible bimodal distributions. The graphical method of analysis by Harding (1949) for polymodal frequency distributions was attempted, but was found to be very subjective and was therefore not used.

In order to determine whether differences in adult activity were inherited by moths of the filial (F_1) generation, as inferred by Wellington (1964) and shown in Onconotus by Dingle (1968), those moths of both sexes and species which recorded a mean of 9.5 or more periods of 30 min continuous activity per night (active forms) were confined together for the purpose of mating. The same procedure was carried out for the inactive moths, that is, those which recorded nine or less 30 min periods per night. The F_1 adults were then introduced into the activity recorders, under the same conditions used for recording the activity of the parental (P_1) moths. Due to the difficulties in obtaining sufficient active and inactive moths of both sexes at the same time for mating purposes, relatively few individuals were tested. Results were pooled, that is, males and females of each

species, and then partitioned into an active and inactive group as was done for the P_1 moths. The significance of the differences between the proportions of active and inactive moths in the P_1 and F_1 populations was tested by a method approximating to a "t" test, given by Chambers (1964, pp. 46 and 47).

9.2.3. Sex Pheromone

Once the pheromone gland in the terminal abdominal segments of the virgin female moth of A. segetum was located, it was vivisectioned into the solvent dichloromethane, macerated by means of a glass rod and pure sea-sand, and then filtered. The filtrate was made up to volume, so that the extract contained a pheromone concentration equivalent to four females per ml (4 FME/ml) and kept at 5°C over sodium sulphate.

The laboratory test method for pheromone activity was adapted from a method described by Shorey, Gaston and Fukuto (1964). The apparatus consisted of a Buchner funnel through which clean air was passed, at a flow rate of about 6 litre/min, over impregnated filter paper. A glass cylinder, closed at both ends with nylon gauze and containing male moths, rested in the funnel over the impregnated filter paper. The apparatus was placed in front of a fume cupboard and a photographic safelight was used for observation during the tests. A control test with solvent only was carried out before each pheromone test. The tests were carried out between 2340 h and 0100 h.

Two virgin female moths of A. segetum, three days old, were kept at 5°C overnight and their pheromone glands vivisectioned into 10 ul of dichloromethane. The glands were ground with sodium sulphate using a glass rod, and the solution was allowed to settle before being injected

into a gas-liquid chromatograph by Dr J.S. Read. The column of the chromatograph was packed with a 1:1 mixture of 10 per cent QF-1 and 10 per cent DC 200 on Gas Chrom Q (100/120 mesh). A flame ionisation detector was used with argon at 60 ml/min as the carrier gas. The oven temperature was 180°C, and the detector temperature was 240°C.

9.3. Results

9.3.1. Oviposition Sites

The total number of eggs laid by female moths on the various substrates available to them within caged areas are shown in Table XI.

An analysis of variance was carried out on the data, but it was found that there was great heterogeneity of variance. Application of transformations of the data still indicated heterogeneity. However, it is interesting to note that a high percentage of eggs was deposited on debris, varying from 50 to 71 per cent, and it was found that oviposition on this substrate occurred in 80 per cent of the trials. Andrewartha (1961) quotes an experiment where oviposition by Pieris rapae was determined in a randomised block design, and which also showed great heterogeneity in the variances. He was able to show, however, that differences in the mean numbers of eggs laid on plants in the family Brassicae and on all other sorts of plants tested were so consistent that they were taken as being highly significant without calculating precise probabilities. From this it would seem that the high percentage of eggs laid on debris by A. ipsilon and A. segetum, whether confined over maize plants or tobacco, may be taken as being real despite variance heterogeneity.

TABLE XI. OVIPOSITION SITES OF A. SEGETUM AND A. IPSILON IN CAGED AREAS.

	Substrate	Total eggs laid		% laid per substrate	
		<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>
Maize	Funnel	0	87	0.00	5.11
	Lower leaves	190	149	15.64	8.76
	Weeds	155	300	12.76	17.64
	Debris	866	1 148	71.28	67.49
	Soil	4	17	0.32	1.00
	Totals	1 215	1 701	100.00	100.00
Tobacco	Lower leaves and stems	202	149	25.38	17.74
	Weeds	165	135	20.73	16.07
	Debris	403	546	50.63	65.00
	Soil	36	10	3.26	1.19
	Totals	796	840	100.00	100.00

The few oviposition sites that were found in the field confirmed the results obtained under caged areas. Of four batches of eggs found in the field, all were on dry plant debris lying on the soil surface. A total of 56 eggs were found in the four batches, and no eggs were found on any other substrate within the surrounding 2 m² of each site. These oviposition sites were located in plots with young maize and groundnut plants.

9.3.2. Capacity for Activity

Results of recording the activity of P₁ moths based on the arbitrary division of active and inactive forms are shown in Table XII. The histograms of the frequency of activity periods are shown in Figs. 26 and 27.

It is seen that A. ipsilon has a higher percentage of active moths than does A. segetum, and if the 30 min periods are taken as a measure of sustained activity, then it is seen that A. ipsilon is relatively more active than A. segetum.

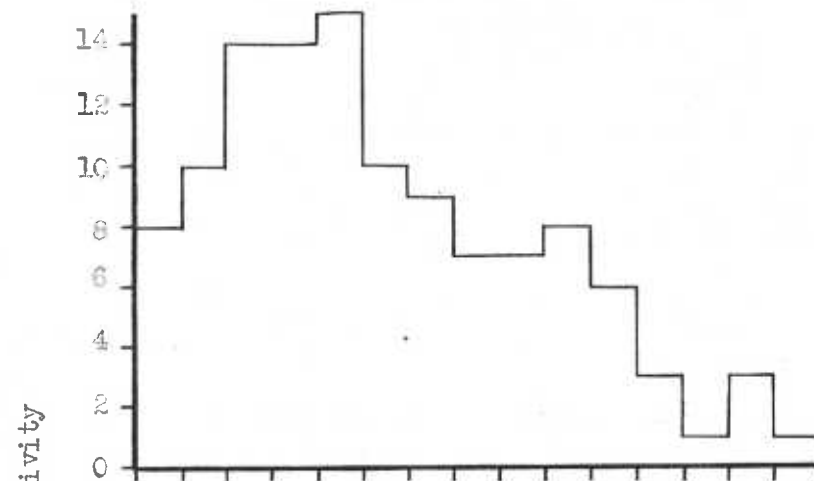
The heritability of activity characteristics, based on the arbitrary division of active and inactive forms and on the mean number of 30 min continuous activity periods, are shown in Table XIII. Histograms of the frequency of activity periods of the F₁ moths from either active or inactive parents (P₁) are shown in Figs. 28 and 29.

The changes in the percentage of active and inactive moths in the F₁ populations from the mean percentages (male and female) of active and inactive moths in the P₁ populations are shown in Table XIV. The differences between the proportions of moths that were classified as active and inactive in the F₁ and P₁ populations are significant for

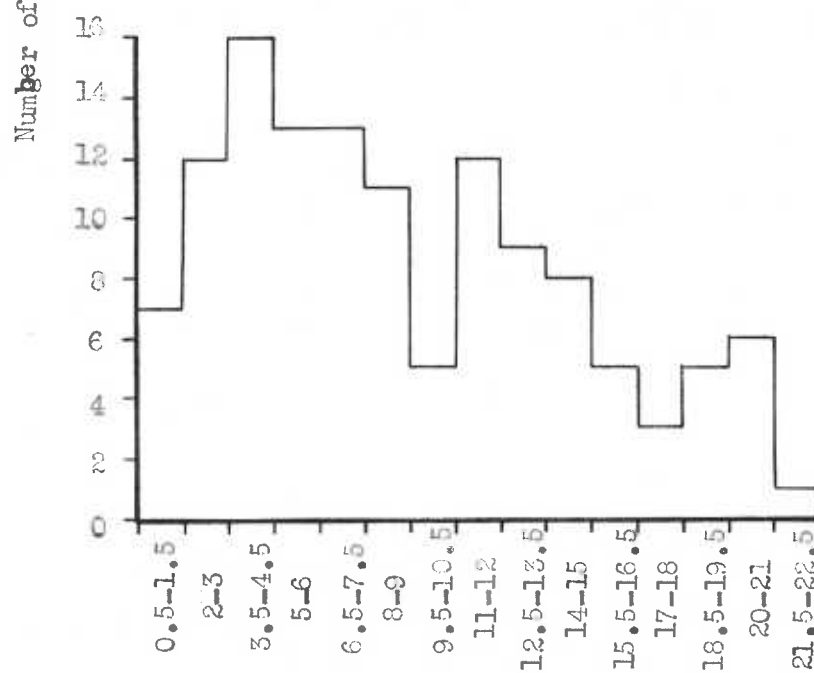
TABLE XII. PERCENTAGE OF ACTIVE AND INACTIVE MOTHS
OF AGROTIS SEGETUM AND A. IPSILON.

Species and sex	Per cent of poulation active or inactive					
	30 min periods			5 min periods		
	Active	Inactive	n	Active	Inactive	n
<u>A. segetum</u> male	38.79	61.21	116	60.61	39.39	99
<u>A. segetum</u> female	42.86	57.14	126	63.30	36.70	109
<u>A. ipsilon</u> male	57.14	42.86	42	70.27	29.72	43
<u>A. ipsilon</u> female	60.00	40.00	65	68.33	31.67	60

A. segetum males, n = 116



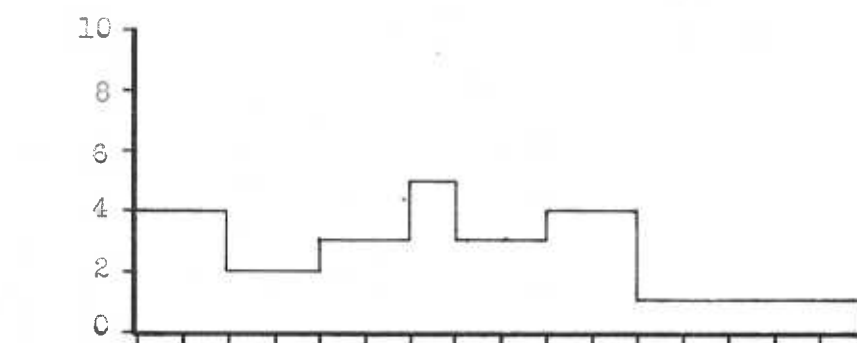
A. segetum females, n = 126



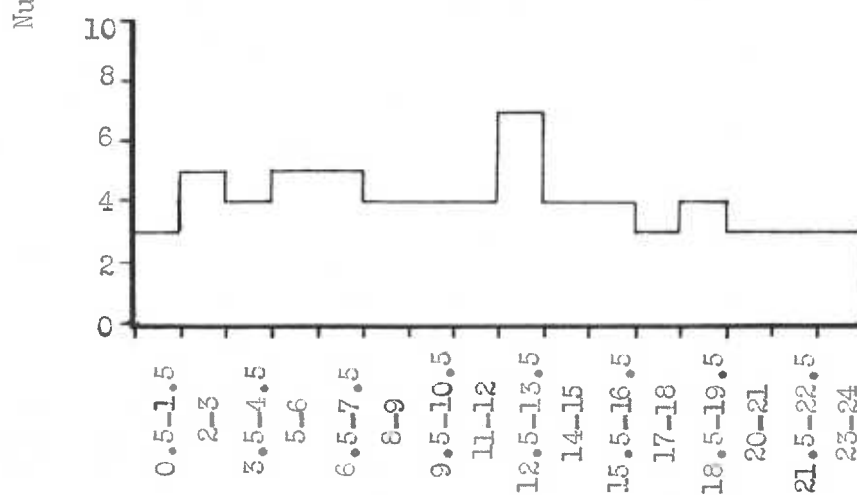
Mean number of 30 min periods of continuous activity of each moth during two nights observation.

FIG. 26. DISTRIBUTION OF ADULT A. SEGETUM ACTIVITY BASED ON 30 MIN PERIODS OF CONTINUOUS ACTIVITY.

A. ipsilon males, n = 42



A. ipsilon females, n = 65

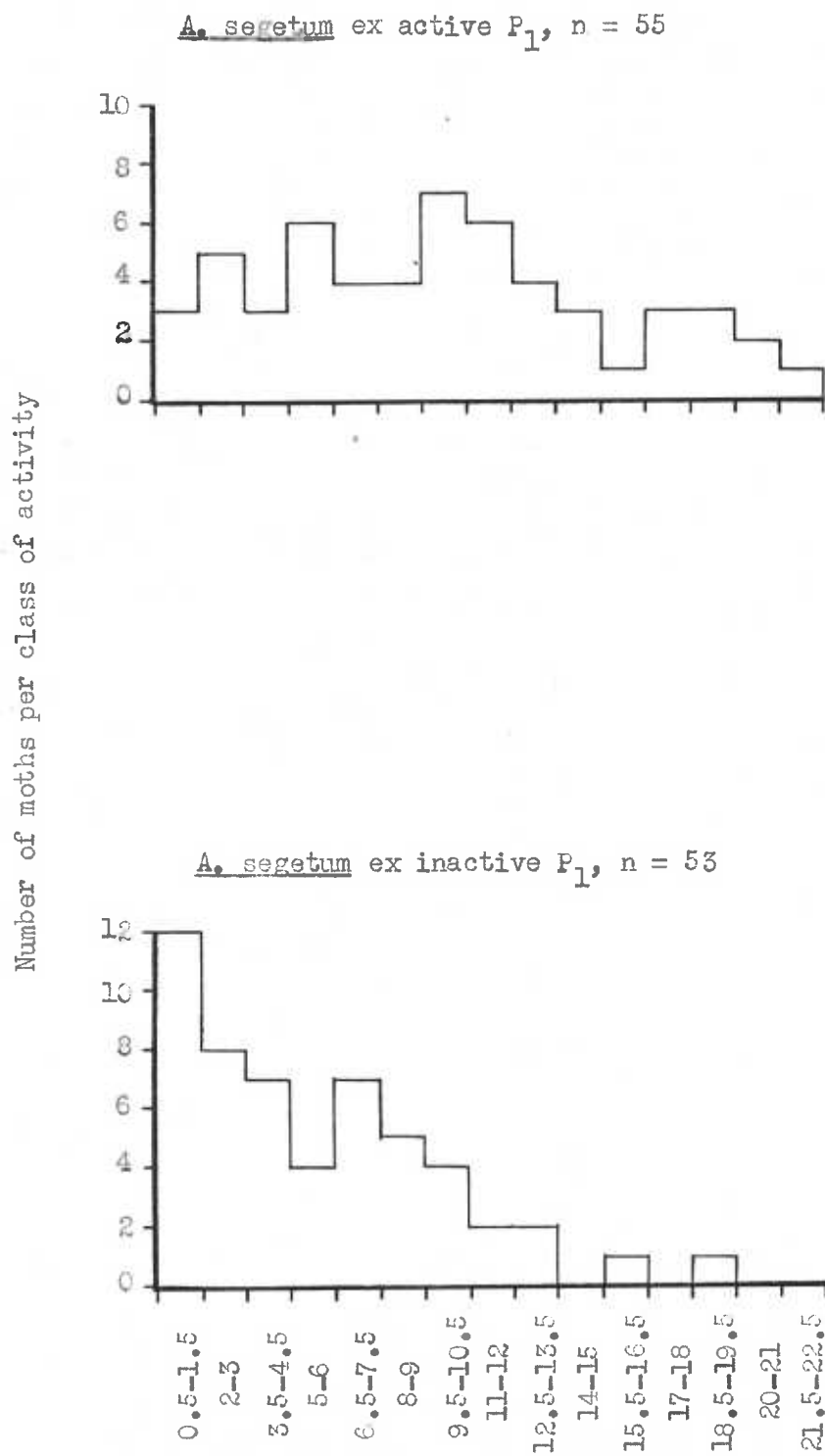


Mean number of 30 min periods of continuous activity of each moth during two nights observation.

FIG. 27. DISTRIBUTION OF ADULT A. IPSILON ACTIVITY BASED ON 30 MIN PERIODS OF CONTINUOUS ACTIVITY.

TABLE XIII. PERCENTAGE OF ACTIVE AND INACTIVE FILIAL MOTHS
RESULTING FROM ACTIVE AND INACTIVE PARENTS.

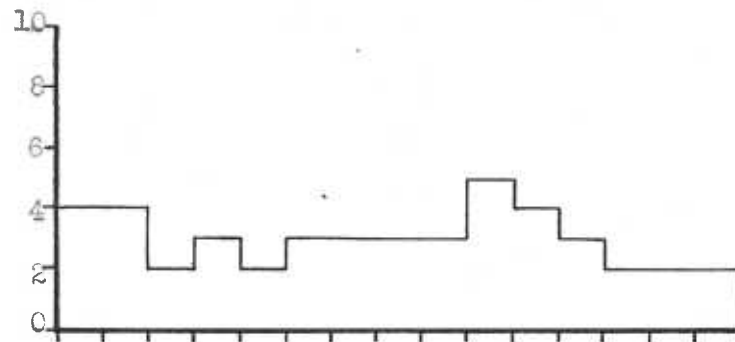
Species	Parent type	% F ₁ population active or inactive		
		Active	Inactive	n
<u>A. segetum</u>	active	54.44	45.45	55
	inactive	18.87	81.13	53
<u>A. ipsilon</u>	active	60.00	40.00	45
	inactive	40.00	60.00	40



Mean number of 30 min periods of continuous activity of each moth during two nights observation.

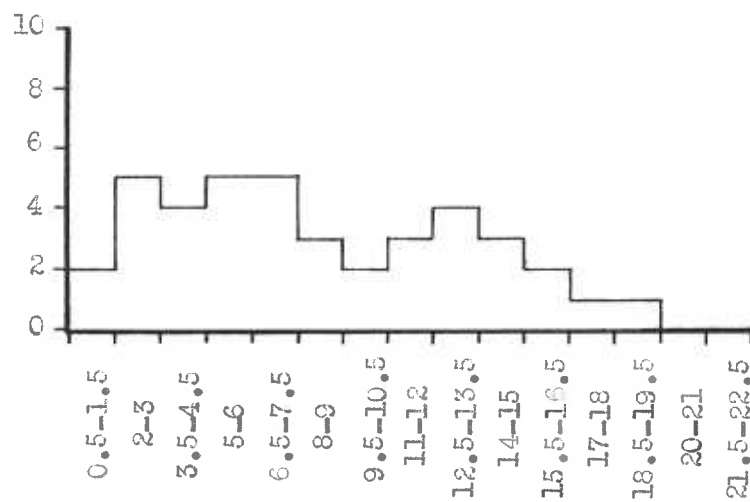
FIG. 28. DISTRIBUTION OF ACTIVITY OF FILIAL A. SEGETUM ADULTS.

A. ipsilon ex active P_1 , n = 45



Number of moths per class of activity

A. ipsilon ex inactive P_1 , n = 40



Mean number of 30 min periods of continuous activity of each moth during two nights observation.

FIG. 29. DISTRIBUTION OF ACTIVITY OF FILIAL A. IPSILON ADULTS.

TABLE XIV. COMPARISON OF THE MEAN PERCENTAGES (MALE AND FEMALE) OF ACTIVE AND INACTIVE PARENTS WITH THE PERCENTAGES IN THE FILIAL POPULATION.

Species	Mean % P_1 moths		Parent type	% F_1 moths		% change in F_1 from P_1
	Active	Inactive		Active	Inactive	
<u>A. segetum</u>	40.32	59.12	active	54.55	45.45	13.73
			inactive	18.87	81.13	21.95*
<u>A. ipsilon</u>	58.57	41.43	active	60.00	40.00	1.43
			inactive	40.00	60.00	18.57*

* denotes that differences between F_1 and P_1 are significant

for the inactive moths of A. segetum and A. ipsilon, and almost significant for the active moths of A. segetum. The capacity for activity would thus appear to be a heritable trait.

The moths that did not record any activity, as measured by periods of 30 min and 5 min continuous activity, are shown in Table XV. In all populations there is less than 6 per cent that did not show any activity.

9.3.3. Sex Pheromone

During exposure of the male moths to the pheromone extract of A. segetum, three different responses were noted whereas no response was observed when only the solvent dichloromethane was tested. At the beginning of an exposure, responding males would have alert antennae and vibrating wings, then they would take to active flight and finally attempt to copulate with each other. It was found that male moths would respond to 0.1 FME.

From these tests it was apparent that the virgin female moths of A. segetum possess one or more pheromones that serve to recruit a sexual partner, and as a releaser of male copulatory behaviour (Shorey, 1973).

Graphic traces obtained on a gas-liquid chromatograph from pheromone extracts of two A. segetum virgin female moths showed very small peaks. Injection of standard compounds of different chain lengths and functionalities, under the same conditions as the extracts, produced traces for comparison with the pheromone extracts (Klun and Brindley, 1970) and the retention times obtained with a chart speed of 30.5 cm per h were:

TABLE XV. PERCENTAGE OF MOTHS IN ALL POPULATIONS NOT
RECORDING ANY ACTIVITY.

Species	Generation	% of population completely inactive	
		30 min periods	5 min periods
<u>A. segetum</u>	P ₁	3.94	0.48
<u>A. ipsilon</u>	P ₁	5.66	0.97
<u>A. segetum</u>	F ₁ active	1.82	0.00
	F ₁ inactive	5.66	0.00
<u>A. ipsilon</u>	F ₁ active	2.22	0.00
	F ₁ inactive	0.00	0.00

Moth 1	:	2.76, 3.94, 4.93, 6.11 min
Moth 2	:	2.96, 3.94, 5.22, 6.70 min
Fatty acid	}	a. : 2.76(C_{14}), 4.14(C_{15}) min
methyl ester		
standard		
		b. : 3.15(C_{14}), 4.43(C_{15}) min
Tetradecenyl	}	: 2.86(C_{14} methyl ester), 3.94(C_{14} acetate) min.
acetate		

From this preliminary work it appears that the pheromone(s) molecule has a chain length of 14 to 15 carbon atoms, as the gas-liquid chromatography indicates that either (i) C_{14} fatty acid methyl esters or (ii) C_{14} fatty acid methyl ester and C_{14} acetate, or (iii) C_{14} and C_{15} fatty acid methyl esters and C_{14} acetate are present in the gland extract of A. segetum.

The pheromone gland was found to be situated in the inter-segmental membrane between abdominal segments VIII and IX of the female moth. When the gland is extruded, it appears as a white ring with ventral development.

Flaschenträger and Amin (1950) have demonstrated that the female moths of A. ipsilon attract males of the same species. The attractant odour appears an hour after eclosion and is restricted to the last two abdominal segments. The pheromone can be extracted from the abdominal segments by ether, and the ethereal extract shows the same power of attraction as the living moths. The pheromone of A. ipsilon does not appear to have been characterized, so that no comparisons with the preliminary analysis performed on that of A. segetum can be made.

9.4. Discussion

The biological significance of ovipositing on debris is not clear, since it has been shown (section 8.3.3.) that larvae are unable to survive on this substrate for any appreciable time. Chapman (1969) maintains that in the selection of an oviposition site by an insect, two phases can be recognised. The initial selection is based on a general reaction to the environment followed by a final selection, which depends on more specific responses. The latter often includes contact chemoreceptors on the antennae, tarsi, and ovipositor (Dethier, 1947). It is felt that fertilised female moths must initially be attracted to an area where food plants are growing in a favourable condition for young larvae to develop, that is, plants in the early stages of growth (section 7.3.2.), and then specifically select deposition sites. The final selection may well be dependent on chemoreceptors as proposed by Dethier, but it is also thought that thigmotaxis may play a role. The reason for the latter is that the preferred oviposition substrate of debris, and the fairly high proportion of eggs deposited on the 'unnatural' substrate of gauze (26 per cent), are both irregularly shaped with recesses.

With the results showing preferred oviposition sites to be on debris, field observations of cutworm outbreaks by Rose (1962) and other entomologists in Rhodesia, can be explained. An accumulation of records shows that outbreaks are more likely to occur where agricultural lands have been treated with manure or compost, or where green crops such as dhal have been ploughed in and not completely buried. The surface debris in these cases would provide sites for oviposition. The adaptive significance of ovipositing on debris may be explained as follows. The debris acts as a mulch and is able to retain soil

moisture, particularly from light showers at the beginning of the rainy season. Weed seeds that may be present in, or under, the mulch will be able to germinate and provide new plant growth on which young larvae can develop.

Wellington (1957) has suggested that the role of individual differences in the population dynamics of animals has been relatively neglected. The factors believed to regulate population requires detailed observations of the qualities of different types of individuals, apart from extrinsic mortality factors. Wellington (1964) has shown in Malacosoma pluviale (Dyar) that inactive moths oviposit near their birthplace, and most of their offspring are also inactive. More active moths can travel farther before they oviposit, and always have a higher proportion of vigorous individuals among their progeny. Such polymorphism allows the insect to cope with environmental diversity; for example, inactive residents exploit favourable habitats and active migrants colonise more severe habitats, or replenish the vigour of other populations. Because the most active moths usually export the most vigorous progeny, the population left behind becomes less vigorous during successive generations. This steadily decreasing vitality eliminates local populations that are not replenished by vigorous immigrants. The ideas of Wellington would seem to be applicable to A. segetum and A. insilon, since in both cases there is an overlapping range of individual differences in a population as opposed to a distinct bimodality.

Although numerous studies have suggested the importance of environmental factors affecting flight in various species (Dingle, 1968; Johnson, 1965), there is a paucity of information about behavioural

variation caused by genetic differences. So far most evidence of genetic variation for flight has been derived from the presence of polymorphisms with respect to morphometric characters, such as wing length. Rose (1972) distinguished short and long fliers in populations of Oicadulina spp. (Homoptera), and showed that differences in flight behaviour were inherited. The Oicadulina populations could be divided into these two fractions according to durations of tethered flight of individuals. Clear bimodal activity curves were not obtained for the Agrotis spp., and it seems more likely that inheritance of this trait is polygenic for A. segetum and A. ipsilon. Caldwell and Hegmann (1969) maintain that flight is a continuous variable, probably dependent on allelic differences at many loci: heritability is a population-specific parameter describing the ratio of the additive genetic variance to the total variance for the trait. With the current emphasis on the importance of behavioural differences in migration (Kennedy, 1961), quantitative genetic analysis of such differences may be useful in discerning strategies of migration and dispersion.

As mentioned in the introduction to this chapter, A. ipsilon appears to be more variable than A. segetum. It was also suggested in section 6.4. that A. ipsilon was the more opportunist of the two species. It is seen from Table XIII that the P_1 populations of A. ipsilon have a higher proportion of active individuals than A. segetum, and that this trait is inherited in higher proportions. Thus, from the hypothesis of Wellington (1964) that active migrants colonise more severe habitats, it would be expected that A. ipsilon could cope with a greater environmental diversity than could A. segetum. This adds to the idea that A. ipsilon is the more opportunist of the two species.

10. SEASONAL ABUNDANCE OF AGROTIS SEGETUM AND A. IPSILON.

10.1. Introduction

Insect control depends greatly on knowledge of the seasonal trends in abundance of pests, and this is, therefore, an important aspect in the understanding of the biology of A. segetum and A. ipsilon. Once a knowledge of the seasonal trends in populations is available, and the number of generations that each species is able to complete in a calendar year is known, the factors causing fluctuations in numbers can be investigated. With this data, a better understanding of the factors causing outbreaks of the pests can be obtained. This could lead to possible methods of forecasting such events.

10.1. Methods

The seasonal abundance of adult A. ipsilon and A. segetum has been determined by the use of Robinson light-traps (Robinson and Robinson, 1950) equipped with 125 W mercury-vapour lamps and situated at Salisbury, Chiredzi and Gatooma Research Stations. These three traps are sited adjacent to experimental plots of annual crops, which are grown throughout the year. During the latter part of the study, the light-trap grid in Rhodesia was enlarged to form part of the Southern African Light-Trap Grid (Blair, 1972 a) and data from Kariba, Mount Darwin, Victoria Falls and Matopos was obtained. Each calendar year has been divided into 52 weeks beginning 1 - 7 January and ending 25 - 31 December. In order that the weeks of any one year can be compared with those of other years, two adjustments are made. Week 26 (June/July) contains eight days, that is, 1 and 2 July data are pooled; in a Leap year the data of 29 February is pooled with that of 28 February. Since catches are

generally small during the cool season, and Leap years only occur one in every four, these adjustments should not materially affect the data. Lewis and Taylor (1967), in their standard calendar for the analysis of annual records (such as light-trap catches), have dropped the dates of 29 February and 31 December. The latter date is during the northern winter when insect numbers are low and, therefore, not important in recording abundance. However, 31 December is during the southern summer when insect numbers are high; thus the date that is lost in the southern winter is 1 July.

In attempting to explain peaks of moths from light-trapping (section 10.3.1.), factors such as the influence of lunar phases on flight activity, the immigration of moths on convergent wind streams, and the successful breeding of the resident population in the latter part of the previous year have been considered. The relevant lunar phases, that have been thought by a number of authors to influence flight activity, were extracted from meteorological records for the period embracing the first 10 weeks (1 January to 11 March) of each trapping year (1969 - 1973). This 10-week period was selected as it was during this time that peak moth catches were recorded in certain years. The date of the height of each phase was used as a pivot with $\pm$ three days on either side as the extent of each phase.

Meteorological records were consulted to ascertain the number of days that convergence lines, or areas, were present over Salisbury in the months of January and February of each year; these months were selected as it is during this period that peak catches were recorded in certain years, and to establish whether these peaks were due to immigration of moths.

With the difficulties involved in observing natural populations of a soil-inhabiting insect such as cutworms, no field population estimates could be made. However, in an effort to obtain a comparative indication of population levels prior to the moth peaks at the beginning of certain years, the number of reports received by the Plant Protection Research Institute of larval damage by A. segetum and A. ipsilon were extracted for the months of October, November and December.

In an attempt to ascertain whether the low numbers of moths recorded during the cool season were due to the possible inhibiting effects of low temperature on flight activity, or were a reflection of the population level, the minimum temperatures recorded by the meteorological station adjacent to the light-trap at Salisbury were considered with moth catches during June and July (cool season).

By using the temperature-velocity curves (logistic curves) that were obtained from laboratory studies (Figs. 8 to 13) and the mean weekly temperatures at Salisbury in 1969, the average per cent development per day for each stage in the life cycle was determined. In this way it was possible to calculate the duration of each successive generation through the year. There are, however, disadvantages in using laboratory data for extrapolation to field conditions, as the former are based on constant temperatures and on a semi-synthetic bean diet. Despite the differences in meteorological screen temperature and temperature of the insect, particularly in view of the effects of insolation, many workers have successfully used screen temperatures to predict events in field populations (for example, Phelps and Burrows, 1969; Druzhelyubova and Makarova, 1963; Apple,

1952; Glen, 1931). The year 1969 was selected for the study since there were discernible peaks of moths from light-trapping results (section 10.3.1.), which could then be used for comparison with the calculated number of generations possible per calendar year. The starting point was taken as 1 January, with the deposition of eggs, because the adult populations of both species were at a low level at this time (Fig. 30).

The total rainfall recorded during the post-rainy season (March, April, May and June) at Salisbury was plotted against the number of moths recorded in the light-trap, at the same site, during August or August and September. Such data was taken for 10 separate years in an effort to forecast the general trend of the local population during this period.

Records of parasites and predators of A. segetum and A. ipsilon were obtained from literature and from data filed by the Plant Protection Research Institute of the Rhodesian Ministry of Agriculture.

10.3. Results

10.3.1. Annual Population Cycle

The seasonal change in numbers of A. segetum and A. ipsilon moths captured in the light-trap at Salisbury during 1969 to 1973 are shown in Figs. 30 to 34. It can be seen that the numbers are at a low ebb during the cool season, that is during the period from week 20 to week 30. With the increase in ambient temperatures from mid-August (hot season) there is a corresponding increase in the moth populations, reaching a peak at around week 35 and another at around week 45. The major peak of the year is usually during the first 10 weeks. From the

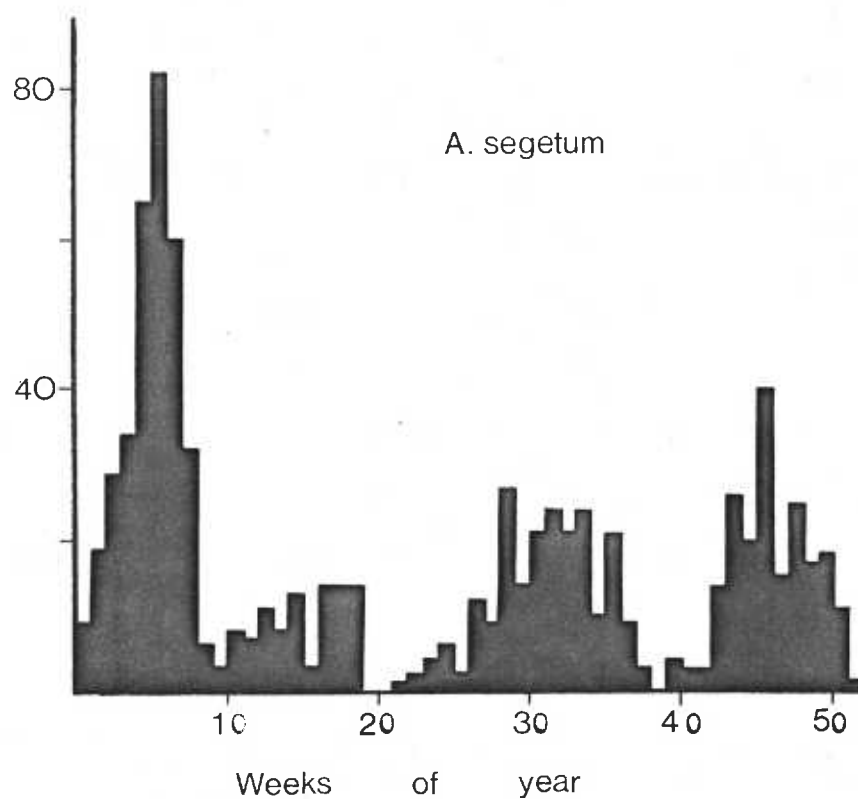
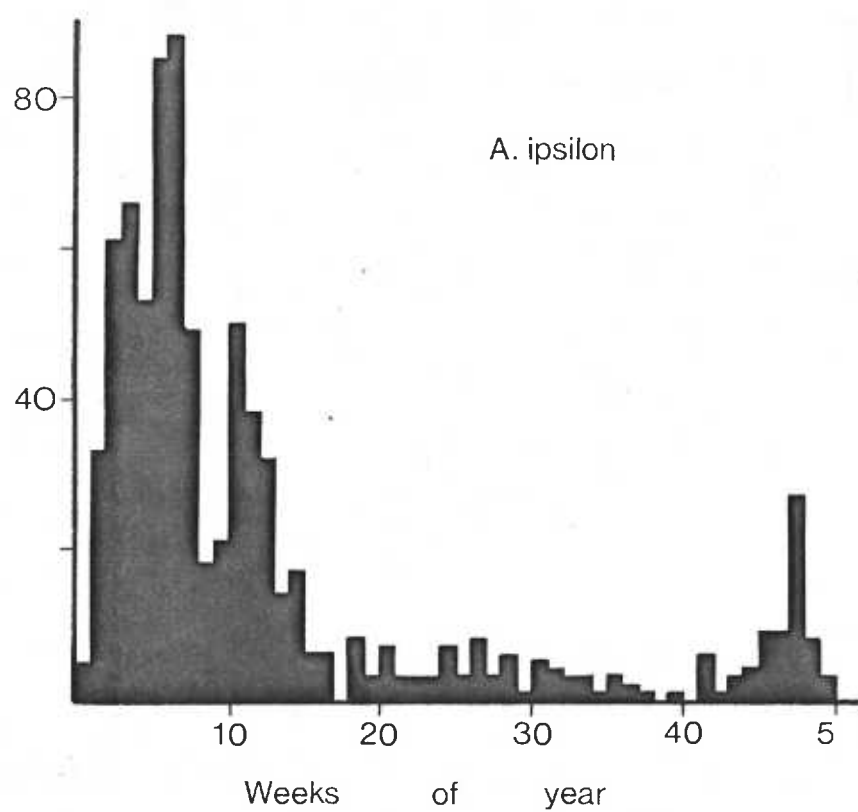


FIG. 30. WEEKLY CATCHES OF A. IPSILON AND A. SEGETUM MOTHS IN THE SALISBURY LIGHT-TRAP IN 1969.

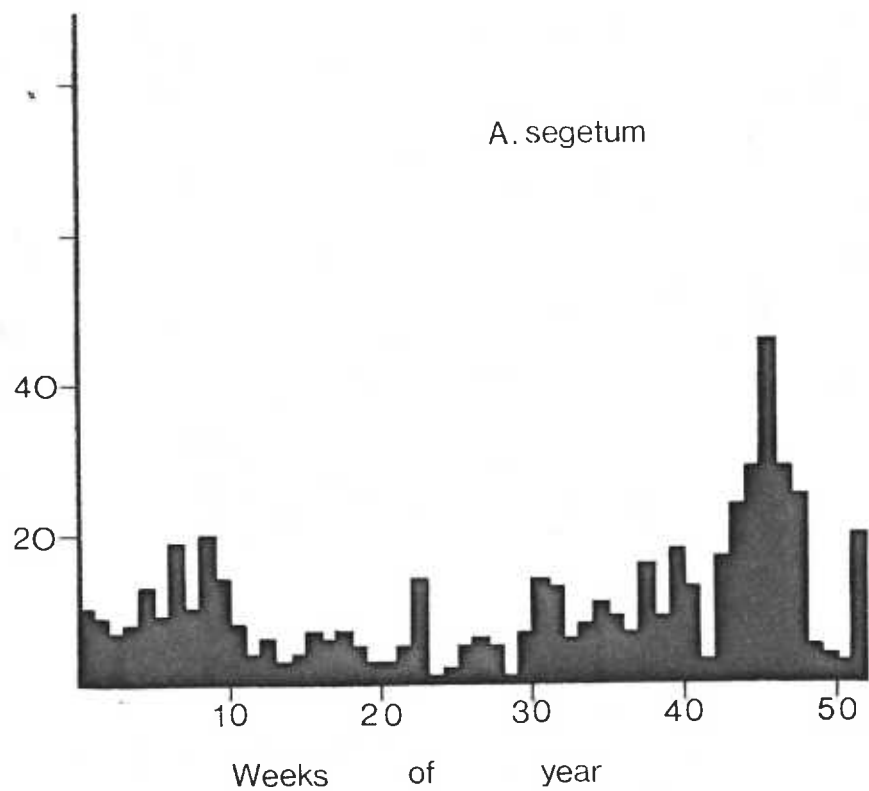
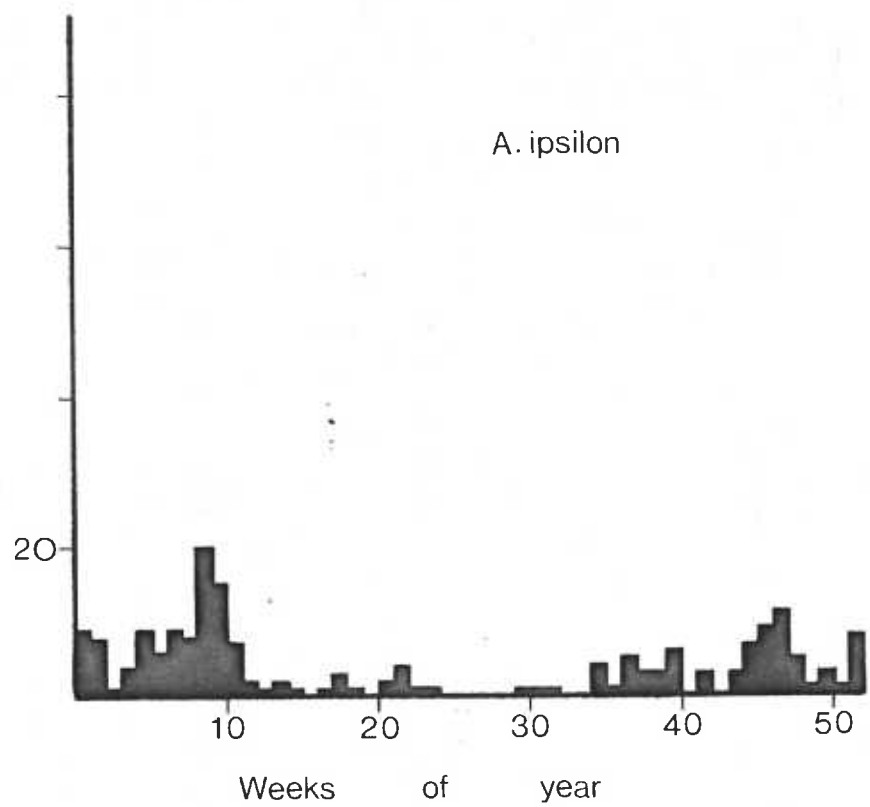


FIG. 31. WEEKLY CATCHES OF A. IPSILON AND A. SEGETUM MOTHS IN THE SALISBURY LIGHT-TRAP IN 1970.

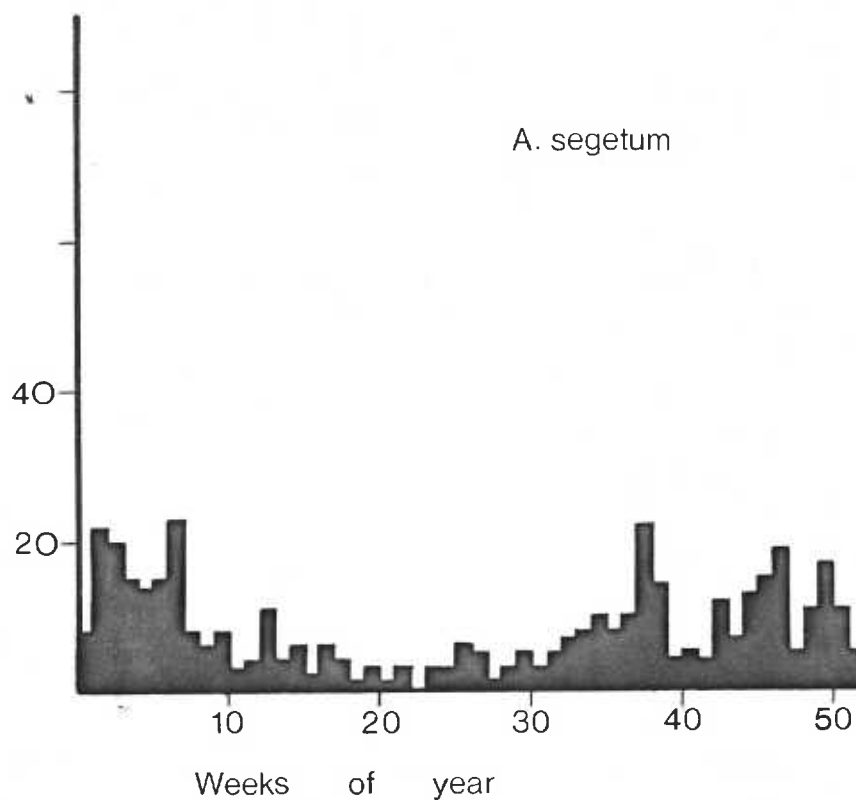
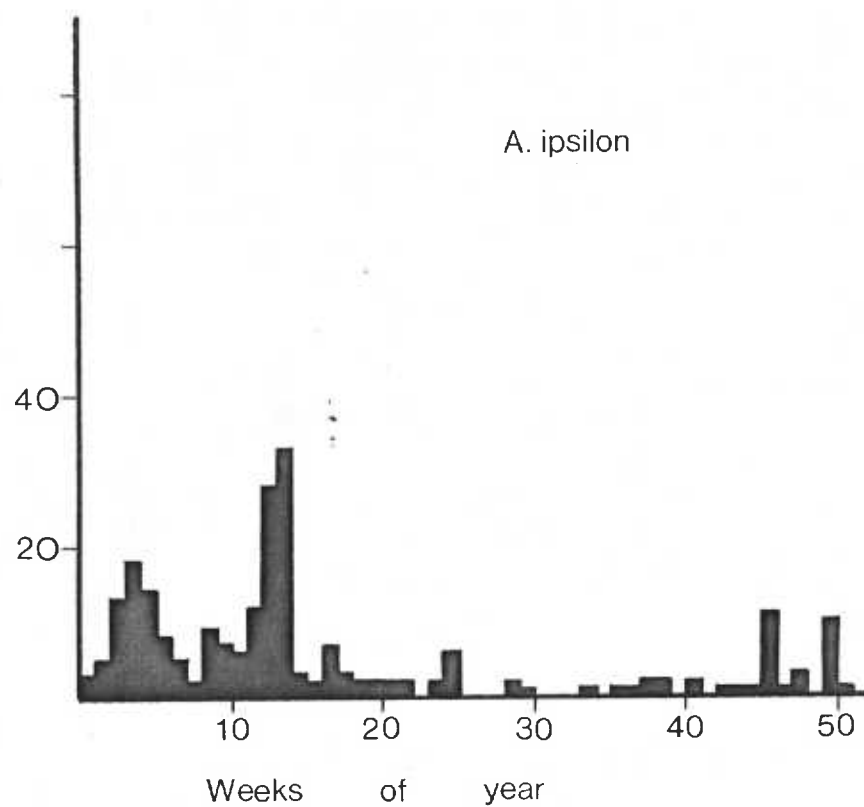


FIG. 32. WEEKLY CATCHES OF A. IPSILON AND A. SEGETUM MOTHS IN THE SALISBURY LIGHT-TRAP IN 1971.

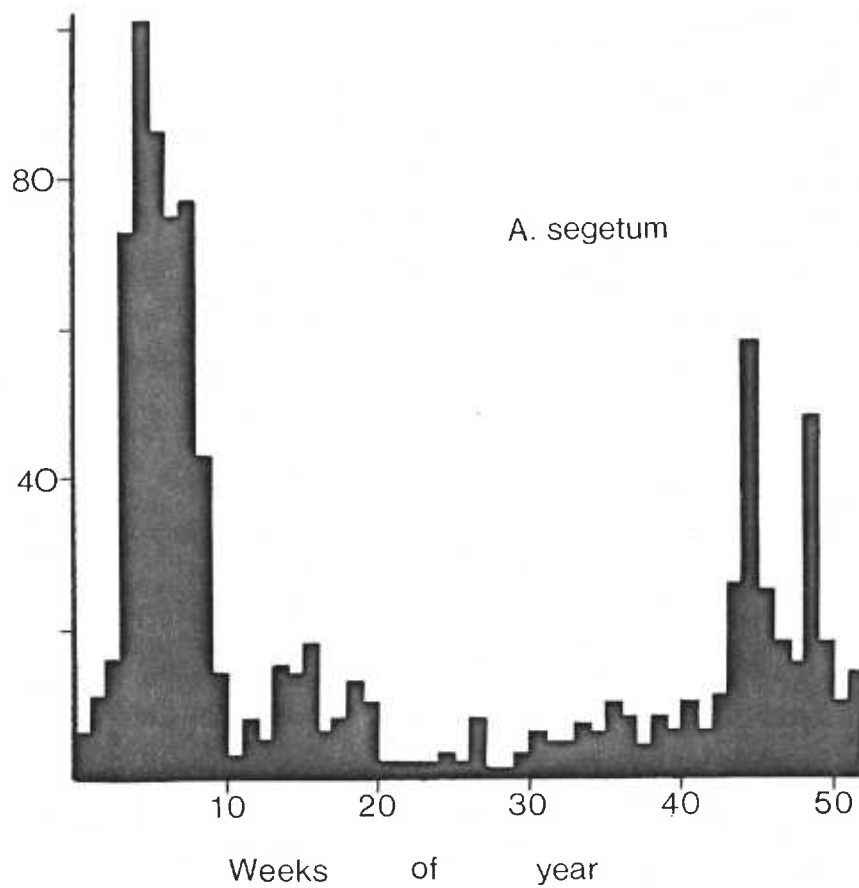
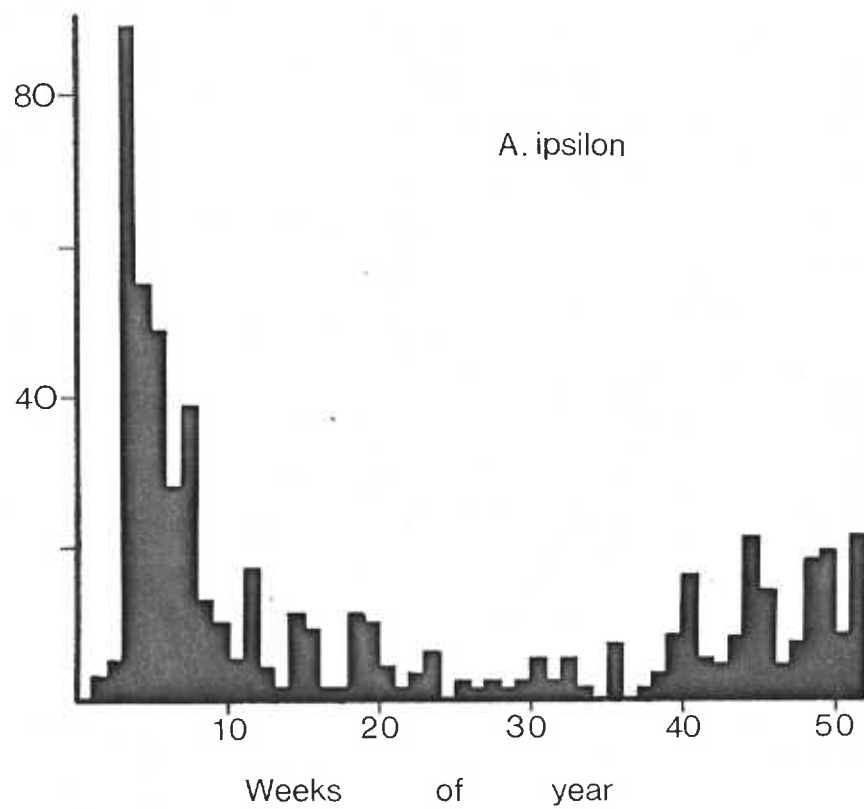


FIG. 33. WEEKLY CATCHES OF *A. IPSILON* AND *A. SEGETUM* MOTHS IN THE SALISBURY LIGHT-TRAP IN 1972.

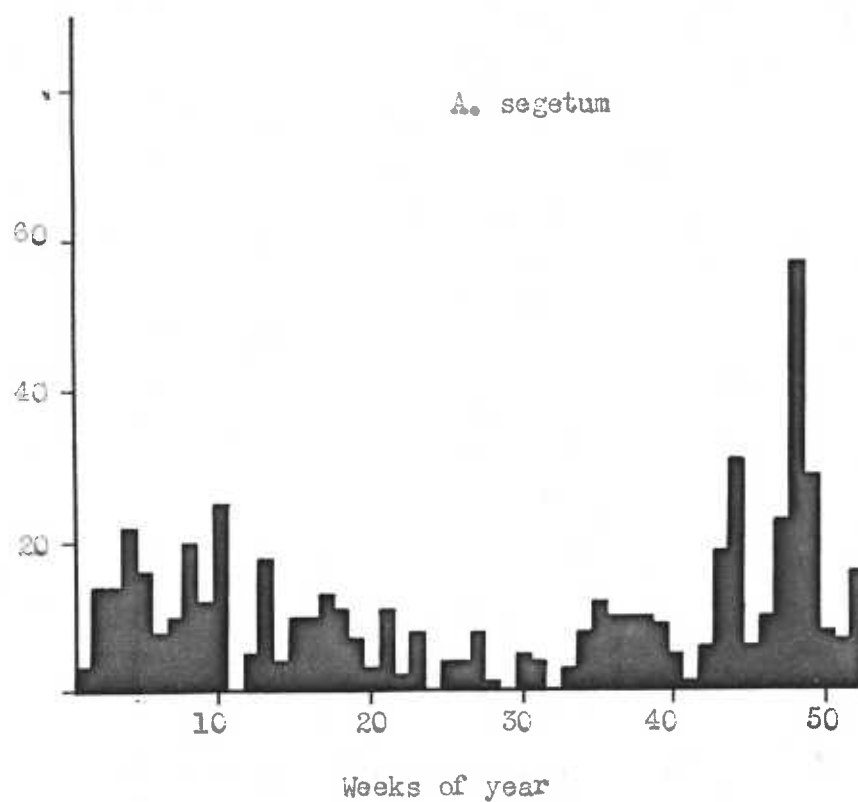
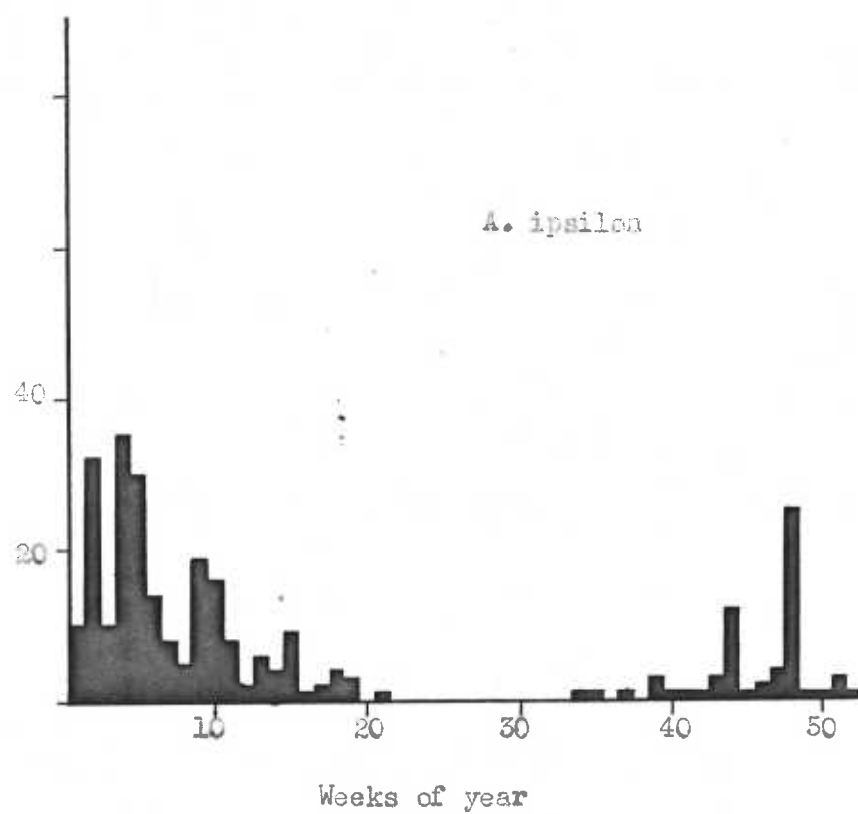


FIG. 34. WEEKLY CATCHES OF *A. IPSILON* AND *A. SEGETUM* MOTHS IN THE SALISBURY LIGHT-TRAP IN 1973.

records of the other trapping sites in Rhodesia much the same picture emerged, though numbers of moths varied from site to site.

From the light-trapping it is seen that the life cycle of A. segetum and A. ipsilon continues throughout the year in Rhodesia, with seasonal fluctuations, and that there does not appear to be any time of the year without moths. The exception to this is A. ipsilon during the cool season of 1973, when no moths were recorded for a period of 12 weeks; a fairly severe drought was experienced in this year and may be the cause of the apparent disappearance of this species during the cool, dry, season. Another point of interest is that in 1969 and 1972, high numbers of both species were recorded during the first 10 weeks and that fairly distinct peaks were discernible for the remainder of the year. The possible factors causing these peaks will be dealt with in the following sections.

10.3.2. Influence of Lunar Phases on Light-Trap Catches

The number of moths trapped at Salisbury in each lunar phase during the first 10 weeks (1 January to 11 March) of each year are shown in Table XVI.

It is seen, from the five-year means, that there is little difference between the numbers of moths trapped at each lunar phase. From this it would appear that the gross differences in moth numbers in the first 10 weeks of 1969 and 1972 (Figs. 30 and 33), and the other three years, would not appear to be due to any favourable lunar phase. However, the influence of lunar phases on the numbers of moths caught in light-traps has been shown by a number of authors (Williams, 1936, 1937, and 1940; Williams and Singh, 1951; Williams, Singh and El-Ziady,

TABLE XVI. MEAN NUMBER OF MOTHS TRAPPED PER NIGHT DURING EACH LUNAR
PHASE IN THE FIRST TEN WEEKS OF EACH YEAR.

Year	First quarter		Full-moon		Last quarter		New-moon	
	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>
1969	3.9	7.9	3.6	3.8	6.2	7.9	5.8	10.0
1970	2.0	1.0	1.1	0.5	2.0	1.7	1.9	1.6
1971	1.8	1.5	2.1	0.9	2.9	1.1	1.5	1.3
1972	6.8	5.3	11.6	8.0	5.3	3.0	6.5	2.3
1973	1.6	2.9	1.9	1.2	3.0	3.3	2.0	2.5
5-yr mean	3.2	3.7	4.1	2.9	3.9	3.4	3.5	3.5

1956; Nemec, 1971) to be reduced during periods of full-moon and be increased during periods of new-moon (no moon). If one takes the views of these authors that moonlight has an effect on nocturnal insects and that light-trap catches are reduced at full-moon, then from Table XVII the following may be expected. In 1969 and 1971 there are more nights of full-moon than new-moon during the first 10 weeks, and so catches should be depressed. In 1970 and 1973, one would expect the catches to be increased as there are more nights of new-moon than of full-moon, whereas in 1972 no overall effect would be expected with an equal number of nights of new- and full-moon. Despite the expectations, it is seen from Table XVII that more moths of both species were trapped in 1969 and 1972 than in the other years.

Brown and Taylor (1971) found in Kenya that A. segetum moths were more abundant in light-traps (1.52 m from the ground - a similar height of the Rhodesian traps) during the first week after full-moon. The number of nights of this lunar parameter within the period from 1 January to 11 March of each year, and the number of moths trapped, are shown in Table XVIII.

From the five-year means of the moths trapped in the first week after full-moon and during the periods between this lunar parameter, it is seen that there is little difference between the two categories for A. segetum, and that slightly more A. ipsilon were trapped during periods other than in the first week after full-moon.

However, the results are in agreement with the views of Hanna and Atries (1969) who suggest that moonlight has no effect on flight activity of A. ipsilon, since in Egypt the largest catches are recorded

TABLE XVII. NUMBER OF NIGHTS OF NEW-MOON AND FULL-MOON
AND NUMBER OF MOTHS TRAPPED IN FIRST TEN WEEKS OF EACH YEAR.

Year	Number nights		Number moths trapped	
	Full-moon	New-moon	<u>A. segetum</u>	<u>A. ipsilon</u>
1969	20	14	156	220
1970	14	21	55	40
1971	17	14	56	33
1972	14	14	250	134
1973	14	21	64	70

TABLE XVIII. NUMBER OF NIGHTS IN THE WEEK AFTER FULL-MOON
WITHIN THE FIRST TEN WEEKS OF EACH YEAR, AND THE NUMBER OF MOTHS TRAPPED.

Year	Nights in week after full-moon	Mean moths trapped in week after full-moon		Mean moths trapped in remaining period	
		<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>
1969	21	3.6	4.2	5.1	7.8
1970	14	1.8	1.2	1.7	1.3
1971	14	3.1	0.9	1.7	1.3
1972	14	7.4	5.1	7.0	4.0
1973	14	2.7	2.2	1.9	2.6
5-year mean		3.7	2.7	3.5	3.4

at new-moon in February, April and October, at first quarter in June and August, at full-moon in May and September, and at last quarter in December, January, March, July and November.

Thus, none of the theories pertaining to moth catches and lunar phases appear to hold with the data obtained in this study. As suggested from Table XVI, there appears to be little difference in the number of moths trapped at each lunar phase, and the large numbers trapped in 1969 and 1972 appear to be a reflection of a real increase in the population available for sampling.

10.3.3. Number of Moths in Relation to Convergence of Airstreams

The second factor that could account for the large number of moths in the first 10 weeks of 1969 and 1972 is immigration. Before dealing with the possibility of immigration, it was necessary to ascertain whether the two species were known to be migrants. Much evidence has been accumulated to show that A. ipsilon is a migrant (Fletcher, 1925; Williams, 1926; Williams, Cockbill, Gibbs and Downes, 1942; Rivnay, 1964), while A. secretum is suspected as being a migrant (Williams et al., 1942; Wiltshire, 1957). The two species are thus on record as being migratory, or at least being suspected as such.

(1963) in which
~~Brown~~ (1970) and Rainey (1974) have shown that insect ~~flight~~ direction of flying insects
~~direction~~ insects down and is greatly influenced by wind direction, the former being in
the same general direction as the latter. Brown, Betts and Rainey
(1969) have shown that moths are concentrated above a zone of convergent winds and are then deposited with rain. The number of days that convergence of airstreams was recorded in January and February of each year over Salisbury are shown in Table XIX.

TABLE XIX. NUMBER OF DAYS ON WHICH CONVERGENCE OF AIRSTREAMS
WAS RECORDED OVER SALISBURY AND NUMBER OF MOTHS TRAPPED AT
SALISBURY DURING JANUARY AND FEBRUARY OF EACH YEAR.

Year	Days of convergence	Number moths trapped	
		<u>A. secretum</u>	<u>A. ipsilon</u>
1969	5	333	451
1970	1	93	59
1971	4	136	92
1972	6	481	276
1973	1	114	156

It is seen from Table XIX that most convergence was recorded at Salisbury in 1969 and 1972, and that there is a corresponding trend in the number of moths trapped. The correlation coefficient of the days of convergence and the number of A. segetum trapped at Salisbury is +0.88, and of A. ipsilon trapped it is +0.67. The degree of association between these two variables is good for A. segetum and reasonably good for A. ipsilon.

The mean number of moths trapped at Salisbury on days of convergence and non-convergence over the same site during January and February of each year are shown in Table XX. It is seen from the five-year means that there are approximately five more moths trapped on convergent days than on non-convergent days. The larger catches of moths in 1969 and 1972 could, therefore, be due to more extensive immigration of moths into the sampling area in those years.

10.3.4. Breeding Success of Resident Populations

The third factor that was proposed as causing increased moth catches in 1969 and 1972 was the successful breeding of the resident population in the few months prior to the peak catches.

No field observations were carried out on the natural populations of A. segetum and A. ipsilon, due to the difficulties involved in sampling the subterranean larval stages. The number of reports of larval damage recorded by the Plant Protection Research Institute in the last three months of each year may be taken as an indication of population levels prior to the moths emerging in January and February of the following year. The number of reports are shown in Table XXI.

TABLE XX. MEAN MOTHS TRAPPED AT SALISBURY ON
CONVERGENT AND NON-CONVERGENT DAYS.

Year	Mean moths trapped on convergent days		Mean moths trapped on non-convergent days	
	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>
1969	7.6	10.6	5.0	6.8
1970	2.0	2.0	1.6	1.1
1971	5.0	2.3	1.9	1.1
1972	20.2	8.5	6.7	4.2
1973	6.0	16.0	1.8	2.4
5-yr mean	8.2	7.9	3.4	3.1

TABLE XXI. NUMBER OF REPORTS OF LARVAL DAMAGE BY A. SEGETUM
AND A. IPSILON IN OCTOBER, NOVEMBER AND DECEMBER AND NUMBER
OF MOTHS TRAPPED IN JANUARY AND FEBRUARY OF THE FOLLOWING YEAR.

Larval damage		Moths trapped	
Year	Number reports	Year	Number moths trapped
1968	10	1969	784
1969	5	1970	152
1970	4	1971	161
1971	5	1972	757
1972	14	1973	270

It is seen from Table XXI that the number of reports were higher at the end of 1968 and 1972 than in the other three years being considered. The relatively larger resident populations at the end of 1968 could, therefore, account for the larger catches of moths at the beginning of 1969. However, the level of the resident populations in 1971 would not appear to provide moths of the numbers trapped in early 1972.

10.3.5. Number of Moths in Relation to Temperature

In section 10.3.1. it was seen that the level of moths caught in the light-trap during the cool, dry, season was low. As the light-trap catch is a function of both the activity of the moths and the population available for sampling, the decrease in numbers during the cool season could be attributable to a reduction of activity.

Using the method of Lewis and Taylor (1967) for determining flight threshold temperatures, it was found that the scatter diagram resulting from plotting the moth catch against minimum temperature for each day in June and July of 1969 to 1973 (cool season of each trapping year), did not reveal any clear threshold (Figs. 35 and 36). The same procedure was carried out with temperatures recorded at 2000 h, and again no clear threshold was apparent. It was, therefore, not possible to relate temperature with flight activity. However, it is interesting to note that a total of 122 A. segetum moths were trapped when the minimum temperature was between 1°C and 6°C, while 79 were trapped when the temperature was between 7° and 12°C, and that 39 A. ipsilon moths were trapped between 1° and 6°C while 30 moths were trapped between 7° and 12°C. The apparent inverse relation between number of moths and frequency of zero catch (Figs. 35 and 36) is explained by the distrib-

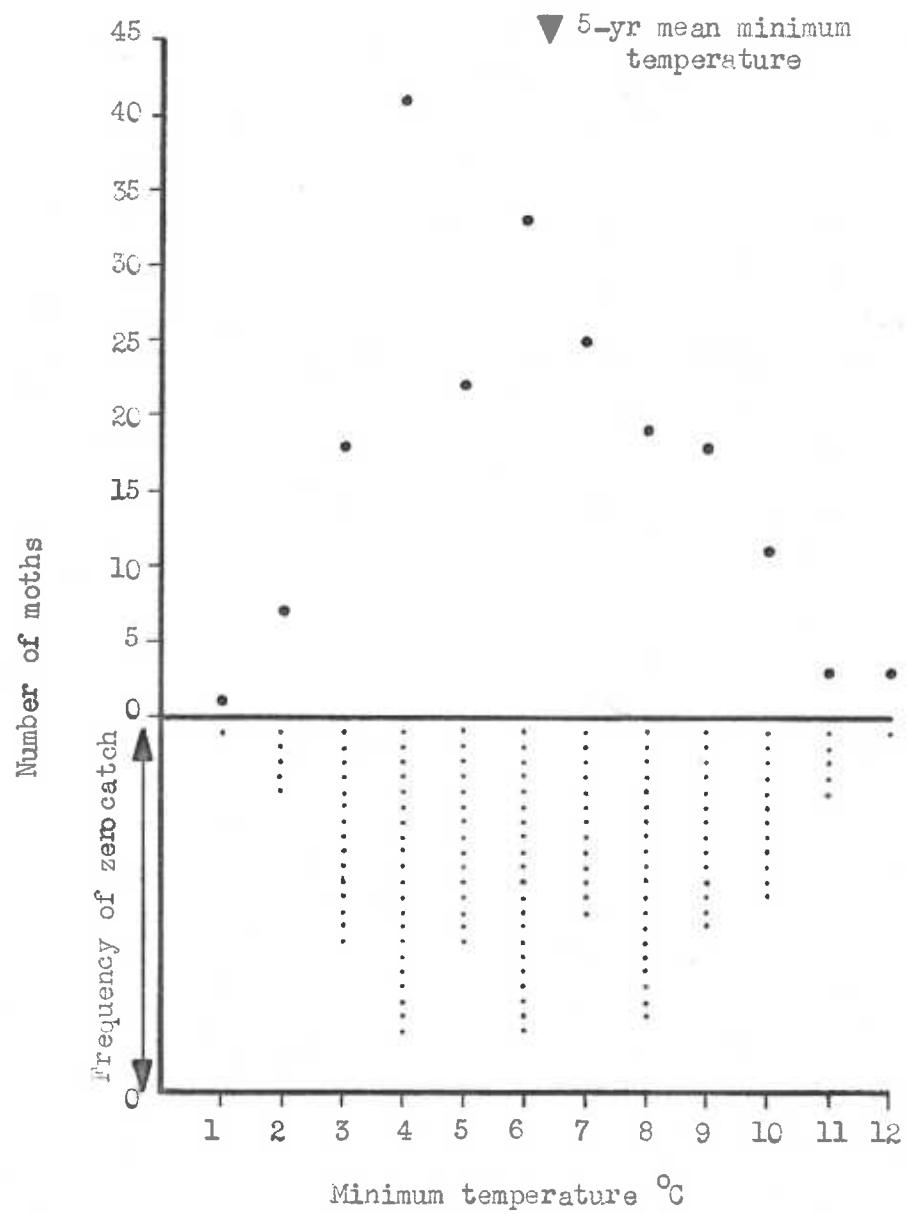


FIG. 35. NIGHTLY CATCH OF A. BEGETUM MOTHS IN JUNE AND JULY (1969-73) PLOTTED AGAINST MINIMUM TEMPERATURE.

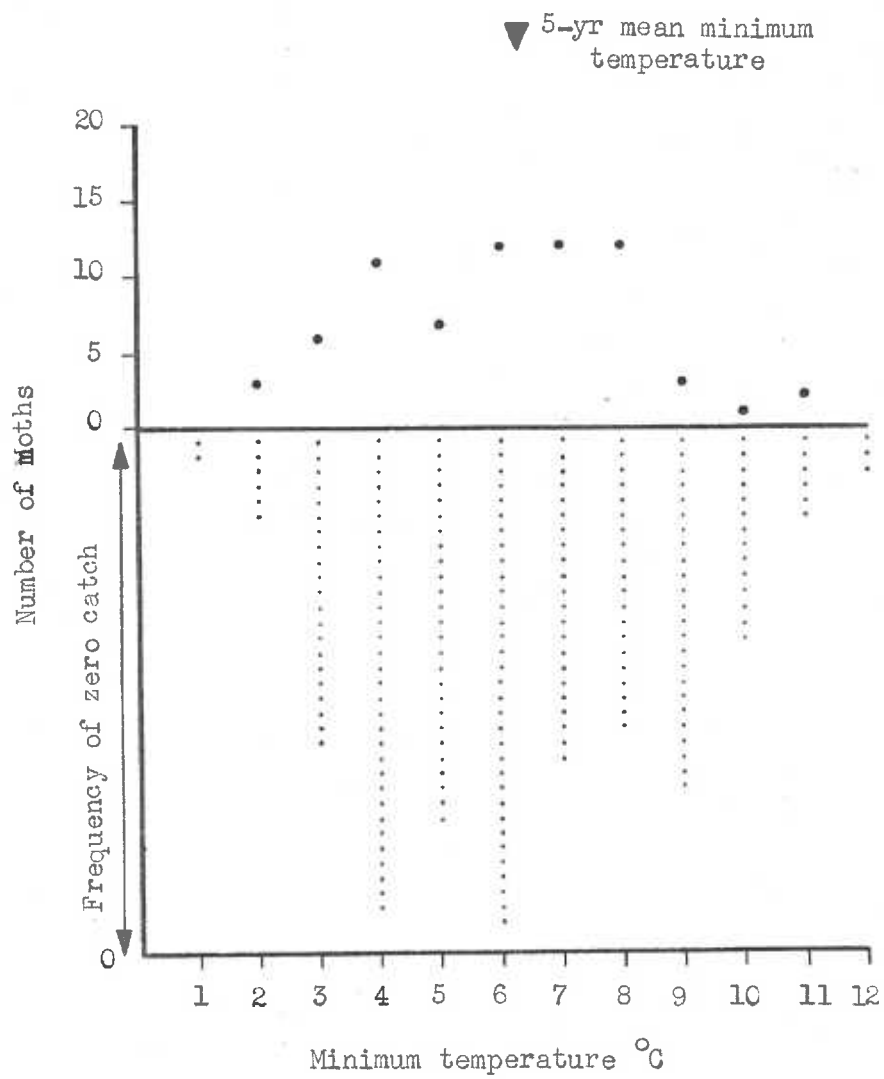


FIG. 36. NIGHTLY CATCH OF A. EPSILON MOTHS IN JUNE AND JULY (1969-73)
PLOTTED AGAINST MINIMUM TEMPERATURE.

ution of the mean minimum temperature, which for the five year period is 6.5°C.

The activity of A. segetum and A. ipsilon moths would not appear to be greatly influenced by low temperatures, and this may be explained as follows. The daily minimum temperature is usually recorded at about 0600 h (J.D. Torrance, 1973, personal communication), and allowing for say 4 to 6 h before this time for the temperature to fall below the flight threshold temperature, moths could possibly fly for 6 to 8 h per night. The low numbers of both species trapped during the cool season would seem to be a reflection of the reduced population available for sampling, and not entirely due to reduced activity with cooler temperatures.

10.3.6. Estimation of Voltinism by Relationships of Temperature and Rate of Development

From the calculation outlined in 10.2., and summarised in Appendix A.1. and A.2., it was found that A. segetum was able to undergo four complete generations, and A. ipsilon was able to complete five. The calculated dates of completion of each generation and the observed dates of completion, as obtained from light-trapping data, are shown in Table XXII.

If these results are compared with the trapping data in Fig. 30, it is seen that both species are at a low ebb in the adult stage on 1 January. In order to compare the results obtained from the logistic curves, the next depression in moth numbers must be located. For A. ipsilon the next depression is at week 9 (26 February to 4 March), the third depression of the year is at week 20 (14 to 20 May), the

TABLE XXII. CALCULATED AND OBSERVED DATES OF COMPLETION OF
EACH GENERATION OF A. SEGETUM AND A. IPSILON DURING 1969.

Generation	Calculated date of completion		Observed date of completion	
	<u>A. segetum</u>	<u>A. ipsilon</u>	<u>A. segetum</u>	<u>A. ipsilon</u>
1	4 Mar	3 Mar	5-11 Mar	26 Feb-4 Mar
2	27 May	12 May	14-20 May	14-20 May
3	14 Oct	26 Aug	25 Sep-1 Oct	17-23 Jul <u>or</u> 28 Aug-3 Sep
4	10 Dec	1 Nov	25-31 Dec	2-8 Oct
5	-	31 Dec	-	25-31 Dec

fourth at week 29 (17 to 23 July) or at week 35 (28 August to 3 September), the fifth at around week 40 (2 to 8 October) and the last at week 52 (25 to 31 December). It is seen that there is close agreement of the calculated dates of completion of each generation and the observed dates of depressions in moth numbers as sampled by light-trapping, with the exception of the fourth generation. For A. segetum, it is seen from Table XXII that the calculated date of completion of the first generation is in close agreement with the light-trapping results (observed), fairly close for the second generation, but those of the third and fourth generations do not appear to be in synchrony.

However, considering that the calculations are based on weekly mean temperatures and on the assumption that there was no diapause at any stage, the calculated and observed results are fairly close in agreement. It is also possible to substantiate the calculations of voltinism of the two species with light-trap data, that is, that A. epsilon is quinvoltine and A. segetum is tetravoltine in Rhodesia.

10.3.7. Factors Causing Outbreaks and a Method of Forecasting

As mentioned in section 10.3.1., large peaks of moths recorded in a light-trap could possibly be attributed to the influence of lunar phases on flight activity, to an influx of migrating moths, or to a successful breeding of the resident population. Southwood (1971) suggests, in general, that for pests of annual crops, migration is often the most important process whose magnitude determines whether or not there will be an outbreak of a pest. The factors that Southwood considers will affect the size of the initial invasion (that is, migration) into a crop will be discussed in section 10.4.

The area of land under crops in Rhodesia is fairly small in comp-

arison with the total area of the country, so that indigenous vegetation is likely to determine the general trend of the local populations. Utilising the technique of Rose (1972), as described in section 10.2., the results obtained are shown in Table XXIII.

The relationship of rainfall and numbers of moths at the end of the cool, dry, season is shown in Fig. 37, and it is seen that there is a fairly high correlation coefficient for each species (+0.65 for A. segetum and +0.73 for A. ipsilon). It would seem that with higher rainfall prior to the cool, dry season, the indigenous vegetation is able to remain green for longer and aid in survival of larvae, and more adults are able to emerge at the beginning of the hot season. The reason for using the number of moths trapped in August, or August and September, is that peaks of moths are recorded in light-traps at this time (week 35 and 45), as shown in section 10.3.1.

10.3.8. Factors Affecting Seasonal Abundance

Factors that are likely to affect seasonal abundance of A. segetum and A. ipsilon in Rhodesia are the availability of larval food, the survival of larvae on crop debris, migration of adults, pressure of parasitism and predation, and the ambient temperatures and soil moisture content.

Some 10 tachinids and one ichneumonid have been recorded as parasites of Agrotis in Rhodesia. The tachinids include Chlorolydella metallica Vill., Cuphocera haemorrhoidalis Macq., Dolichocolon paradoxum B.B., Exorista fallax Mg., Gonia bimaculata Wied., G. munroi Curr., Linnaemya tarsalis Vill., Succingulum mistum Vill., Wagneria nigrans Meig. and Zenillia pillipes Vill. The ichneumonid recorded is

TABLE XXIII. RAINFALL FROM MARCH TO JUNE AND NUMBERS OF MOTHS
TRAPPED IN AUGUST OR AUGUST AND SEPTEMBER.

Year	Log rainfall (mm) March to June	Log moths trapped	
		<u>A. segetum</u> (Aug)	<u>A. insilon</u> (Aug+Sep)
1963	2.21	1.82	0.78
1964	1.43	1.45	0.60
1965	1.69	1.20	0.78
1966	2.25	1.80	1.23
1968	1.65	1.38	0.30
1969	2.49	1.96	1.34
1970	1.96	1.65	1.26
1971	2.16	1.51	0.85
1972	2.36	1.40	1.08
1973	1.96	1.34	0.74

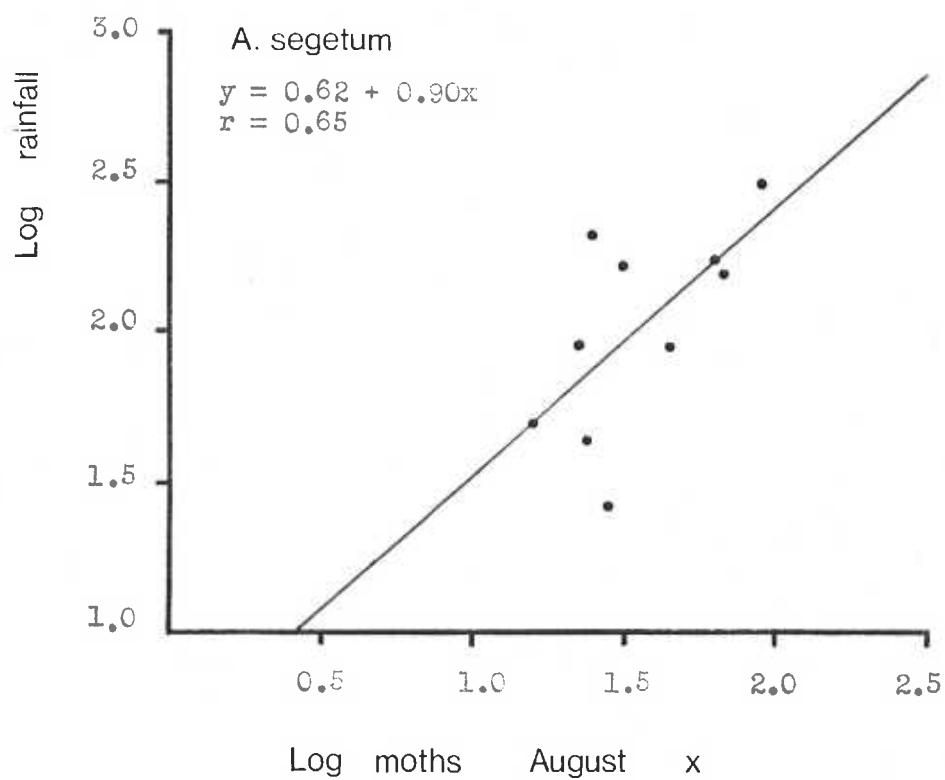
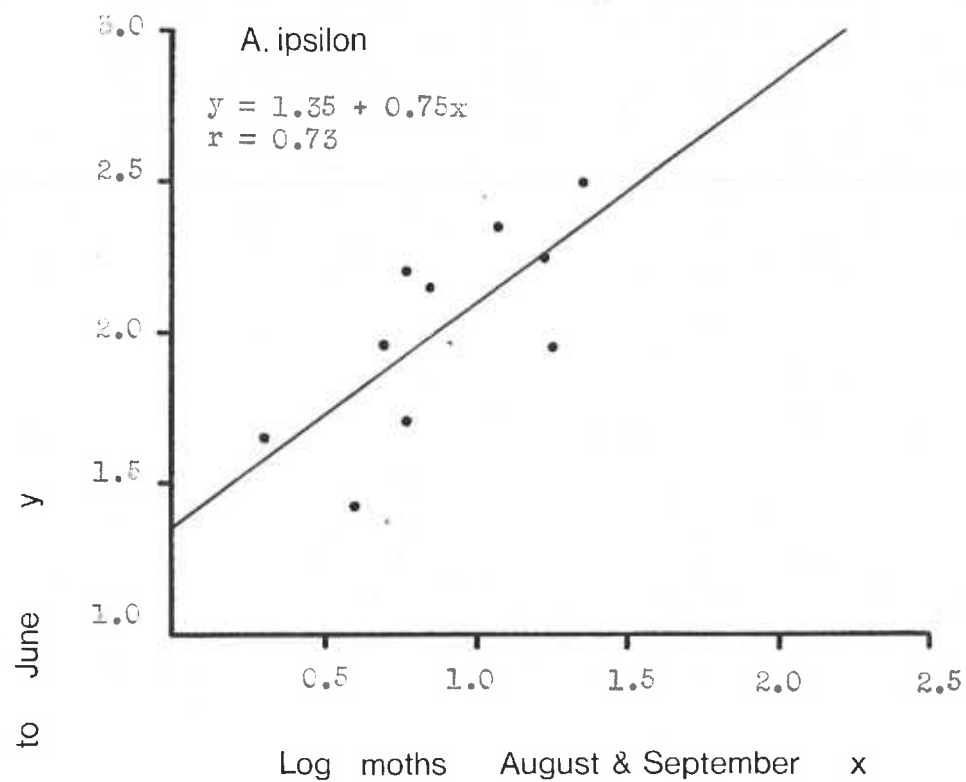


FIG. 37. RELATIONSHIP OF RAINFALL FROM MARCH TO JUNE AND MOTHS TRAPPED IN AUGUST OR AUGUST AND SEPTEMBER.

Enicospilus capensis F. (= Henicospilus euxoae Wilk.). Jack (1918) found the most persistent parasite to be G. bimaculata, but unfortunately does not mention the level of parasitism attained. No parasites were recorded or observed during field work. The formicids Pheidole megacephala F. and Camponotus rufoglaucus Jerd. race gulu Em. were found to be important predators of eggs and young larvae. Seven cases of predation by these formicids were observed in which one or both species were active in removing either eggs or 1st and 2nd instar larvae. When these predators located an area where eggs or young larvae were present, 100 per cent mortality occurred with the exception of one case when 94 per cent mortality was recorded. In the latter case 2nd instar larvae were found feeding between the leaf sheath and stem of a maize plant or were in the soil, both situations affording shelter from the predators. Ants would seem to be important natural control agents of young cutworm populations. Spiders, spp. indet., were observed devouring moths confined in asbestos cylinders during studies on oviposition sites.

10.4. Discussion

The reliability of light-traps as tools for sampling populations has been doubted by a number of workers, due mainly to the influences of lunar phases and temperature on insect flight activity.

Williams (1936) first explained the phenomenon of reduced catches at full-moon by the relative reduction in luminosity of the lamp in competition with moonlight. Subsequently Williams and Singh (1951) used suction traps, thereby removing the light source as an attractant, and obtained similar results to those from light-traps. Williams, Singh and El-Ziady (1956) concluded that moonlight had a definite effect

on nocturnal insects, and that the low catches in light-traps at full-moon are not merely due a physical reduction in efficiency of the traps. The five-year means of moth catches in this study indicate that there is little overall difference between any of the lunar phases (Table XVI), and that the influence of the moon is of little consequence. Hardwick (1972) also found that lunar phases did not affect the activity of noctuid moths, and explains that a mercury-vapour lamp (as was used in the Rhodesian traps) has a great surface brilliance and emits a high percentage of ultra-violet light to which nocturnal insects are particularly sensitive. The mercury-vapour lamp may therefore be less subject to vagaries of moonlight than an incandescent lamp, as used by Williams in his studies.

Williams (1940, 1951, 1961, and 1962) has done much analysis on the captures of insects in light-traps. He states that, "the number of insects caught in the trap in any one night is mainly determined by two factors; (1) the activity of the insects, and (2) the total population available for sampling. The activity varies rapidly and is determined largely by the weather conditions of the moment. The population changes happen more slowly and are determined more by the weather conditions some time previous The catch is therefore proportional to both the activity and the population of phototropic insects." By working with weekly totals of moths caught in the trap, the daily variations due to rapid weather changes are largely cancelled; Selman and Barton (1972) assumed that the use of groups of days allowed short term variations in catches, caused by weather variables, to be avoided. With the poor association of low temperatures on catches of A. seretum and A. insilon, and the fact that catches are represented as weekly totals, it can be said that the

data obtained is a fairly reliable sample of the moth populations in the area of the trap.

Brown (1970) and Rainey (1974) have shown that insect flight direction is greatly influenced by wind direction, and that the former is generally in the same direction as the latter. Brown, Betts and Rainey (1969) have shown that this downwind movement means a net movement towards, and/or with, areas of convergence (defined as being an area across whose boundaries wind directions result in a net inflow of air). Within areas of convergence air is forced to rise, and this has the effect of progressively increasing the area-density of any airborne organisms. These are often confined to the lower limits of the atmosphere by the inhibiting effects, on insect flight musculature, of the lower temperatures at higher altitudes. The rising air above a zone of convergence is cooled by expansion, resulting in due course in condensation and precipitation. Moths that have been concentrated above a convergent zone are then deposited with the rain. The most important zone in Africa is the ITCZ (see chapter 4). It has been shown (Blair, 1972 b) that immigration of Spodoptera exempta (Walker) moths can occur and they can be deposited during short-lived convergence. The immigration of A. segetum and A. ipsilon moths on air-streams and subsequent concentration in areas of convergence would seem to account for the peaks recorded by the light-trap in 1969 and 1972.

The number of generations that each species is able to complete per annum varies tremendously in different parts of the world; for example A. segetum is uni- or bivoltine in Europe (Fiedler, 1936; Herold, 1919), trivoltine in Soviet Central Asia (Druzhelyubova, 1963)

and tetravoltine in Israel (Rivnay and Yathom, 1964), while A. ipsilon is tetravoltine in Israel (Rivnay, 1964) and trivoltine in Bulgaria (Nikolova, 1961) and in the south-east of the United States of America (Satterthwait, 1933).

It has been shown by K.J. Wilson (1973, personal communication) that the predatory ants Pheidole mesacephala and Camponotus rufoglaucus zulu are particularly active on the soil surface from January to June in cultivated lands, so that the period of highest abundance of prey and predator would seem to coincide. The apparent synchronisation would allow the predators to exercise efficient control of young cutworm populations. Jack (1918) recorded the ant Dorylus helvolicus L. as being a frequent predator of Agrotis larvae. Broad (1966), while working on Rhodesian groundnut pests, found that a broadcast application of the insecticide dieldrin encouraged cutworm attack by eliminating natural control agents such as ants; this underlines the importance of ants as predators of cutworms.

The ambient temperatures have an effect on both the growth of food plants and on the rate of development of A. segetum and A. ipsilon. In determining voltinism of the latter two species by means of the logistic curves (section 10.3.6.), it was seen that generations developing over the cool season have a slower rate of development than those during the summer period. For complete development of A. ipsilon about 106 days are required during the cool season and about 60 days during the summer, while for A. segetum about 140 days are required in the cool season and 60 days in summer. The rate of reproduction (natality) is thus slower in the cool season than in summer, and with the scarcity of larval food through low soil moisture content, mortality

will be at a high level. Populations are, therefore, small during the cool season and this is again borne out by light-trap records (section 10.3.1.). With the increase in temperature the rate of reproduction is increased, and with the start of the main rains, plants begin to grow actively to provide suitable larval food which will probably decrease the rate of larval mortality and result in a greater abundance of the species.

It seems that local factors, such as temperature and rainfall, account for most peaks of moths. Although the invasion of moths from distant sources has not been shown clearly, from the good association between days of convergence and number of moths trapped, it would seem that some migration does take place.

11. CONCLUDING DISCUSSION

Several aspects of the biology and behaviour of Agrotis segetum and A. ipsilon have been studied to obtain an understanding of the relationships between the species and their environment. The purpose of this concluding discussion is to show how the various facets are interrelated in the overall biology of the species, and how they can be utilised in developing a pest management system.

Both species are fairly cosmopolitan in distribution, and are found in practically all the zoogeographic regions of the world. They are thus able to adapt to a wide range of climatic conditions, and the need to determine the developmental rates of the local 'races' was evident. In this regard it was found that A. ipsilon was able to develop at a faster rate than A. segetum at each of the temperatures tested. As A. ipsilon has the ability of completing more generations a year, it is better able to capitalise on temporarily favourable conditions and may be said to be the more opportunist of the two species.

In comparing the developmental rates of the two species in Rhodesia with those obtained in other parts of the world, it is apparent that the local 'races' are adapted to warmer temperatures. Extrapolation of the logistic curves obtained in this study indicate that little development takes place below about 10°C, whereas the 'races' in countries with cold climates are able to develop below this temperature.

From the larval behavioural studies, certain points have emerged which could be utilised in formulating a pest management system. It was shown that 1st and 2nd instar larvae were photopositive, that a

change took place in the 3rd instar, and that from 4th instar onwards the larvae showed a negative phototaxis (see section 8.3.1.). This same pattern of reactions was also seen in the field. In section 8.3.2. it was shown that the feeding behaviour of the larvae was related to their phototactic reactions, that is, the larvae feed on tender foliage above the soil surface during daylight hours and from the 4th instar they shelter in the soil during the same period. The time that young larvae would be feeding above the soil during the day is about 10 to 14 days during the warm summer; this has been determined from the logistic curves obtained from laboratory rearing. This period thus represents a vulnerable part of the life cycle which could be utilised in exercising control of these two species. The feeding marks caused by the young photopositive larvae are fairly characteristic (section 8.3.2.), so that the presence of these larvae can be discerned. With the young larvae being above the soil surface during the day, they would be readily accessible to parasites and predators, and to insecticides or other chemicals such as anti-feedants. With the small size of the larvae at this stage, the quantities of insecticide or of anti-feedants necessary to obtain control would also be small. The possible use of anti-feedants would seem to have the advantage over the use of broad spectrum insecticides as they should not have an adverse effect on the important natural control agents, such as ants.

Photonegative larvae, with the exception of those in the last instar, were shown (section 8.3.3.) not to be able to survive on crop debris for longer than about 14 days. It seems that larvae require green plant material in order to develop successfully, which means that populations established prior to the main cropping season probably rely

on weed growth as a food source. The main damage to newly-emerged crops is caused by photonegative larvae, which are very likely to have established themselves on weeds growing in the lands prior to the planting of the crop. The introduction of a bare fallow, with strict control of weeds, for a period of say a month prior to the planting of a crop will probably reduce the resident population through starvation. Regular scouting of newly-emerged crops, and any weeds growing in the lands, should provide a means of determining the presence of new infestations. Scouting for the presence of eggs on crop debris, particularly on fibrous roots, may also show the presence of a new infestation (section 9.3.1.). It may be possible to create piles of such fibrous material in agricultural lands, so that standard sampling can be undertaken by farmers.

With regard to the control of cutworms by the tobacco grower, it was seen (section 8.3.2. (b)) that 1st instar larvae are unable to successfully establish on 'hardened' tobacco plants, which secrete alkaloid from the distal ends of the trichomes. Until the tobacco seedlings are hardened, the amount of alkaloid produced is small and it is possible that infestations could become established. However, the seedlings are grown in seedbeds of small area, so the scouting for feeding marks should pose no great problem and an appropriate control measure could be taken against the young larvae. The seedbeds are normally fumigated with methyl bromide to control nematodes, and any resident cutworms are sure to succumb to this treatment. Invasion of the seedbed area by photonegative larvae may be prevented by the use of barriers, such as steep-sided ditches or a water moat. When the seedlings are planted out into the lands, any resident population of cutworms may be reduced by the introduction of a bare fallow.

As pupation does not occur at any great depth, the pupal stage could be managed by mechanically working the soil to cause death directly. By tilling the soil, weed growth would also be checked and would probably render the area unattractive to ovipositing females (it was suggested in section 9.4. that female moths are initially attracted to areas where young, green, foliage was present). An area of bare fallow would also be unable to support a population of larvae.

It was suggested in section 10.4. that A. segetum and A. ipsilon moths are migratory. Southwood (1971) and Fletcher (1925) maintain that migration is a most important factor in the invasion of pests into annual crops. This type of dispersal need not involve long distances, but as a high proportion of moths in a population are capable of sustained activity (section 9.3.2.), dispersal flights over long distances are feasible. Many of the economic host plants of A. segetum and A. ipsilon are annual crops, and so the invasion of these crops by dispersing moths is worthy of discussion.

Southwood (1971) enumerated four factors that affect the size of the initial invasion (migration) into a crop:

- (1) Numbers of potential invaders;
- (2) Distance of source of invaders;
- (3) Conditions for invasion and settling;
- (4) Attractiveness of the crop.

The number of potential invaders will depend on the availability of food plants during the cool, dry season and since cutworms are polyphagous, practically any growing plant may be considered as food. With the increasing area of winter crops, such as wheat, being grown

under irrigation in Rhodesia, and the trend of planting crops such as maize earlier each year (from the beginning of August), more food is becoming available for the winter and spring generations of cutworms. The more favourable conditions are likely to increase the number of potential invaders into the main rain-planted crops. From the increased numbers resulting from winter cultivation, and from the early planted summer crops, it would be necessary to know the migratory potential of the moths so that the number of potential invaders could be determined. The proportion of moths in the laboratory populations designated as being 'active' has been determined (section 9.3.2.), and although the proportions of the active and inactive morphs are likely to change with environmental and intra-population factors, an approximate number of potential invaders could be related to catches of moths in light-traps.

The identification of the origin of the immigrants would provide sites for sampling the numbers of potential invaders, on a longer term, and also provide information on distances over which migration can occur. No work has been undertaken on this aspect during the present study.

The number of potential invaders that actually settle on and invade a crop will depend on meteorological conditions, and on the attractiveness of the crop. Winds have been shown by Brown (1970) to be important for the transport of moths over long distances, and that these migrants are concentrated in zones of convergence and finally deposited with rainfall. In order that young larvae can develop unhindered, an ample supply of young tender foliage near ground level is necessary. In other words, the crop or other plants must be in the

early stages of growth at about the time of oviposition. With the present trend of extending the cropping season in Rhodesia by irrigation, there is a corresponding extension of the period during which crops will provide food for unhindered development of young larvae, and also attract female moths for oviposition. These favourable conditions should increase the chances of survival of larvae hatching from eggs laid by moths during the winter and spring, so that the local populations should expand, probably exponentially, by the time the main rain-planted crops germinate. It is only during the rainy season that immigration of moths from distant sources will be of any consequence (see chapter 4) in reinforcing local populations, but these invaders will nevertheless be of significance in potential outbreaks.

The outbreaks of cutworms prior to the introduction of methods for extending the cropping season, therefore, were probably due to suitable meteorological conditions bringing invaders into localities having a favourable environment of young plants. With the extension of the cropping season, the chances of establishment of an infestation are increasing and more outbreaks can be expected than in the past.

It was shown that the total rainfall in March, April, May and June can be utilised to forecast the number of potential invaders into areas under early-planted crops (section 10.3.7.).

The availability of larval food, the survival of larvae on crop debris, dispersal of adults, pressures of parasitism and predation, and the ambient temperatures and soil moisture content are factors that are likely to affect seasonal abundance of the two species.

The first two factors are interrelated and may be considered together. Newly-hatched larvae require tender foliage to survive, and if prevented from feeding through mechanical means (such as sticky tobacco) then high mortality results in a few days. Fourth instar larvae were shown (section 8.3.3.) to be unable to survive on crop debris for longer than about 14 days, indicating that older larvae also require green plant material to undergo satisfactory development. In areas where irrigation is not carried out, the condition of the vegetation is dependent on rainfall in the rainy and post-rainy seasons. The amount of suitable food during the cool, dry, season will therefore be scarce, and cutworm populations would be expected to be at a low level. This is clearly seen in the light-trap catches of moths (section 10.3.1.). However, as was indicated earlier in this discussion, the increasing area being brought under irrigation during the dry season should provide a suitable habitat for continued development of Agrotis populations.

With suitable winds and zones of convergence, adults having the potential of prolonged activity are able to migrate into favourable habitats. This was indicated by light-trap catches of moths in 1969 and 1972 (section 10.3.1.), and since migration is of great importance in the colonisation of annual crops, this phenomenon would seem to be fundamental in the abundance of the species. Areas of convergence are only of consequence during the rainy season, so it is at this time that long distance migration can be expected to take place. Again, this is borne out by light-trapping. Large peaks of moths were recorded in January and February of 1969 and 1972; these two months represent the height of the main rains in Rhodesia. The arrival of immigrants serves to augment the resident populations, and increase the abundance and vigour of the species.

12. SUMMARY

- i. Six species of cutworms have been found in Rhodesia. These are Agrotis segetum (Benis & Schiff.), A. ipsilon Hüb., A. spinifera Hüb., A. longidentifera Hampson, Mentaxya albifrons Geyer, and M. ignicollis Walk.
- ii. The most important species economically are A. segetum and A. ipsilon.
- iii. The developmental periods at constant temperatures for the two species, A. ipsilon and A. segetum, have been shown to be different. A. ipsilon develops faster than A. segetum at each of the temperatures tested between 15° and 33°C. Equations have been calculated for the logistic curves which express the rate of development for eggs, larvae, and pupae.
- iv. Means of distinguishing the two species in all stages of development, except the pupa, have been found.
- v. Laboratory observations were made on the influence of rearing temperature on the fecundity and fertility of moths.
- vi. Phototaxis of both species of larvae has been investigated; the larvae are photopositive for the first two and a half instars, and then become negatively phototactic.
- vii. Larval feeding behaviour was found to be related to their phototactic reactions. When photopositive, the larvae feed on or above the soil surface during daylight and once they become

photonegative, they feed below the surface during daylight and on the surface at night.

- viii. Trichomal secretions from tobacco leaves were found to be effective in trapping 1st instar larvae, and causing appreciable mortality.
- ix. Larvae in 4th instar were unable to survive on crop debris, whether moistened or dry, for longer than 14 days at a temperature of 24°C. Sixth instar larvae were able to pupate, though the resulting pupae were significantly smaller than those resulting from larvae given fresh food.
- x. The depths at which larvae pupated were found to be within the top 25 mm of soil, and that the higher the soil moisture content, the shallower the depth of pupation.
- xi. Patterns of emergence of photonegative larvae from burrows and of re-entry into burrows were elucidated.
- xii. Preferred oviposition sites by moths in caged areas were found to be on plant debris, and this was verified in the field. The preferred substrate would seem to be one with crevices and uneven surfaces.
- xiii. The capacity of moth activity was studied. A. ipsilon moths were generally more active than A. segetum. The characteristics of activity seem to be inherited, with active moths giving rise to a population with a greater proportion of active individuals, and vice versa.

- xiv. Virgin female moths of A. segetum were found to possess a pheromone(s) that serves to recruit a sexual partner and to be a releaser of male copulatory behaviour.
- xv. The seasonal abundance of moths of A. segetum and A. ipsilon were monitored by light-trapping, and showed that moths were present throughout the year. The influences of lunar phases and low temperature on flight activity appear to be minimal.
- xvi. Moths of both species are believed to be migratory.
- xvii. A. ipsilon was found to be quinvoltine, while A. segetum was tetravoltine. Voltinism was determined by calculations based on the logistic curves and mean weekly temperatures, and also compared with light-trap catches.
- xviii. Major factors causing outbreaks of cutworms are thought to be due to influxes of migratory moths, good late-season rainfall, and a supply of tender foliage for larval food.
- xix. A good correlation has been obtained between the total numbers of moths captured in a light-trap during August, or August and September, and the total rainfall recorded at the end of the rainy season. This is useful in predicting the population levels that can invade early-planted summer crops.
- xx. The predatory formicids, Pheidole megacephala F. and Camponotus rufoglaucus Jerd. zulu Em., were found to be efficient predators of Agrotis eggs and young larvae.

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15. APPENDIX

A.1. Calculated Development of *A. segetum* in 1969 at Salisbury

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
Jan	1- 7	20.0	Egg	105.00	105.00
	8-14	20.7	Larva	17.50	17.50
	15-21	21.3		19.25	36.75
	22-28	21.1		18.20	54.95
	29- 4	21.6		19.60	74.55
Feb	5-11	21.2		18.20	92.75
	12-14	21.1		7.80	100.55
	15-18	21.1	Pupa	20.00	20.00
	19-25	21.4		40.60	60.60
	26- 4	21.3		36.40	97.00
Mar	5-10	20.9	Egg	102.00	102.00
	11	20.9	Larva	2.60	2.60
	12-18	20.6		16.80	19.40
	19-25	19.6		14.70	34.10
	26- 1	20.2		16.10	50.20
Apr	2- 8	19.9		14.98	65.18
	9-15	20.4		16.66	81.84
	16-22	18.0		11.20	93.04
	23-26	18.8		6.40	99.44
	27-29	18.8	Pupa	16.40	16.40
May	30- 6	18.2		26.60	43.00
	7-13	15.9		19.60	62.60
	14-20	14.6		16.10	78.70
	21-27	16.4		21.00	99.70

continued /

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
May	28- 3	14.9	Egg	42.00	42.00
Jun	4-10	14.0		31.50	73.50
	11-14	15.4		26.40	99.90
	15-17	15.4		2.10	2.10
	18-24	12.7		2.24	4.34
	25- 1	15.0		5.18	9.52
Jul	2- 8	14.6	Larva	4.48	14.00
	9-15	13.7		3.22	17.22
	16-22	13.7		3.22	20.44
	23-29	12.6		2.24	22.68
	30- 5	16.0		6.72	29.40
Aug	6-12	15.8		6.72	36.12
	13-19	15.1	Pupa	5.18	41.30
	20-26	16.3		7.56	48.86
	27- 2	17.9		11.20	60.06
Sep	3- 9	18.3		12.04	72.10
	10-16	19.1		13.44	85.54
	17-23	17.3		9.80	95.34
	24-25	21.5	Egg	5.56	100.90
	26-30	21.5		26.00	26.00
Oct	1- 7	21.0		35.00	61.00
	8-14	23.2		40.60	101.60
	15-19	21.7		92.50	92.50
	20-21	21.7		19.46	19.46
	22-28	20.4	Larva	16.66	36.12
	29- 4	19.6		14.70	50.82
Nov	5-11	21.5		19.32	70.14

continued

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
Nov	12-18	20.2	Larva	16.24	86.38
	19-22	23.9		12.80	99.18
	23-25	23.9	Eupa	18.30	18.30
	26- 2	23.3		41.30	59.60
Dec	3- 9	20.3		32.90	92.50
	10	22.8		5.70	98.20
	11-15	22.8		100.00	100.00
	16	22.8	Larva	3.04	3.04
	17-23	20.7		17.08	20.12
	24-30	20.0		15.68	35.80

A.2. Calculated Development of *A. ipsilon* in 1969 at Salisbury

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
Jan	1- 6	20.0	Egg	102.00	102.00
	7	20.0	Larva	2.40	2.40
	8-14	20.7		17.00	19.40
	15-21	21.3		18.90	38.30
	22-28	21.1		18.55	56.85
	29- 4	21.6		19.25	76.10
Feb	5-11	21.2		18.55	94.65
	12-13	21.1		5.30	99.95
	14-18	21.1	Pupa	28.00	28.00
	19-25	21.4		38.50	66.50
	26- 3	21.3		32.40	98.90
Mar	4	21.3	Egg	18.60	18.60
	5- 8	20.9		73.60	92.20
	9-11	20.9	Larva	7.95	7.95
	12-18	20.6		17.85	25.80
	19-25	19.6		16.80	42.60
	26- 1	20.2		17.50	60.10
Apr	2- 8	19.9		17.15	77.25
	9-15	20.4		17.50	94.75
	16-18	18.0		6.30	101.05
	19-22	18.0	Pupa	16.40	16.40
	23-29	18.6		30.80	47.20
	30- 6	18.2		30.10	77.30
May	7-12	15.9		21.00	98.30
	13	15.9	Egg	10.20	10.20

continued

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
May	14-20	14.6	Egg	60.20	70.40
	21-23	16.4		32.40	102.80
J	24-27	16.4	Larva	7.20	7.20
	28- 3	14.9		11.55	18.75
Jun	4-10	14.0		10.50	29.25
	11-17	15.4		11.90	41.15
	18-24	12.7		9.45	50.60
	25- 1	15.0		11.55	62.15
Jul	2- 8	14.6		11.20	73.35
	9-15	13.7		10.15	83.50
	16-22	13.7		10.50	94.00
	23-27	12.6		6.75	100.75
	28-29	12.6		5.00	5.00
	30- 5	16.0		24.50	29.50
Aug	6-12	15.8		23.80	55.30
	13-19	15.1		22.40	75.70
	20-26	16.3		25.20	100.90
	27- 2	17.9		92.40	92.40
Sep	3- 9	18.3	Larva	15.05	15.05
	10-16	19.1		15.75	30.80
	17-23	17.3		14.00	44.80
	24-30	21.5		19.25	64.05
Oct	1- 7	21.0		13.55	32.60
	8-13	23.2		13.30	100.90
	14	23.2		6.40	6.40
	15-21	21.7		39.20	45.60
	22-28	20.4		35.70	81.30
	29- 1	19.6		18.80	100.10

continued

Month	Dates	Mean temp. °C	Stage	% development	Cumulative %
Nov	2- 4	19.6	Egg	47.40	47.40
	5- 7	21.5		57.60	105.00
	8-11	21.5		11.00	11.00
	12-18	20.2	Larva	17.50	28.50
	19-25	23.9		22.75	51.25
	26- 2	23.3		21.35	72.60
Dec	3- 9	20.3		17.50	90.10
	10-12	22.8		9.00	99.10
	13-16	22.8		24.80	24.80
	17-23	20.7	Pupa	36.40	61.20
	24-30	20.0		34.30	95.50
	31	22.0		5.80	101.30