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To the Graduate Council:

I am submitting herewith a thesis written by Samuel Glover Breeland entitled "The Armyworm, Pseudaletia unipuncta (Haworth), and Its Natural Enemies." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Entomology and Plant Pathology.

Arthur C. Cole, Major Professor

We have read this thesis and recommend its acceptance:

A.J. Sharp, Royal Shanks

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

December 11, 1957

To the Graduate Council:

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Arthur C. Cole
Major Professor

We have read this thesis and recommend its acceptance:

A. J. Sharp

J. Ives Townsend

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Royal E. Shanks

Accepted for the Council:

Dale Wantling
Dean of the Graduate School

THE ARMYWORM, PSEUDALETIA UNIPUNCTA (HAWORTH) AND ITS NATURAL ENEMIES

A THESIS

Submitted to
The Graduate Council
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Doctor of Philosophy

by

Samuel Glover Breeland

December 1957

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TABLE OF CONTENTS

SECTION		PAGE
I.	INTRODUCTION	1
II.	REVIEW OF LITERATURE	4
III.	MATERIALS AND METHODS	7
IV.	SYSTEMATIC HISTORY AND SYNONYMY	16
V.	GEOGRAPHICAL DISTRIBUTION	19
VI.	FOOD PLANTS	21
VII.	LIFE HISTORY AND HABITS	23
	General life history in Tennessee	23
	The moth	25
	Description	25
	Sex differences	26
	Daily activities	29
	Food	29
	Attraction to light	30
	The seasonal flights	39
	Emergence	40
	Mating	40
	Oviposition without fertilization	41
	Time and place of oviposition	41
	Manner of oviposition	46
	Rate of oviposition	47
	Egg masses	49
	Duration of oviposition and egg production	53

SECTION | PAGE

VII. (continued)

Light and oviposition 54

Time elapsing between emergence and oviposition . . 55

Longevity 55

The egg 59

Description 59

Length of incubation period 59

Fertility and hatching percentages 61

The larva 63

General description of the sixth instar 63

Description of other instars 67

General habits 68

Duration of larval life 70

Annual broods 72

Outbreaks 74

Other noctuid larvae with the armyworm habit 76

The pupa 78

General description 78

Place of pupation 80

Duration of the pupal stage 80

VIII. SEASONAL STUDIES 83

Seasonal cycle in Tennessee 83

Winter studies, 1956-57 86

Winter study number one 86

SECTION PAGE

VIII. (continued)

Winter study number two 93

Winter study number three 99

IX. NATURAL ENEMIES OF THE ARMYWORM 105

Parasites 105

Hymenoptera: Braconidae 115

Hymenoptera: Ichneumonidae 124

Hymenoptera: Eulophidae 129

Diptera: Larvaevoridae 129

Predaceous enemies 136

Insects 137

Amphibians 138

Birds 138

Mammals 140

Diseases 140

Virus diseases 140

Bacterial diseases 145

Fungus diseases 145

X. DISCUSSION 146

XI. SUMMARY 153

LITERATURE CITED 156

APPENDIX 165

LIST OF TABLES

TABLE		PAGE
I.	Some Records of Light Trap Catches of Various Workers Showing Ratio of Female and Gravid Female Armyworm Moths	31
II.	Records of Light Trap Catches of Armyworm Moths in Tennessee, 1957, Showing Sex Ratio and Percentage of Gravid Moths	33
III.	Sex Ratio of Insectary Reared Armyworm Moths, *Pseudaletia unipuncta*, 1957	35
IV.	Weekly Record of the Number of Armyworm Moths Caught in Light Traps during 1956 in Tennessee	36
V.	Weekly Record of the Number of Armyworm Moths Caught in Light Traps during 1957 in Tennessee	37
VI.	Numbers of Eggs Deposited by Females of *Pseudaletia unipuncta* on Various Oviposition Media, 1957	45
VII.	Rates of Oviposition of Six Female Moths, *Pseudaletia unipuncta*, May 23, 1957	48
VIII.	The Egg Laying Records of Several Armyworm Moths, Knoxville, Tennessee, 1957	50
IX.	Number of Egg Masses and Number of Eggs per Mass Deposited by Females of *Pseudaletia unipuncta* during Each of the Five Oviposition Periods, 1957 . . .	51

TABLE PAGE

X. Number of Eggs Deposited by Females of *Pseudaletia unipuncta* during Each of the Five Oviposition Periods, 1957 52

XI. Time Elapsing between Emergence and Oviposition of *Pseudaletia unipuncta* at Various Times during 1957 in Tennessee 56

XII. Records of Length of Time between Emergence and Oviposition of *Pseudaletia unipuncta* during Each of the Five Flight Periods in Tennessee, 1957 . . 57

XIII. Longevity in Days of Adults of *Pseudaletia unipuncta* during Each of the Five Flight Periods in Tennessee, 1957 58

XIV. Length of Incubation Period of Eggs of *Pseudaletia unipuncta* during Each of the Five Broods, 1957 60

XV. Hatching Records of Eggs of *Pseudaletia unipuncta* during Each of the Five Oviposition Periods, 1957 . . 62

XVI. Duration of the Various Instars and Length of Larval Life in Five Groups of *Pseudaletia unipuncta*, June 12, 1957, through July 12, 1957 71

XVII. Duration of Larval Life of *Pseudaletia unipuncta* in Each of the Four Full Broods in Tennessee, 1957 . . 73

XVIII. The Species of Noctuid Larvae Exhibiting the Armyworm Habit 77

TABLE PAGE

XIX. Duration of Pupal Life of Pseudaletia unipuncta in Each of the Four Full Broods in Tennessee, 1957 . . 82
XX. Soil Temperatures in Winter Field Cage, 1956-57 90
XXI. Records of All Instars of Pseudaletia unipuncta Larvae Released into Field Cages during the Fall and Winter of 1956-57, Knoxville, Tennessee 92
XXII. Soil and Container Temperatures Associated with Winter Studies Two and Three, 1956-57 95
XXIII. Development Records of the Twelve Specimens of Winter Study Two Completing Growth to Adult 97
XXIV. Survival Records of Pseudaletia unipuncta Larvae of Various Instars during the Winter of 1957 in Tennessee 101
XXV. Gross Development Records of Armyworm Larvae of Various Instars Reared during the Winter of 1957 in Tennessee 103
XXVI. Summary of Parasite Conditions Associated with Six Clusters of Wheat Stubble in an Armyworm Infested Field, Monroe County, Tennessee, June 1, 1956 110
XXVII. Summary of Extent of Parasitism in Eleven Groups of Field Collected Armyworms, Pseudaletia unipuncta, 1956 111

TABLE		PAGE
XXVIII.	Relative Numbers and Percentages of Parasites Reared from the Armyworm during 1956	112
XXIX.	Summary of Extent of Parasitism in Fourteen Groups of Field Collected Armyworms, Pseudaletia unipuncta, 1957	113
XXX.	Relative Numbers and Percentages of Parasites Reared from the Armyworm during 1957	114
XXXI.	Duration of Larval and Cocoon Stages in Four Generations of Apanteles militaris during the Summer of 1957	121

LIST OF FIGURES

FIGURE		PAGE
1.	Cage Used for Capturing Living Armyworm Moths	8
2.	Jar Used for Housing Moths for Observations on Mating, Longevity, and Oviposition	9
3.	Tennessee Model Light Trap	13
4.	U. S. Department of Agriculture Light Trap	14
5.	Map Showing Locations of Light Traps in Tennessee by Counties	15
6.	Stages in the Life History of _Pseudaletia unipuncta_ . .	24
7.	Genitalia of the Male and Female of _Pseudaletia unipuncta_	27
8.	Comparison of Male and Female Sexual Characters	28
9.	Graphic Representation of the 1956 Seasonal Flight Pattern of the Armyworm Moth in Tennessee	38
10.	Egg Masses of _Pseudaletia unipuncta_ Showing Manner of Concealment	43
11.	External Features of the Sixth Instar Larva of _Pseudaletia unipuncta_ with Details of the Head and Mouthparts	64
12.	External Features of the Thorax of the Sixth Instar Larva of _Pseudaletia unipuncta_	65
13.	External Features of the Abdomen of the Sixth Instar Larva of _Pseudaletia unipuncta_	66

FIGURE PAGE

14. Terminal Segments of the Male and Female Pupa of *Pseudaletia unipuncta* to Show Sex Differences 79

15. Graphic Representation of the Seasonal Cycle of *Pseudaletia unipuncta* in Tennessee 85

16. Containers Used for Releasing Armyworm Larvae under Natural Field Conditions 88

17. Portable Screen Cage Used for Confining Armyworms under Natural Conditions 89

18. Graph Showing the Winter Development Records of Twelve Field Collected Armyworms under Natural Temperature Conditions in Tennessee, 1956-57 98

19. Graph Showing the Winter Development Records of the Various Larval Instars of *Pseudaletia unipuncta* . . . 104

20. *Apanteles militaris*, an Important Parasite of the Armyworm 116

21. Larvae of *Apanteles militaris* Emerging from an Armyworm Host 117

22. Cocoons of *Apanteles militaris* 118

23. Cocoon and Adult of *Meteorus autographae* 123

24. Cocoon and Adult of *Rogas terminalis* 125

25. Cocoon and Adult of *Campoletis oxylus* 127

26. Cocoon and Adult of *Hyposoter* sp. 128

FIGURE PAGE

27. Puparium and Adult of *Winthemia rufopicta*, an Important Parasite of the Armyworm 131

28. Larvae of *Winthemia rufopicta* Emerging from Host Armyworm 133

29. Puparium and Adult of *Archytas apicifer* 135

30. Progressive Symptoms of the Polyhedral Virus Disease of the Armyworm 143

INTRODUCTION

The armyworm is the larva of a noctuid moth, known as *Pseudaletia unipuncta* (Haworth). This species is one of the most destructive pests of American agriculture and gets its common name from its habit of traveling in great numbers, ravaging field after field of growing crops on its march of destruction. For the most part, the armyworm is a pest of small grains and other grasses.

The armyworm has long been known as an extremely unpredictable species, appearing in unexpected places with remarkable suddenness. This element of surprise is the key to the success of the species as a destructive pest. The armyworm frequently inflicts serious losses before its presence is detected. The disappearance of the species from the scene is as sudden as its appearance. The sporadic invasion by great hordes of armyworms is referred to in the literature as an "armyworm outbreak."

A study of the past history of the armyworm shows that outbreaks follow no particular pattern and that indeed they have not usually occurred in successive years in a given area, but rather have appeared at irregular intervals. The species typically goes for years without attracting undue attention, and then suddenly a severe outbreak occurs during which the worms build enormously large populations. This sporadic behavior of the armyworm results in tremendous losses to agriculture in outbreak years.

Of the impact of the armyworm, Slingerland (1896) says, "fully to realize the destructive capabilities of this insect one must see (no description will suffice) an army of the worms on the march and at work." Flint (1854) said of an early outbreak, "millions of devouring worms threatening to cut off every green thing."

In 1953, Tennessee suffered a serious armyworm outbreak. During that year this insect inflicted an estimated loss of ten million dollars on farmers of the state (Mullett, 1954). As a result of this outbreak, a project was inaugurated by The University of Tennessee Agricultural Experiment Station, with federal aid, to study the ecology of the armyworm with an eye toward causative factors of outbreaks. Such knowledge would possibly permit a warning system which would allow the early detection of incipient armyworm outbreaks, thereby assuring more effective control and the possible prevention of outbreaks in a given area.

To embark upon such a program of investigation, a thorough knowledge of the basic biology of the armyworm with reference to its seasonal cycle was necessary. Miner (1954) states:

> The greatest single cause of crop loss to armyworms is lack of vigilance. Insecticidal controls are highly satisfactory. However, if a grower fails to examine his field carefully for a week or two in spring, the crop may be ruined before he knows it. Also local supplies of insecticide may soon be exhausted if there was no warning. Thus the greatest service which the entomologist can render is to predict damage so that farmers may not be taken by surprise . . . . The biological information necessary for such prediction service is greater than it was a few years ago, but in many respects armyworm biology is still a huge mystery.

In the spring of 1956, the writer commenced basic biological studies on the armyworm. A review of the literature revealed that a great majority of workers had investigated the armyworm during outbreaks only, a practice which resulted in a surprising lack of factual information on this important species between periods of its conspicuous abundance. Information on the overwintering habits of the species is particularly scanty; in fact, almost non-existent. This gap in our knowledge has resulted in a vague and inadequate understanding of the seasonal aspects of the armyworm life history.

The objective of this dissertation is to report the research findings of the writer over a two-season period (1956-57) on the biology of the armyworm. An effort has been made to concentrate on those features of armyworm biology which are inadequately covered or lacking in existing literature.

REVIEW OF LITERATURE

The first comprehensive work on the biology of *Pseudaletia unipuncta* was that of C. V. Riley, published in his Second Missouri Report (1870). Riley added to this work in his Eighth Missouri Report (1876), and published a complete compilation of his work in the Third Report of the United States Entomological Commission (1883). In the interim years, 1870-1882, Riley published many separate articles on various phases of armyworm biology, but all of his findings as well as a good review of all that was known about the species up until that time are included in the 1883 report of the Entomological Commission. In this report, Riley included sections on nomenclature, geographical distribution, capacity for injury, past history, descriptive characters, habits and natural history, generation studies, hibernation, natural enemies, control measures, and a complete bibliography.

After Riley's work, the next important armyworm contribution came in 1896 when Slingerland published on the subject in Cornell Bulletin 133. This publication gave an account of the life history of the species, described a serious outbreak, and included a brief discussion of parasites. In that same year, 1896, Flagg and Field in Rhode Island, and Warren in Pennsylvania, published on the life history of the armyworm in their respective states. Garmon, in 1908, published a detailed bulletin on the armyworm and its habits in Kentucky.

During the years 1914-1916, many writings appeared in the literature following a severe outbreak over much of the United States and Canada in 1914. The best of these treatises appear to be those of Fernald in Massachusetts (1914), Britton in Connecticut (1915), Baker and Gibson, both in Canada (1915), Davis and Satterthwait in Indiana (1916), Knight in New York (1916), and the United States Department of Agriculture Farmer's Bulletin 731 (Walton, 1916). Collectively, these publications give much information on the 1914 outbreaks in the respective areas, historical accounts, life history and seasonal cycle notes, distribution records, and lists of natural enemies, and they impress upon the reader the severity with which the armyworm attacks in outbreak years.

Flint (1920) published a brief but good account of the life history, habits, and control of the armyworm in Illinois. In 1921 Tryon published an article giving the life history and description of stages of the armyworm in Queensland. Several natural enemies were dealt with in detail.

Mickel, in 1932, published a brief account of Minnesota armyworm outbreaks of that year. In 1938, Britton reported a Connecticut outbreak as being the worst since 1914 and gave notes on life history and parasites.

Walton and Packard reported on the armyworm in the United States Department of Agriculture Farmer's Bulletin 1850, in 1940, and a revision appeared in 1947. Both of these publications give a description of all stages, a discussion of parasites, and detailed control measures.

Of the publications listed in this review, the more important ones are those of Riley (1883), Slingerland (1896), Gibson (1915), Davis and Satterthwait (1916), Knight (1916), Flint (1920), Mickel (1932), and Walton and Packard (1947).

To the writer's knowledge, not since the work of Davis and Satterthwait (1916) has there been any original research reported on the life history of the armyworm.

Aside from the basic references listed here, many hundreds of articles and reports have been written in which the armyworm has been mentioned, or has been the principal subject. Most of these articles, however, are of the type that report the occurrence, outbreak damage, occasional reared parasites, or some incidental observation in governmental, state, or industrial entomological reports. There are several papers, rather detailed, which deal with parasites, predators, diseases, or other specific areas of investigation, but by far the majority of references in the literature contribute, at best, only minor bits of information. In this work, the author has endeavored to draw from as many sources of information as possible and all contributions in the literature which have come to his attention have been considered. A comprehensive bibliography is included in the appendix.

MATERIALS AND METHODS

A stock colony of armyworms in various stages was maintained in the insectary at all times during the course of this project. Because of the structure of the insectary, temperature, moisture, and light conditions were much the same as outside. The upper half of the insectary building was open on two sides with no artificial heating or cooling devices. For the major part of this work, data were gathered from especially designated colony groups reared in this half-enclosed insectary. The colony was started by capturing living adult armyworm moths in a cage designed for that purpose over which a light trap head was placed (figure 1). Each captured gravid female moth was given a collection number, a corresponding record sheet was prepared, and the moth was placed in a one-gallon wide-mouth jar. The top of the jar was cut out and replaced with screen wire to allow a free passage for air and a place to attach an oviposition paper. On the top of the screen was placed a cotton plug saturated with a weak sugar solution on which the moth fed. The oviposition paper was prepared by tightly folding strips of regular note paper in accordion style and taping around either end with Scotch tape. The folded paper was about six inches in length, one-fourth to one-half inch wide, and contained about six folds. It was suspended from the screen top by a small wire. Very satisfactory oviposition was obtained by this method. The entire apparatus is shown in figure 2. Each day the contents of the jar were

Figure 1. Cage used for capturing living armyworm moths.

Figure 2. Jar used for housing moths for observations on mating, longevity, and oviposition.

examined, the condition of the moth recorded, any eggs counted and designated by lot number, and fresh food and oviposition paper supplied. The eggs were transferred immediately to metal salve boxes of two or four-ounce size and allowed to hatch. A small amount of food, usually Johnson grass, corn, or small grain leaves, was placed with the eggs to assure sufficient moisture and immediate food supply for hatching larvae. Emerging larvae were counted and the results recorded. The larvae were kept in the salve boxes by egg lot number until they began to be crowded, at which time they were transferred to one-gallon wide-mouth jars of the type used for adult oviposition. The jars were labeled and the specimens were fed daily. The dates of the first and last pupations were recorded for each jar to determine the duration of larval development for each group. The pupae were removed daily from all groups and kept collectively by date of pupation. The first and last days of adult emergence were recorded to determine the duration of the pupal stage. The adults obtained from the insectary-reared material of the original stock were used to maintain the colony. Typically, two adult males were placed in a jar with one female and allowed to mate. The female subsequently was allowed to oviposit as has been previously described. The combination of two males to one female proved to be superior to other combinations in earlier experiments. Complete records of condition, oviposition, and longevity were kept on the adults placed in the jars. This rearing procedure, with detailed records on each moth and its progeny, was begun with the first flight of moths in

early spring of 1957 and continued through the fifth flight of 1957. Rearing methods were similar in 1956, but records were not as detailed and were used only for working out the number of annual broods.

In addition to the rearing jars, a larger cage, two feet by two feet by four feet, of plastic screen over a wooden frame was used to provide supplementary material for brood studies. This cage could satisfactorily house fifty moths. As many as twenty thousand eggs were obtained in one week from this cage. The eggs gathered from this larger cage were handled in the same manner as were those from the jars.

During the course of this investigation, many field collections were made for parasite emergence studies. Specimens were collected alive in various larval stadia, given a field collection number, and brought immediately to the insectary. The specimens were subsequently isolated, one each, in two-ounce metal salve boxes and were given an identification number. A corresponding record form was prepared for each specimen. The isolated specimens were kept at room temperature, examined daily for changes, and given fresh food. When parasites emerged they were allowed to harden, were subsequently killed and pinned or otherwise preserved, and given an identification number. Pertinent data were recorded.

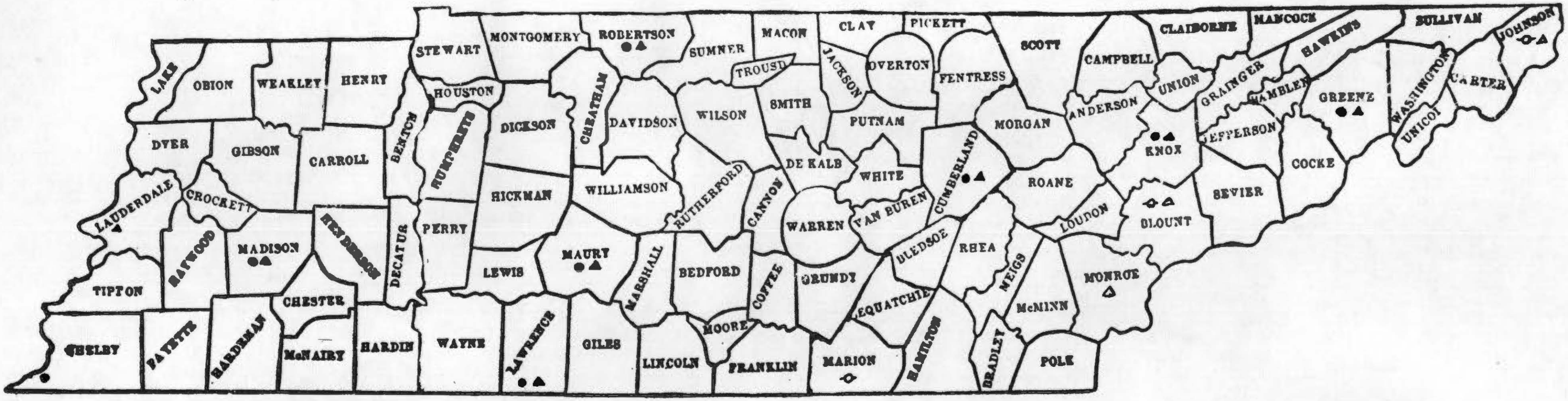
Frequent observations were made in the field for information to correlate with insectary data. Collections were made during each month of the study from March, 1956, through October, 1957. Material and observations from these collections were carefully handled and pertinent data were recorded.

During both seasons of this study, comprehensive light trap operations were employed for the purpose of obtaining information on flights of the armyworm moth in the state. These data were used to supplement life history studies in the field and insectary. During both seasons, eleven traps were in operation with the exception of the early part of the 1956 season, when only eight were used. Eight traps were the property of the Tennessee Agricultural Experiment Station and three were supplied by the United States Department of Agriculture. Figure 3 shows the Tennessee trap which was designed by Mr. W. W. Stanley and figure 4 shows the trap supplied by the U. S. Department of Agriculture. The lamps in both traps were 15-watt black light tubes manufactured by General Electric. The Tennessee trap used two of these lamps while the government trap used only one lamp. The killing agent was 70 per cent isopropyl alcohol. The trapped insects were collected by the writer or were mailed to him weekly by cooperating individuals throughout the state. Figure 5 shows the locations of traps.

Special studies in this work called for the development of various methods which may be best explained in the text.

Figure 3. Tennessee model light trap; left, trap in operating position; right, trap dismantled.

Figure 4. U. S. Department of Agriculture light trap of the type used in this study.



● - University of Tennessee light trap. Operated March 5, 1956 - November 12, 1956.
▲ - University of Tennessee light trap. Operated March 11, 1957 - November 11, 1957.
○ - U. S. Department of Agriculture light trap. Operated May 7, 1956 - November 12, 1956.
△ - U. S. Department of Agriculture light trap. Operated March 11, 1957 - November 11, 1957.

Figure 5. Map showing locations of light traps in Tennessee by counties.

SYSTEMATIC HISTORY AND SYNONYMY

The armyworm, Pseudaletia unipuncta (Haworth), has at various times since its description been known under several combinations of names. These names are due mainly to changes in generic concepts through the years. The species was first described by A. H. Haworth in 1810 upon the breaking up of Francillon's collection in London. Haworth described the species from a Francillon specimen without locality label as Noctua unipuncta. In 1829, Stephens published a description of the same specimen, now in Haworth's collection, by mistake as impuncta instead of unipuncta, a lapsus calami. In 1850, Stephens corrected his mistake in the specific name, placed it in the genus Leucania, and stated the insect to be North American. In 1852, Guenee, overlooking previous descriptions, described the species as new from numerous specimens in Parisian collections as Leucania extranea.

The species has been placed in several genera following the classifications set forth in various systematic groupings. The two most commonly applied generic names prior to the twentieth century were Heliophila Huebner, 1806, and Leucania Ochsenheimer, 1816. The former name has been used by those who accept the "tentamen" of Huebner, the latter by those who reject it. In this connection, I quote from Riley (1876).

> This long known and familiar generic term (Leucania), applied to a well defined genus, has recently been dropped from our nomenclature--in the writings and in the "List" and "Check List" of N. A. Noctuidae by Mr. A. R. Grote. It has been replaced by Heliophila of Huebner. By this

> change we pass from light into darkness. I consider that the reasons so long urged by entomologists against the adoption of the classification of the "Tentamen" and "Verzeichniss," and particularly those given by Guenee for not following this last in his admirable work on the Noctuidae, are good and sound. The Huebnerian classification is essentially unreal, and the generic divisions so inadequately defined that I doubt if any one would attempt to make use of the works in question, were it not for the references to the admirably illustrated works of the same author. The introduction of his generic terms into American Lepidopterology has so upset its nomenclature, without in the least advancing our knowledge, and the grounds for this introduction are so questionable, that those who make these insects a speciality are apt in the future to divide into two factions--the Huebnerites and the anti-Huebnerites; in which event the latter will certainly have strong support from entomologists in general.

In 1905, Hampson included *unipuncta* in the genus *Cirphis* Walker. This name, *Cirphis unipuncta*, is the more familiar one to workers of the present generation. However, McDunnough (1937) pointed out that the use of the name *Cirphis* for our North American species is incorrect, based as it is on the genitalia of the genotype, *costalis* Walker, a Tasmanian species, and recommended the reversion to *Leucania* Ochs. Franclemont (1951) confirmed McDunnough's observations and stated that the name *Cirphis*, which Hampson applied to the *unipuncta* group, is untenable because the genotype is not congeneric with any of the American species. Franclemont erected a new genus, *Pseudaletia*, for the *unipuncta* group with *Leucania unipuncta* Haworth as the type (Proc. Ent. Soc. Wash. 53(2):64). This name has seemingly met with full acceptance. The synonymy follows.

Pseudaletia unipuncta (Haworth)

1810. Noctua unipuncta Haworth. Lepidoptera Brittanica, Pars 2, p. 174.
Location of Type: British Museum (Natural History).

1829. Noctua impuncta Stephens. Illustrations of British Entomology, Haustellata, vol. 3, p. 80. (Lapsus calami.)

1852. Leucania extranea Guenee. Histoire Naturelle des Insects, Species General des Lepidopteres, vol. 5 (Noct. 1), p. 77.
Type Locality: "Ameriq Septentrion., Bresil, Columbie, etc."
Location of Type: United States National Museum.

1951. Pseudaletia unipuncta Franclemont. Proc. Ent. Soc. Wash., vol. 53, p. 65. (New combination.)
Location of Lectotype: United States National Museum. (USNM Type No. 60993.)

GEOGRAPHICAL DISTRIBUTION

Pseudaletia unipuncta is cosmopolitan in distribution. It is undoubtedly North American in origin and reaches its destructive peak in the United States east of the Rocky Mountains and in Canada. It is particularly abundant throughout the region from Iowa and Maine south to Texas, including the Atlantic and Gulf States and all of New England. To the west of the Rockies this species is not common but has been reported from California (1902), New Mexico, Arizona, Utah, Oregon, Washington, and Montana; also from British Columbia and Alberta, Canada (Crumb, 1956). It occurs in all of the eastern provinces of Canada, more notably in Ontario and Nova Scotia (Gibson, 1915). Curran (1927) and Ramirez (1917) record the species from Mexico, and it has been reported from Guatemala by Duran (1931).

In South America, the armyworm is recorded from Argentina (Blanchard, 1943), Brazil (d'Utra, 1902), Chile (1921), Colombia (Toro, 1929), and Venezuela (Riley, 1883). It has been reported from Cuba by Cook and Horne (1906).

Gurney (1918) reports P. unipuncta from Europe. Farther east the species is well distributed. d'Emmerez de Charmoy (1927) reports it from Africa. It is reported from Siam by Ladell (1933), and from Russia by Engel'hardt (1927 and 1929). There are numerous records of its occurrence in India (Hectar, 1924; Fletcher, et al., 1919; Husain, 1935; and Joannis, 1913), Burma (Ghosh, 1924, 1925, 1927, and 1931), and China (Chao and Chen, 1947; Chu, 1938; Duport, 1913;

Fu, 1937; Hu and Tse, 1936). Oishu (1940) and Ueno (1930) have reported the species from Japan; NaKayama (1929) has reported it from Korea; and Sonan (1940) from Formosa.

The species has been recorded numerous times from Australia (Davidson, 1932; Girault, 1925; Gurney, 1918; Jarvis, 1922; and Lea, 1928). Blick (1953) reports the armyworm from New Zealand, and Froggat (1939) from New Guinea. Goot (1929) and van Hall (1916) have reported P. unipuncta from the Dutch East Indies. The species has further been recorded from the Philippine (Otanes and Karganilla, 1940; Uichanco, 1928) and Hawaiian (Fullaway, 1909; Kelly and Krauss, 1909; Pemberton, 1923) Islands.

The foregoing records of distribution are by no means complete, but were selected to show the cosmopolitan range of the species.

FOOD PLANTS

Although the armyworm feeds on a great variety of plants the world over, the grasses must be considered its basic food. It particularly attacks small grains, i. e., wheat, oats, barley, rye, and rice. With equal relish it attacks pasture grasses of all types, e. g., blue grass, timothy, sudan grass, etc. The large-stem grasses, e. g., corn, millet, sugar cane, and sorghum are readily attacked. In addition to grasses, it frequently attacks alfalfa and occasionally clover.

The worms occasionally become so numerous in their breeding grounds as to devour their food supply before they have attained full growth, and search for food elsewhere. Under such stress of hunger, they are almost omnivorous. Forbes (1905) reports the species feeding on strawberry, bean, sugar beet, sweet potato, parsley, watermelon, cucumber, apple, pepper, honeysuckle, ragweed, and amaranth. The same author reports that in confinement they have grown and completed their development when fed exclusively on poppy, beet, lettuce, cabbage, raspberry, onion, parsnips, radish, carrot, or pea. The writer has observed the species feeding on numerous garden crops on a farm near Sweetwater, Tennessee, after their having devoured their breeding area food, a field of barley. Massachusetts cranberry bogs have often been attacked by the armyworm (Franklin, 1915, 1945, 1949). Peaches and plums have been infested in Queensland (Jarvis, 1926), artichokes in California (Lange, 1941), flax in Minnesota (Ruggles, 1921), and in

Japan, Kumashira (1938) reported the armyworm attacking a rush, Juncus effusus decipiens, used for mat making.

Almost without exception, large populations of armyworms develop only in rank-growing grass crops, damage to other crops being secondary.

LIFE HISTORY AND HABITS

General Life History in Tennessee

The armyworm overwinters in Tennessee as a partially grown larva. Upon the advent of extended warm weather in early spring the overwintering larvae complete their development, pupate in the soil, and begin emerging as adults in early March, with the peak of spring emergence occurring in mid-April. The spring flight is the beginning of the first of five broods of a given year. The moths deposit their eggs in tightly compact masses in or near rank-growing fields of young grain or other small grasses. The eggs (figure 6), numbering up to 1800 from a single moth over a period of several days, hatch in from three to fourteen days from the time they are deposited, depending upon prevailing temperatures. The newly hatched larvae begin feeding immediately on young tender blades of grass, eating the epidermis and having a skeletonizing effect. This type feeding is characteristic of the first two of the six larval instars. The remaining instars, third through sixth, straddle the outer margin of the grass blade and cut holes from the margin to the midrib until the blade is stripped clean. The duration of larval development from eclosion to pupation averages about thirty-four days for the first brood. The first brood worms reach maturity in late May and pupate in early June. Pupation is preceded by a short prepupal period of a day or more during which time the worms do not feed. The pupal stage is

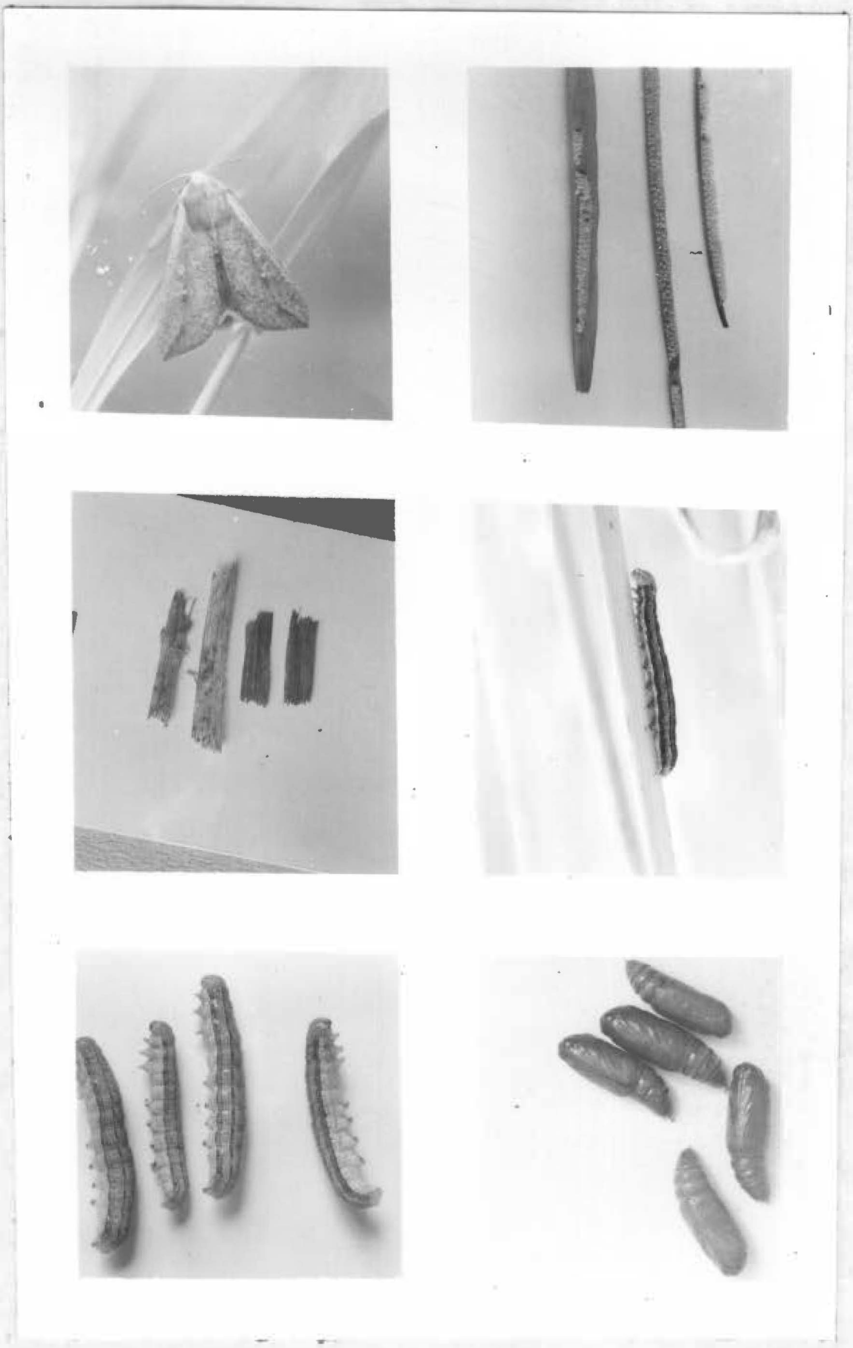


Figure 6. Stages in the life history of Pseudaletia unipuncta: upper left, moth; upper right, egg masses; middle left, young larvae; middle right, mature larva in feeding position; lower left, a group of mature larvae; lower right, pupae. Natural size.

spent in the soil at a depth of from one inch to three inches and lasts for an average of thirteen days, producing moths in mid-June which are the parents of the second brood. There are four complete broods and a partial fifth brood which enters the winter as partially grown larvae to complete the annual cycle. The length of time necessary to complete a brood varies with the season and details are given in the studies of the seasonal cycle. The first brood is the damaging one in Tennessee and any outbreaks which occur are likely to come no later than the first week of June.

The Moth

Description (see figure 6)

The author cannot improve upon the description of Riley (1883) which follows:

> The parent moth is variable in size, the average individual measuring about 40 mm. (an inch and a half) in wing expanse. The front wings are pointed at the tips, and are of a reddish gray or fawn color, much specked with black atoms. Anterior of the center of each wing are two rather large, indistinct spots, distinguished from the rest of the wing by an absence of black specks, and by a clearer reddish coloring. Immediately posterior to the outermost of these spots is a white point indistinctly surrounded by blackish. A series of black points parallel with the outer margin; one on each vein is usually perceptible. An oblique black streak starts from this line of dots, and ascends to the apex of the wing, and, with the form of the wings, principally characterizes the species. Just inside the fringe is a series of black dots, one between each of two veins. The hind wings are translucent, gray, with the terminal border and the nervures blackish (in the front wing the nervures are whitish). The sexes differ from each other but little.
>
> The under side of the wings is of an opalescent yellowish white. Along the outer margin, particularly of the hind wings, are many black specks, so nearly confluent as to form a definitely limited

dusky terminal band. On the costal margin of each forewing, near the tip, is a small, distinct, black dot, and at the center of each hind-wing is a similar dot. The body is concolorous with the wings, and the legs are light gray, slightly tinged with reddish, and speckled with black dots.

Drawings of both the male and female genitalia are given in figure 7. Franclemont's (1951) drawings have been checked against the genitalia of several specimens of Tennessee moths of each sex and a favorable comparison was found.

An excellent color figure of the moth appears in Holland's (1903) "Moth Book," plate 23, figure 40.

Sex Differences

Superficially, the sexes of P. unipuncta moths are not easily distinguishable, but reliable characters for their separation do exist. Differentiating characters are as follows:

Male	Female
1. Tip of abdomen rather blunt.	1. Tip of abdomen more pointed.
2. Antennae hairy, especially at base (figure 8A).	2. Antennae relatively smooth (figure 8A).
3. Paired claspers prominent feature of external genitalia (figure 8B).	3. Single ovipositer prominent feature of external genitalia (figure 8B).

The genitalia may be easily seen in freshly killed specimens by rolling a round pencil or similar object from about the middle of the venter of the abdomen posteriorly, causing the external genitalia to protrude. A similar protrusion may be accomplished on living specimens by applying very slight pressure, so as not to injure the moth,

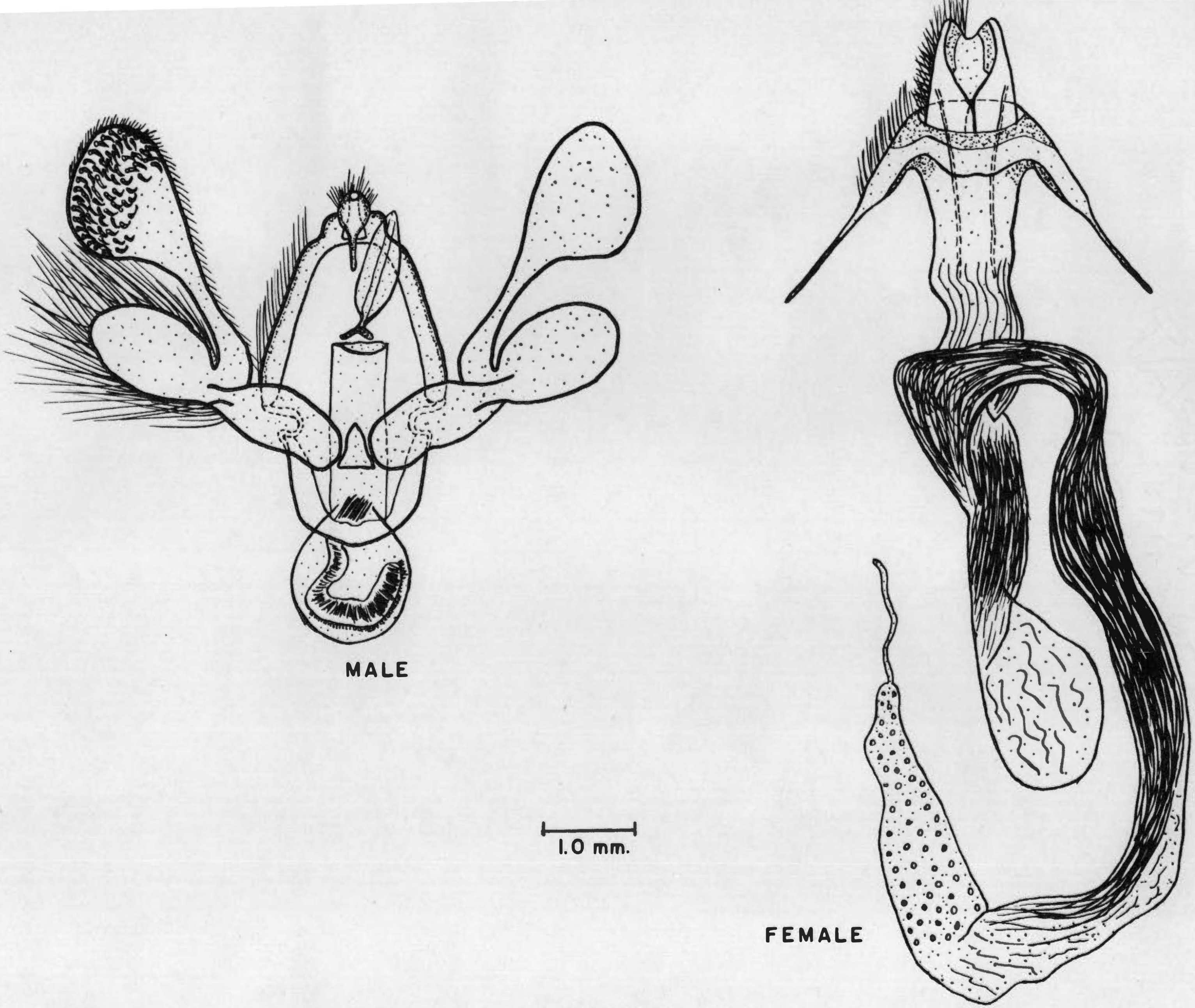


Figure 7. GENITALIA OF <u>Pseudaletia</u> <u>unipuncta</u> (Haworth). The right half of each is denuded.

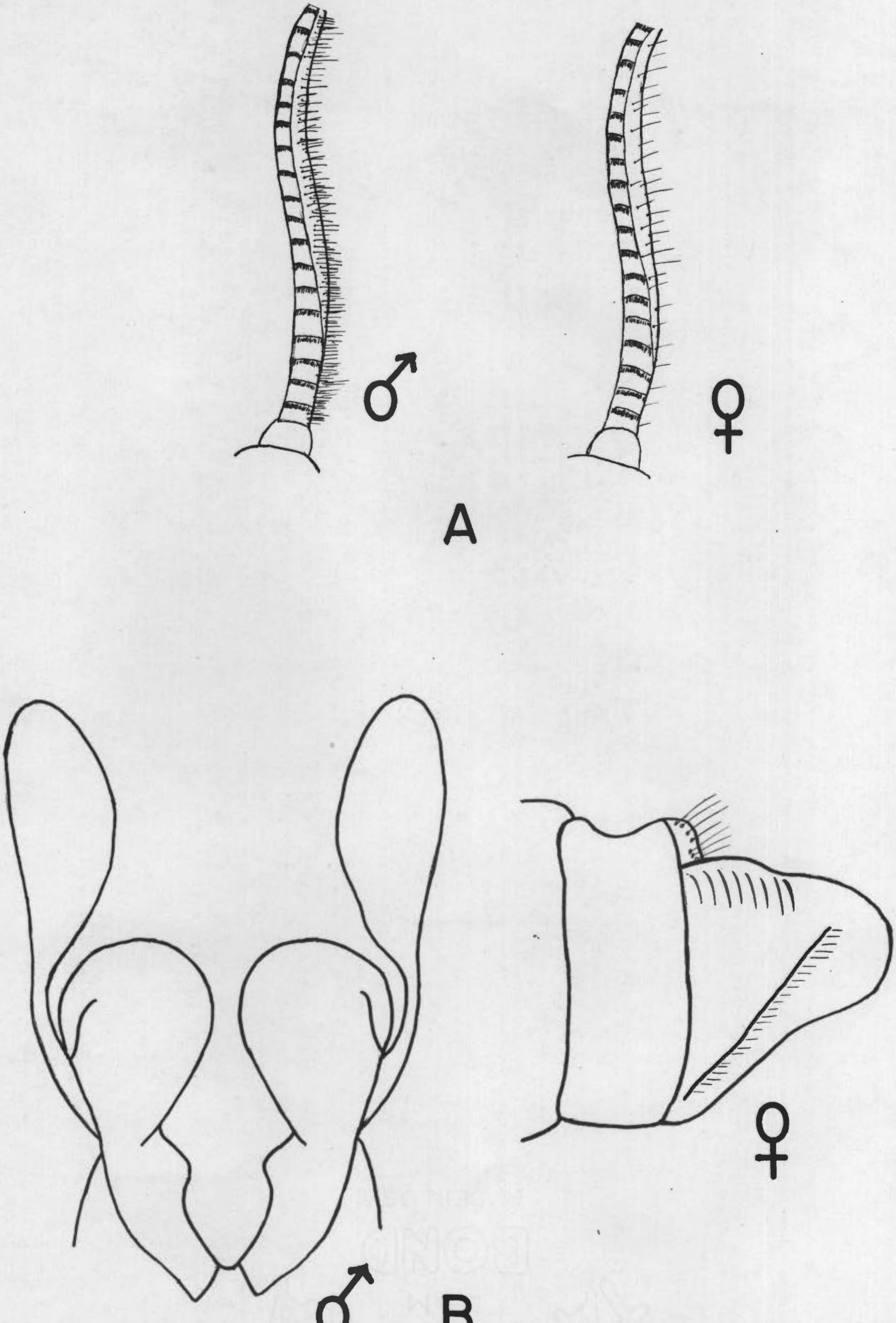


Figure 8. Comparison of male and female sexual characteristics: A, male and female antennae; B, male (ventral view) and female (lateral view) genitalia.

with the thumb and forefinger just anterior to the terminal segments. The female genitalia may best be seen from a lateral view, the male from a ventral view.

Daily Activities of the Moth

The armyworm moth normally remains quiescent during the greater part of a day, becoming active only after sunset. At dusk the day's activity (*i. e.*, feeding mating, or ovipositing) of a particular moth is begun, and continues until the impulse is satisfied. The writer has never observed a moth in flight during the bright part of the day either in nature or captivity unless the moth was disturbed, but he has observed a number of moths in active flight during twilight hours and after dark in the field and in captivity. Mating and oviposition have been seen at dusk and after dark and on some occasions oviposition, but not mating, has been noted during daylight hours on overcast days. Feeding may be observed at any hour among confined moths.

Food of the Moth

The armyworm moth is not injurious in its feeding and consequently little work has been done concerning its food habits. Forbes (1905) reports that the moth is fond of sweets and may be captured in large numbers at night by using sugary substances as bait. Riley (1883) states that the moth undoubtedly feeds upon the nectar of various flowers and reports that it has been taken in the evening from the blossoms of clover, apple, honeysuckle, and yucca. Walkden (1937) reports that in Kansas between 1921 and 1931, the armyworm moth was

one of only five species caught for the eleven consecutive years of a bait trap operation in which a bait of crushed banana and a 10 per cent solution of molasses in water was used. Knight (1916) reported moths feeding on mashed and decaying apples, sipping the nectar of catnip, and observed one feeding on a ripe apple hanging on a tree. The writer fed moths on a weak sugar solution approximating .02 per cent. It is probable that the moths in nature prefer the nectar of flowers, but will feed on any sweet exudation available.

Attraction to Light

The armyworm adult, like other noctuid moths, is strongly attracted to light. For this reason light traps have been employed to supplement field and insectary studies.

The early theory was that lepidopterous insects taken at light were practically all males and that the relatively few females taken had previously oviposited. If this were true, the use of light traps would be of little value as an instrument for studying habits of the moth.

Turner (1918 and 1920), Dirks (1937), and Knutson (1944) have all conducted studies which contribute information on the sex-ratio of light-collected armyworm moths. In addition to the sex-ratio, Turner and Dirks give the percentage of females which were found to be gravid. Table 1 is a compilation of data from the above sources. From these data, it is apparent that, for the armyworm moth, a higher percentage of males are caught at light than females. Chi-square tests

TABLE I

SOME RECORDS OF LIGHT TRAP CATCHES OF VARIOUS WORKERS SHOWING RATIO OF FEMALE AND GRAVID FEMALE ARMYWORM MOTHS

Source of Data	Dates	Location of Traps	Number Moths	Number Females	Per cent Females	Per cent Gravid	Chi-Square	Probability
Turner (1918)	1916	Md.	976	424	43.5	80.0	16.8	<.0001
Turner (1920)	1918	Md.	55	21	38.0	62.0	3.07	.08
Dirks (1937)	1931-34	Me.	947	428	45.0	45.0	8.75	.003
Knutson (1944)	1927-40	Minn.	949	371	39.0	-	45.2	<.0001

for difference from a 1:1 sex-ratio showed a significant difference in the sexes in the work of Turner (1918), Dirks (1937), and Knutson (1944). A total of 976, 947, and 949 moths sexed by the above workers respectively, showed 43.5, 45.0, and 39.0 per cent females respectively. Turner (1920) sexed a total of fifty-five moths, twenty-one (38.0 per cent) were females. Although a chi-square test to determine difference from a 1:1 ratio was not significant, it must be noted from the data of table 1 that the percentage of females in this case was the lowest of the several groups represented in the table. The fact of no significant difference is undoubtedly due to the small sample, since higher percentages of females in other groups showed a significant difference by the same statistical test.

During the 1957 season the writer sexed 12,054 armyworm moths which had been caught at light in Tennessee. Of these 5,785, or 47.9 per cent, were females. The chi-square test for difference from a 1:1 ratio for all moths sexed showed a significantly higher number of males for the season. However, as can be seen from the data of table 2, the percentage of females was higher than that of males in the first two broods and continued to regress with time until the last brood when the percentage of females increased from the previous brood.

From the data in both tables 1 and 2, it can be seen that a relatively high percentage of light-collected female armyworm moths is gravid, indicating that they had not deposited all of their eggs before being caught.

TABLE II

RECORDS OF LIGHT TRAP CATCHES OF ARMYWORM MOTHS IN TENNESSEE, 1957, SHOWING SEX RATIO AND PERCENTAGE OF GRAVID MOTHS

Flight Number	Flight Period	Total Sexed	Number Males	Number Females	Per cent Females	Per cent Gravid
I	March 11-May 20	1854	566	1288	69.5	*63.0
II	June 3-June 24	1657	774	883	53.3	-
III	July 15-Aug. 12	4958	2828	2130	42.9	-
IV	Aug. 26-Sept. 16	2207	1343	864	39.1	-
V	Oct. 14-Nov. 11	1378	758	620	44.9	-
Totals		12054	6269	5785	47.9	

Chi-square for totals = 19.4; probability = < .0001

* Represents 17 of 27 moths caught alive from which fertile eggs were obtained. Routinely caught specimens were sent to Louisiana State University for special studies.

To determine whether the light-collected samples of moths show a significantly higher percentage of males because of their greater numbers in the population or whether this difference might be due to other factors not associated with the actual sex-ratio, insectary-reared armyworm moths from the various colony groups were sexed during 1957. A total of 1,478 moths sexed showed 711, or 48.1 per cent, to be females, a figure not significantly different from the number of males. On the basis of these tests, it appears that the population approaches a 1:1 sex-ratio, but that extrinsic and intrinsic factors are in operation which result in a significantly larger number of males being caught in light traps. These data are given in table 3.

Extensive light trap operations were conducted during both seasons of this study. The data obtained were used to supplement seasonal history studies in the insectary and in the field. The trap descriptions and their locations have been given previously in the materials and methods section of this work. A summary of catches for the 1956 and 1957 seasons is given in tables 4 and 5 respectively. Figure 9 is a graphic illustration showing the 1956 flight pattern based on light trap records for the state as a whole and for two East Tennessee traps in areas where most of the field observations were made.

Since the first generation eggs must be deposited by the first flight of moths in spring and since the first brood is the damaging one in Tennessee, it is the opinion of the writer that light trap data might be used successfully to time expected dates of armyworm damage.

TABLE III

SEX RATIO OF INSECTARY-REARED ARMYWORM MOTHS, *Pseudaletia unipuncta*, 1957

Flight Number	Flight Period	Males		Females	
		Number	Per cent	Number	Per cent
I	March 11-May 20	36	43.9	46	56.1
II	June 3-June 24	195	50.5	191	49.5
III	July 15-Aug. 12	287	48.2	206	51.8
IV	Aug. 26-Sept. 16	156	52.4	142	47.6
V	Oct. 20 Nov. 11	93	42.5	126	57.5
Totals		767	51.9	711	48.1

Chi-square for totals = 2.12; probability = 0.15

TABLE IV

WEEKLY RECORD OF THE NUMBER OF ARMYWORM MOTHS CAUGHT IN LIGHT TRAPS DURING 1956 IN TENNESSEE

Date Week Ending	Location of Traps by Counties											
	Shelby	Madison	Lawrence	Maury	Robertson	Cumberland	Knox	Greene	Blount	Marion	Johnson	Total
Mar. 5	0	1	-	1	0	0	0	0	-	-	-	2
12	44	24	3	8	1	0	0	4	-	-	-	84
19	23	0	4	3	1	1	0	-	-	-	-	32
26	14	1	-	7	1	2	0	-	-	-	-	25
Apr. 2	62	52	25	47	6	1	2	9	-	-	-	204
9	243	34	22	53	30	6	35	76	-	-	-	419
16	386	21	22	120	32	6	21	44	-	-	-	652
23	67	8	5	21	0	2	11	17	-	-	-	131
30	51	0	10	140	26	-	36	74	-	-	-	337
May 7	225	126	-	119	66	-	45	123	134	-	-	838
14	76	-	-	18	0	-	-	31	69	86	95	375
21	120	64	5	8	12	6	5	43	11	21	27	322
28	-	15	-	8	5	2	18	16	33	4	11	112
Jun. 4	-	48	0	0	160	5	22	10	12	-	4	261
11	-	-	-	136	96	6	104	72	34	-	168	616
18	10	-	-	80	120	16	78	48	-	-	144	496
25	6	-	40	76	45	8	33	182	48	-	11	449
Jul. 2	-	8	40	12	152	8	12	112	28	-	128	500
9	14	64	54	32	76	32	6	32	24	-	478	812
16	-	22	20	88	56	35	22	72	32	-	487	834
23	42	48	32	105	87	118	154	158	88	-	294	1126
30	40	-	16	42	44	78	148	216	216	-	102	902
Aug. 6	-	294	156	108	380	377	144	285	156	-	-	1900
13	51	144	68	42	52	44	58	48	100	-	34	641
20	57	40	28	34	44	18	32	44	28	-	-	295
27	0	-	28	18	36	13	33	44	38	-	26	236
Sept. 3	39	113	16	18	94	32	40	32	8	-	98	490
10	75	27	36	75	120	18	71	125	0	-	263	810
17	-	79	26	6	177	82	26	32	6	7	109	550
24	42	-	4	20	20	35	7	31	-	-	107	266
Oct. 1	81	20	12	20	12	18	3	42	-	-	275	483
8	-	32	-	4	64	28	26	36	4	-	142	336
15	6	18	-	-	20	25	32	12	5	-	141	259
22	36	6	-	34	15	3	28	65	16	6	104	313
29	10	26	11	-	20	12	38	108	20	-	176	421
Nov. 5	38	31	-	-	84	-	49	95	27	-	107	431
12	-	2	-	16	64	38	21	71	9	-	92	313

- No collection

TABLE V

WEEKLY RECORD OF THE NUMBER OF ARMYWORM MOTHS CAUGHT IN LIGHT TRAPS DURING 1957 IN TENNESSEE

Date Week Ending	Location of Traps by Counties											
	Lauderdale	Madison	Lawrence	Maury	Robertson	Cumberland	Knox	Greene	Blount	Monroe	Johnson	Total
Mar.11	-	11	-	10	0	3	-	-	-	57	-	81
18	39	17	42	19	1	31	5	18	1	43	3	219
25	211	32	25	58	5	10	13	9	1	140	5	509
Apr. 1	159	93	47	35	2	4	8	14	7	107	2	478
8	323	170	36	114	6	6	17	14	30	175	41	932
15	1	4	10	65	5	2	0	4	0	6	3	100
22	54	-	-	436	22	28	-	75	24	1018	30	1687
29	-	540	53	320	24	34	186	233	25	557	758	2730
May 6	27	154	38	181	16	13	86	95	9	97	313	1029
13	-	20	-	18	19	22	36	14	-	23	34	186
20	-	46	-	2	2	2	2	6	1	4	30	95
27	208	3200	90	-	50	2	10	8	-	20	6	3594
Jun. 3	64	784	34	30	12	9	22	12	1	3	-	971
10	84	63	9	26	26	13	43	48	4	72	618	1006
17	-	12	-	24	10	6	18	12	-	2	44	128
24	-	21	8	34	12	3	42	32	-	-	85	237
Jul. 1	32	210	10	8	84	8	29	12	2	8	888	1291
8	-	-	12	32	24	16	132	40	14	-	-	270
15	2	7	-	9	2	2	35	4	24	7	44	136
22	48	56	12	12	104	-	120	208	24	3	246	833
29	-	54	40	24	238	6	346	220	33	-	768	1729
Aug. 5	220	162	108	76	588	16	338	332	-	152	-	1992
12	80	140	-	-	36	17	114	50	16	100	84	637
19	55	-	40	-	144	48	128	132	32	156	180	915
26	-	217	24	-	28	44	96	48	34	200	256	947
Sept.2	35	56	32	4	32	6	76	64	-	89	64	458
9	64	192	24	13	4	26	60	8	13	32	48	484
16	8	28	37	14	22	10	84	26	12	-	84	325
23	-	56	-	92	48	-	32	60	16	-	324	628
30	-	120	8	24	40	32	36	32	6	-	196	494
Oct. 7	-	40	-	20	24	32	42	8	16	-	568	750
14	-	8	-	12	10	18	40	8	8	-	27	131
21	-	132	-	-	40	-	40	38	8	-	92	350
28	-	172	-	31	9	-	31	-	13	-	75	331
Nov. 4	-	122	-	100	100	-	36	-	17	-	5	380
11	-	148	-	-	11	-	7	-	6	-	14	186

- No collection

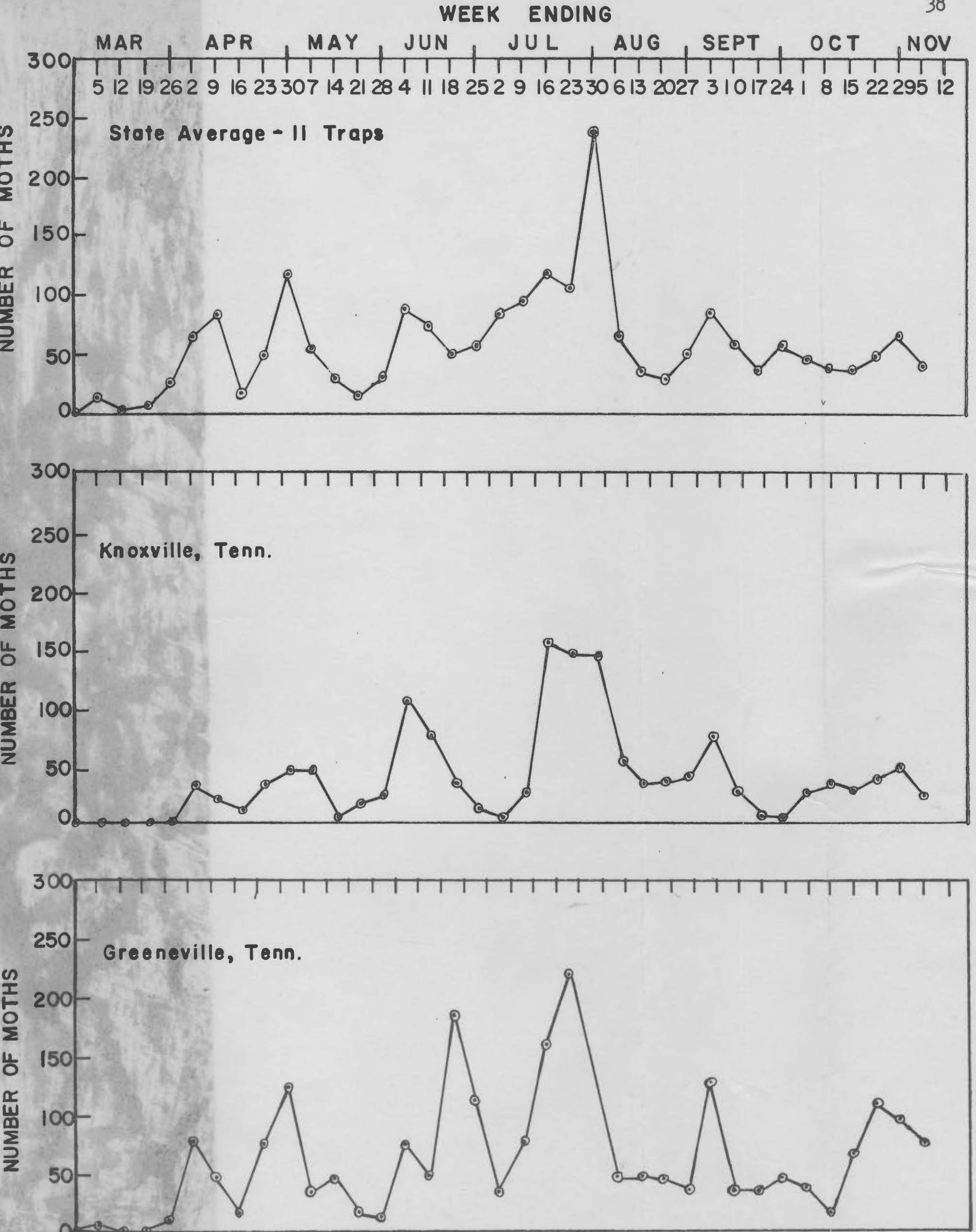


Figure 9. Graphic representation of the 1956 seasonal flight pattern of the armyworm moth in Tennessee.

By utilizing life history data and calculating the earliest possible date for the appearance of mature worms from the time of the peak of the spring flight in a general climatic area, the development of an effective warning system is possible. As has already been pointed out, light trap records are further useful in working out the number of annual broods in a given area. Such records must be used only to supplement carefully planned insectary rearings and field observations since there is a tendency for much overlap in late-season broods.

The Seasonal Flights

There are five annual flights of the armyworm moth in Tennessee, producing four complete broods and a partial fifth brood which over-winters as partially grown larvae. These flights occurred in 1956 as follows:

Flight I - March 3 to May 7

Flight II - June 8 to July 1

Flight III - July 23 to August 13

Flight IV - September 1 to September 30

Flight V - October 30 to November 15

The flights can be seen in the peaks of the line graphs of figure 9 showing some light trap records for 1956. The flight records as indicated by light traps compared favorably with records from the insectary colony and from field observations.

Adult Emergence

The armyworm pupates in the soil to a depth rarely exceeding two inches, more often at an inch or less. The pupal cell, formed from a small amount of silk spun by the prepupa, is oval in shape and incompletely formed. The cell usually forms a little earthen pocket in loose soil or in cracks of harder soil. After breaking through the pupal coverings, the moth pushes its way to the surface and hangs on debris or foliage until its wings have stretched and its body has hardened, a process which usually requires about three hours.

In experiments to determine if one sex emerged earlier than the other, results were essentially negative. There was some indication that of specimens pupating on the same day, the females began emerging slightly earlier than the males, but this time advantage of the females in eleven such groups was never greater than one day. However, in no case did male emergence begin earlier than did female emergence.

Mating

Mating usually occurs in from one to three days after emergence of the adult. Apparently only one mating is required to fertilize the entire life production of eggs of a female. One female, isolated from males after mating, deposited 1759 eggs, all of which were fertile. The mating position is end to end. The moths occasionally become stuck together in the mating process and cannot be separated. The frequency of this occurrence is greatest during hot, dry weather.

Experiments were conducted to determine whether polygamy occurs among female armyworm moths. Two containers were set up with two females and one male in each; three with three females and one male; and six with four females and one male. In no case was there evidence of polygamy. Fertile eggs were obtained from only one female in any of the combinations. Infertile eggs were obtained from more than one female in several cases, indicating that oviposition without fertilization occurs in the species.

Oviposition without Fertilization

Fifteen virgin females were isolated for further observations on oviposition without fertilization. Only three of the fifteen moths deposited eggs, one of these moths deposited fifty and another only four. These observations indicate that oviposition without fertilization is infrequent and the haphazard arrangement of the eggs indicates that the deposition of infertile eggs might require greater effort than the deposition of fertile eggs. The same situation has been reported in the case of the fall armyworm, *Laphygma frugiperda*, by Luginbill (1928).

Time and Place of Oviposition

The writer has not observed the ovipositing act of the moth in the field, but he has observed it at numerous times among caged moths. Riley (1876) once offered a reward of ten thousand dollars to anyone finding the eggs of the species in the field; the fact that there were no takers testifies to the difficulty of such a discovery. This is due to the moth's habit of concealing the eggs in tight places. Despite

shortcomings in actual field observations of the eggs, much knowledge on the preferred oviposition sites of the moth has been gained through breeding cage work, field observations of freshly hatched larvae, and in the writings of some who have succeeded in finding the eggs in nature.

From all evidence available, it seems that the moth oviposits most frequently in tight places as provided by the narrow space between the sheath and blade of growing grasses or the same in cut, dried straw or corn stalks. In experiments in which the moths were given a choice, they showed a decided preference for the latter. Also the moth will deposit her eggs readily in a narrow, tender grass blade which has a tendency to fold lengthwise and stick (figure 10).

Subsequent to his 1876 work, Riley persisted in his study of the armyworm egg and in his 1883 report stated that there was satisfactory proof that early in the season the moths oviposited by preference in the cut straw of haystacks, and even in old fodder shocks of corn stalks. He reported that old bits of corn stalk from various localities had repeatedly been found with armyworm eggs thrust under the outer sheath. He also reported that year-old stalks of grass likewise contained eggs. The writer is pretty well convinced that such are the favorite, but not necessarily the usual, oviposition sites of the armyworm moth for reasons outlined below:

1. In early spring the first young worms are found almost exclusively beneath old straw in the fields or under new grain which has been trampled, mowed, or blown down. In such situations, even when

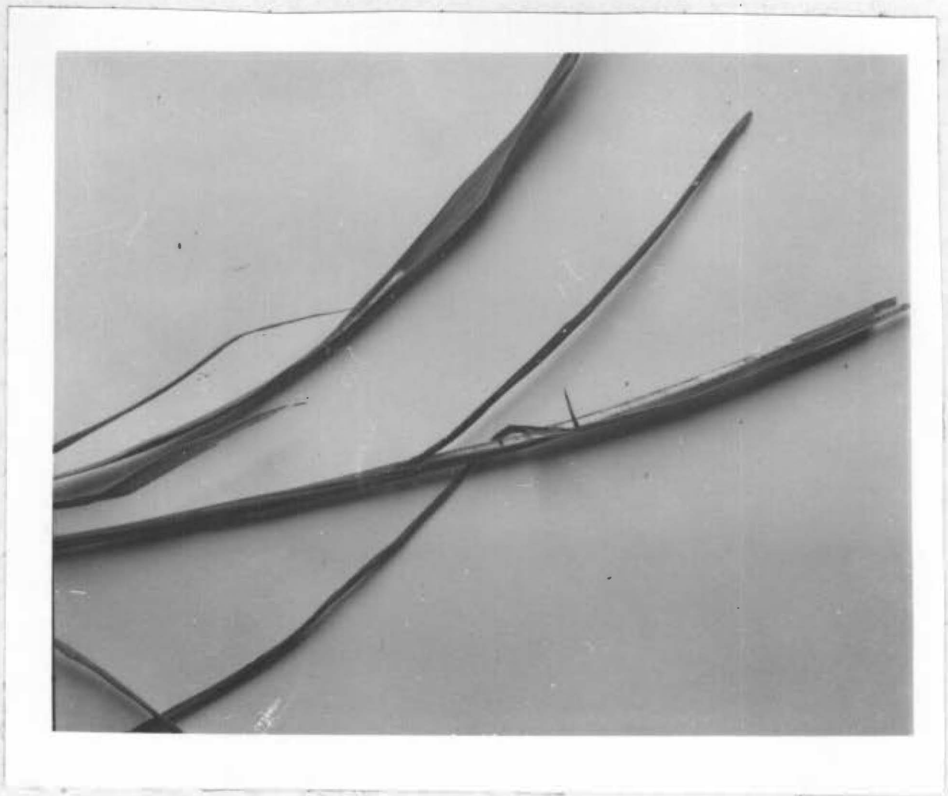


Figure 10. Egg masses of Pseudaletia unipuncta showing manner of concealment.

other forms of protection from the elements are available, a greater concentration of young worms is found under the straw.

2. Adult moths discovered in nature are invariably found resting in old or trampled straw.

3. Riley (1883) reported that numerous eggs had been found in old straw and fodder.

4. Experiments by the writer showed more frequent oviposition on straw than on grass. Further experiments showed more frequent oviposition on folded paper strips than on fresh, succulent, potted grass plants. The strips more nearly resemble straw than grass in physical properties.

5. The moths show a distinct preference for cracks and crevices which are more numerous in stubble than in a fresh plant.

Despite this apparent preference for stubble, the space between the sheath and blade of fresh grasses is readily utilized as an oviposition site and although not favored, is probably used more than stubble because of its greater availability.

The fact that folded paper strips as described in the materials and methods section are superior oviposition sites is evidenced by the data obtained from experiments utilizing various grasses and the paper strips. The tests were run for three days during the peak of the second brood oviposition period. Paper strips and six kinds of grasses were used (see table 6). The grasses were planted in individual clay flower pots and the paper was inserted into the dirt of the flower pot. Four replications were used on each of the three days. The results are given in table 6.

TABLE VI

NUMBERS OF EGGS DEPOSITED BY FEMALES OF *P. unipuncta* ON VARIOUS OVIPOSITION MEDIA, 1957

Date	Wheat	Oats	Barley	Sudan Grass	Dallis Grass	Johnson Grass	Folded Paper Strips
July 13	0	0	19	0	40	78	2040
July 14	178	24	50	0	106	88	857
July 15	32	0	88	15	35	0	425
Total	210	24	157	15	181	166	3322

In the absence of good oviposition sites, the moth will deposit her eggs in available places, but almost always in a tight place. Eggs were frequently found beneath the paper covering on the floor of rearing jars and in crumpled paper towels placed in cages for hiding places. The most unusual site which the writer observed was on the narrow portion of the wing of a luna moth, when both specimens were caught in a live trap. It is interesting to note that the site in this case was surprisingly similar to a grass blade.

Oviposition normally begins after light begins to fade in late afternoon and seemingly continues until all eggs ready for deposition on a given day have been deposited. Oviposition is completed during the early hours of the night unless the act is delayed by excessive artificial light. Oviposition has been observed in some instances in daylight, but only on heavily clouded days.

The writer has records of oviposition at temperature readings as low as 38° F. and as high as 95° F.

Manner of Oviposition

The method of oviposition in the species was observed by allowing the moth to oviposit in a small slit between two glass microscope slides. The slides were prepared by placing a piece of matchbox cardboard at each end between the slides which were held together with Scotch tape, thus leaving a slight space between the slides.

A female moth ready for oviposition shows a slightly nervous behavior. Typically her wings vibrate at a quick, jerky pace, and she

crawls or flutters about with her abdomen bent forward and downward with ovipositor extended. In this position she crawls nervously forward moving her abdomen from side to side in an arc with the ovipositor in contact with the substrate. When she finds a suitable oviposition site such as the glass slides described above, folded paper, or under more natural conditions, straw or a grass blade, she thrusts her ovipositor far forward in the slit and begins to deposit her eggs singly. In a grass blade, her ovipositor serves to form a crease and a sticky secretion from her colleterial glands seals the blade. The first egg is deposited at the greatest distance inward to which her ovipositor will reach. The ovipositor is then moved outward with each successive egg deposition until the edge is reached. This continues until the female is disturbed, until she reaches an obstruction, or until all of her mature eggs have been deposited.

Rate of Oviposition

On the evening of May 23, 1957, in Knoxville, six female moths, isolated in rearing jars, were observed in the act of oviposition. The time that oviposition commenced was recorded for each female and at the end of a particular period of oviposition, the paper was removed, the time interval written on the paper, and the old paper replaced by a fresh one. At the end of all oviposition the totals were recorded. The results are in table 7.

From the data in this table, it can be seen that the moths deposited their eggs in masses at a rate which ranged from 3.8 to 7 eggs per minute and averaged about 5 eggs per minute. In the case of these

TABLE VII

RATES OF OVIPOSITION OF SIX FEMALE MOTHS, P. unipuncta, MAY 23, 1957

Female Number	Time of Oviposition	Duration of Oviposition	Number of Eggs Deposited	Rate (No./Min.)
1	6:10-6:40 P. M.	30 Min.	210	7.0
2	6:12-6:25 P. M.	13 Min.	45	
	6:27-6:40 P. M.	13 Min.	50	3.8
3	6:23-6:40 P. M.	17 Min.	78	4.6
4	6:40-7:03 P. M.	23 Min.	110	4.8
5	6:40-6:55 P. M.	15 Min.	75	
	6:57-7:10 P. M.	13 Min.	48	4.4
6	6:40-6:55 P. M.	15 Min.	87	5.8
Average of 8 egg masses		17.5 Min.	88	5.03

six moths, oviposition began at 6:10 p.m. and was completed at 7:10 p.m. The time averaged 17.5 minutes for each of the egg masses and 23 minutes for each moth, two moths each depositing two separate masses. From the average number of eggs obtained daily from numerous females, it would seem that these records closely approximate the daily egg laying habits of the species. However, on occasion, a moth will deposit several egg masses of considerable size in one day. It must be noted that the day of these observations was heavily overcast and much darker at 6:00 p.m. than is usual for the time of year in Tennessee.

Egg Masses

As explained in the preceding section, the armyworm moth deposits her eggs in masses. The mass is usually composed of several rows of eggs covered with a white adhesive fluid which fastens them together and draws the sides of the substrate together so that nothing but a narrow glistening streak is visible. The moth seldom deposits all of her eggs in one mass, but may deposit several masses in a given oviposition period. The lifetime egg laying records of several moths are given in table 8 to show the relationship of the egg mass to the overall oviposition pattern. From the data given in the table, it can be seen that the moth has a preoviposition period of several days after emergence (see also table 12). Once oviposition begins it continues for a period of several days (see table 10) with from one to several masses of eggs being deposited each day. After deposition of all eggs there is usually a postoviposition period of a few days before death of the moth. Table 9 gives the extremes and averages of the number

TABLE VIII

THE EGG LAYING RECORDS OF SEVERAL ARMYWORM MOTHS
KNOXVILLE, TENNESSEE, 1957

Female Number	Date Emerged	Dates of Oviposition	Egg Mass	Number of Eggs	Daily Total	Lifetime Total	Date of Death	Preoviposition Period	Oviposition Period	Postoviposition Period
548	Mar. 31	Apr. 3	A	169	169		Apr. 15	3 days	6 days	7 days
		4	B	210	210					
		5	C	225						
			D	142	367					
		6	E	68	68					
		7	F	21	21					
		8	G	33	33	868				
557	Apr. 4	Apr. 8	A	106			Apr. 15	4 days	3 days	5 days
			B	172	278					
		10	C	110						
			D	128	238	516				
562	Apr. 20	Apr. 23	A	133			Apr. 30	3 days	7 days	1 day
			B	239						
			C	39						
			D	95						
			E	81	587					
		24	F	69						
			G	55	124					
		25	H	224						
			I	176	400					
		26	J	137						
			K	85	222					
		27	L	136	136					
		29	M	32						
			N	152						
			O	106	290	1759				

TABLE IX

NUMBER OF EGG MASSES AND NUMBER OF EGGS PER MASS DEPOSITED BY FEMALES OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE OVIPOSITION PERIODS, 1957

Flight Number	Period of Observations	Number of Masses	Number Females Observed	Number of Egg Masses Deposited by One Female			Number of Eggs Per Mass		
				Range	Ave.	St. Error	Range	Ave.	St. Error
I	Mar. 11- May 20	84	15	1-16	5.6	± 1.19	5-239	110.6	± 6.10
II	Jun. 3- Jun. 24	43	11	2-9	4.8	± .74	15-400	130.2	± 1.89
III	Jul. 15- Aug. 12	88	17	1-16	5.2	± .92	10-345	90.0	± 7.54
IV	Aug. 29- Sept. 23	78	17	1-10	4.6	± .71	3-340	101.3	± 1.00
V	Oct. 20- Nov. 18	34	8	1-6	4.3	± .60	35-260	139.0	± 9.60
Totals	Mar. 11- Nov. 18	327	68	1-16	4.9	± .40	3-400	108.4	± 3.88

TABLE X

NUMBER OF EGGS DEPOSITED BY FEMALES OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE OVIPOSITION PERIODS, 1957

Flight Number	Period of Observations	Number Females Observed	Duration of Oviposition in Days			Daily Egg Production Per Female			Total Egg Production Per Female		
			Range	Ave.	St. Error	Range	Ave.	St. Error	Range	Ave.	St. Error
I*	Mar. 11-May 20	15	1-9	4.0	± 0.63	5-587	154.7	± 21.3	5-1759	619.2	± 131.4
II	Jun. 3-Jun. 22	9	1-9	5.3	± 0.85	15-732	117.3	± 16.4	131-1033	622.1	± 107.0
III	Jul. 15-Aug. 8	29	1-10	4.4	± 0.37	6-377	62.0	± 6.8	58-1345	273.2	± 60.2
IV	Aug. 29-Sept. 23	17	1-7	4.0	± 0.45	6-380	116.2	± 10.3	15-1344	464.7	± 89.1
V	Oct. 20-Nov. 18	8	1-10	4.5	± 1.04	37-392	131.3	± 4.7	37-1021	590.7	± 41.6
Season Totals	**Mar. 11 Nov. 18**	78	1-10	4.3	± 0.24	5-732	105.6	± 5.4	5-1759	454.3	± 41.56

*Moths were all wild caught and some had undoubtedly deposited eggs before confined.

of egg masses and the number of eggs per mass which were deposited by females in confinement during the 1957 season. The data of table 9 shows that the armyworm moth deposited from one to sixteen egg masses during life with an average of 4.8 masses. The number of eggs per mass ranged from three to four-hundred and averaged 108.4. Typical egg masses are shown in figure 6.

Duration of Oviposition and Egg Production

Once oviposition has begun by a moth it normally continues for a week or longer before the female has deposited all of her eggs. The extremes and average duration of the oviposition period for the five 1957 broods of the armyworm moth are given in table 10.

The fecundity of the armyworm moth has been neglected in the literature and figures that have been recorded are much below those observed by the writer. Riley's (1883) extreme figure is 737 eggs counted in the ovaries of a female. Slingerland (1897) gives the same figure and is obviously quoting Riley, and Davis and Satterthwait (1916) state that the largest number of eggs obtained from a single female in their work was 254. The writer has recorded the number of eggs deposited by each of numerous specimens. The number of eggs deposited averages higher than the maximum figure given by Davis and Satterthwait, and the average approaches the extreme figure of other authors. The maximum number of eggs obtained by the writer from a single female was 1759, but it must be noted that this was a captured specimen which oviposited during the first night of captivity and could have conceivably deposited some eggs prior to her capture. At any rate,

the potential of the species would probably be in the neighborhood of 2000 eggs. Data on the number of eggs deposited by the moths per day and during life are presented for all 1957 broods in table 10. From the data given in this table, it can be seen that the armyworm moth, in confinement during 1957 in Tennessee, had oviposition periods which ranged from one to ten days and averaged 4.3 days. The number of eggs deposited by a single female per day ranged from five to 732 and averaged 105.6. The lifetime egg production of the moth varied from a low of five to a high of 1759 and averaged 454.3 eggs.

Light and Oviposition

Preliminary experiments were conducted to determine the effect of light on oviposition. Two gravid females were placed, separately in one-gallon wide-mouth jars of the usual type and kept in constant light. Two gravid females were likewise isolated in jars of the same type, which had been painted black with poster ink so that no light could enter. These dark jars were kept in constant darkness. All other factors were kept constant. All of the moths had normal life spans, but in no case were eggs deposited. Dissection after death yielded numerous eggs from the body of each moth, more than one thousand in each constant-light moth and one constant-dark moth, and nearly two hundred in the remaining constant-dark moth. No conclusions can be drawn from the use of so few specimens, but the indication is that the moth requires for oviposition a photoperiod of alternate light and darkness. It is planned to conduct further experiments on the effect of this and other physical factors on the habits of the moth in future studies.

Time Elapsing Between Emergence and Oviposition

To determine the interval of time between emergence of the female moth from the pupa and oviposition, a series of female moths in each brood was isolated with one or two males, all of which had emerged on the same day. The first day of egg deposition was recorded for each female. Table 11 shows some cage records of female moths concerning the time interval between emergence and oviposition during different months of the year. Table 12 gives the extremes and averages for each 1957 brood. The period ranged from three to seventeen days and averaged 6.05 days for the entire season. Standard errors of the means indicate little difference in the average of this period from brood to brood.

Longevity of the Moth

The average life-span of the armyworm moth in captivity is in the neighborhood of ten days, but moths have been kept alive by the writer for three weeks and longer. In the insectary rearing of 261 moths on which longevity records were kept, the length of life ranged from one to twenty-seven days and averaged nine days for males and ten days for females. The results of longevity records are given in table 13.

Sufficient liquid food and atmospheric moisture were found to be the most important factors influencing the longevity of adults. Extreme summer temperatures were of no consequence except in the absence of sufficient humidity. In July, 1957, a high mortality rate among caged moths on extremely hot days was corrected by draping a wet towel over the cage.

TABLE XI

TIME ELAPSING BETWEEN EMERGENCE AND OVIPOSITION OF *Pseudaletia unipuncta* AT VARIOUS TIMES DURING 1957 IN TENNESSEE

Specimen Number	Date of Emergence	Date of Oviposition	Length of Interval in Days
536A-6	April 23	April 29	6
I-6	April 29	May 6	7
536A-5	April 30	May 8	8
I-4	May 8	May 14	7
22	June 3	June 8	5
24	June 4	June 8	4
22A	July 15	July 18	3
105	August 29	September 3	5
116	September 6	September 11	5
130	September 9	September 13	4

TABLE XII

RECORDS OF LENGTH OF TIME BETWEEN EMERGENCE AND OVIPOSITION OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE FLIGHT PERIODS IN TENNESSEE, 1957

Flight Number	Period of Observations	Number of Females Observed	Length of Interval (Days)		
			Range	Ave.	St. Error
I	Mar. 11-May 20	4	6-8	6.8	± 0.15
II	Jun. 3-Jun. 24	10	3-10	5.9	± 0.70
III	Jul. 15-Aug. 12	23	4-10	5.6	± 0.35
IV	Aug. 29-Sept. 23	17	3-14	5.9	± 0.73
V	Oct. 20-Nov. 11	7	5-17	7.8	± 1.68
Totals	Mar. 11-Nov. 11	61	3-17	6.05	± 0.32

TABLE XIII

LONGEVITY IN DAYS OF ADULTS OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE FLIGHT PERIODS IN TENNESSEE, 1957

Flight Number	Period of Observations	Number Observed		Longevity					
				Males			Females		
		Males	Females	Range	Ave.	St. Error	Range	Ave.	St. Error
I	Mar. 11-May 20	8	9	3-19	11.4	± 1.41	3-18	11.2	± 1.43
II	Jun. 3-Jun. 24	21	11	4-18	10.2	± 0.83	4-24	12.2	± 1.85
III	Jul. 15-Aug. 12	56	47	1-24	8.5	± 0.81	2-22	8.5	± 0.51
IV	Aug. 29-Sept. 23	47	31	3-20	8.3	± 0.58	3-20	8.5	± 0.68
V	Oct. 20-Nov. 11	12	19	5-22	11.7	± 1.51	5-27	15.0	± 1.49
Totals	Mar. 11-Nov. 11	144	117	1-24	9.0	± 0.41	2-27	10.1	± 0.42

The Egg

Description (see figure 6)

The egg of the armyworm moth is perfectly spherical and measures from 0.6 to 0.7 mm. in diameter. Under low magnification the surface appears smooth, but at 54X and above the shell can be seen to be marked with very fine, parallel ridges running from one pole to the other. The color of the egg when first deposited varies from white to pale yellow, becoming a dark yellow after about twenty-four hours. Immediately preceding hatching, the egg becomes from dark gray to black resulting from the dark head of the larva showing through the shell. Infertile eggs never progress beyond the pale yellow color phase.

Length of Incubation Period

Temperature is the most important factor in the duration of the egg stage. Humidity, while playing a major role in the hatching of eggs, apparently is of only minor importance in the length of the incubation period. When eggs kept in a dry place hatch at all, they do so in the same length of time as those in a moist place.

Between March 25, 1957, and November 23, at Knoxville, Tennessee, a total of 271 egg masses was obtained on which incubation period records were kept. During this time the shortest period of incubation was three days, the longest twenty-four days, and the average 6.4 days. The longest periods occurred during a cool spell in mid-April and in fall, while the shortest occurred in mid-summer. Table 14 gives data showing the length of the incubation periods during each of the five 1957 broods.

TABLE XIV

LENGTH OF INCUBATION PERIOD OF EGGS OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE BROODS, 1957

Brood Number	Period of Observations	Number of Egg Masses	Mean Temperature	Incubation Period in Days: Range	Ave.	St. Error
I	Mar. 25-May 13	90	64.3° F.	3-15	6.6	± 1.07
II	Jun. 8-Jun. 21	52	78.6° F.	3-5	3.6	± 0.03
III	Jul. 19-Aug. 10	45	79.7° F.	3-4	3.2	± 0.06
IV	Aug. 30-Sept. 21	43	76.9° F.	3-5	3.6	± 0.09
V	Oct. 25-Nov. 23	41	52.9° F.	6-24	16.0	± 0.77
Totals	Mar. 25-Nov. 23	271		3-24	6.4	± 1.62

The temperature influence may be seen by examining the mean temperatures for each period given in the table.

Fertility and Hatching Percentages

Fertility of the egg of an armyworm moth may be ascertained by the darkening color of the egg. Egg masses or individual eggs in a mass which do not become deep yellow by the second or third day after deposition are always found to be infertile. Most of the eggs in a mass from a fertilized female hatch; however, almost invariably a small percentage fails to hatch. This is probably not due to infertility of the eggs in question, but rather to injury by early emerging larvae of the same mass.

Frequently during extremely hot, dry periods the entire egg production of a female moth fails to hatch, or certain masses do not hatch while other masses from the same female do hatch. The failure of all egg masses of a female to hatch is undoubtedly due to the failure of the moths to mate at high temperature and low humidity rather than to the effect of these factors on the eggs themselves, since moisture supplied to such egg masses upon deposition fails to induce hatching. When some egg masses of a female hatch while others do not, deficient moisture is apparently the limiting factor since half of such an egg mass supplied with moisture hatches, while the other half, without added moisture, fails to hatch. Table 15 gives the hatching percentages of eggs for all five broods of 1957. Data in this table indicate a nearly complete hatching percentage of eggs during the cool months of spring and fall while the hot months of summer show a relatively

TABLE XV

HATCHING RECORDS OF EGGS OF *Pseudaletia unipuncta* DURING EACH OF THE FIVE OVIPOSITION PERIODS, 1957

Flight Number	Period of Observations	Number of Egg Masses	Total Eggs	Number Hatched	Per cent Hatched
I	Mar. 11-May 20	84	9,308	9,127	98.0
II	Jun. 3-Jun. 24	53	5,599	4,392	78.4
III	Jul. 15-Aug. 12	125	11,189	3,270	29.2
IV	Aug. 29-Sept. 23	122	11,955	7,477	62.5
V	Oct. 20-Nov. 11	34	4,726	4,618	97.7
Totals	Mar. 11-Nov. 11	418	42,777	28,884	67.5

Chi-square for homogeneity = 13,676; probability = L.0001

low hatching percentage. The influence of temperature on egg hatching is indicated. As discussed above, this influence is apparently closely associated with moisture requirements of the moths and the eggs.

The chi-square test for homogeneity indicates that the samples are not from a homogeneous population, i. e., there is not a uniform probability for egg hatching from brood to brood.

The Larva

General Description of the Mature Larva (figures 11, 12, and 13)

This description is a modification of that of Crumb (1927).

Head 3.0 to 3.5 mm. broad. Body about 30-35 mm. long and 5.5-6.5 mm. broad at broadest point; skin smooth; general color varying from red through pinkish and pale gray to the more usual dark gray or greenish-gray. The usual coloration as follows: ground color yellowish or grayish or greenish-gray, more or less tinged with pinkish; dorsal area with setigerous tubercles I and II strongly infuscated (figure 13, I and II); setigerous tubercle II with a narrow black stripe near its base; subdorsal area pale, slightly infuscated; spiracular area heavily infuscated or black including the spiracle; sub-spiracular area pale tinged with pink; spiracles entirely black; head pale gray slightly tinged with brown with black submedian stripes and reticulation; frontal punctures (figure 11, Fa) nearly always below the line of the frontal setae; cervical shield concolorous with adjacent parts but with three pale lines strongly outlined in black (figure 12, Cv Sh).

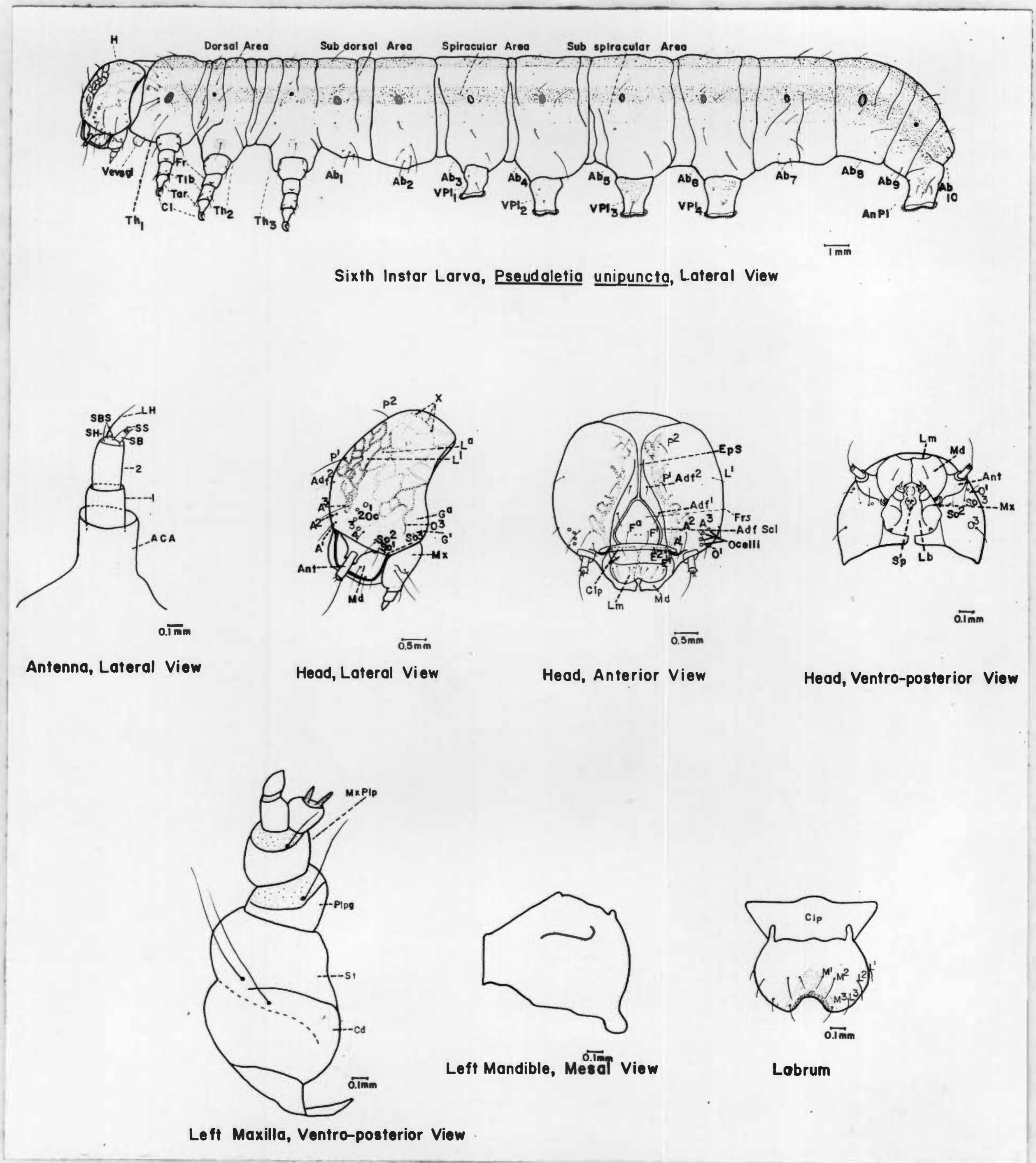


Figure 11. External features of the sixth instar larva of Pseudaletia unipuncta with details of the head and mouthparts. Ab-abdominal segment; ACA-antacoria; Adf Scl-adfrontal sclerite; An Pl-anal proleg; Ant-antenna; Cd-cardo; Cl-tarsal claw; Clp-clypeus; EpS-epicranial suture; Fr-femur; Frs-frons; H-head; LH-long hair (sensillum trichodeum); Lb-labium; Lm-labrum; Md-mandible; Mx-maxilla; MxPlp-maxillary palpus; Oc-ocellus; Plpg-palpiger; SB-sensillum basiconicum; Sh-short hair (sensillum trichodeum); SBS-small sensillum basiconicum; Sp-spinneret; SS-sensillum styloconicum; St-stipes; Tar-tarsus; Th-thoracic segment; Tib-tibia; Vevgl-ventral eversible gland; VPl-ventral proleg. Setae and punctures: Adf-adfrontal; F-frontal; G-genal; L-lateral; M-median; O-ocellar; P-posterior; SO-subocellar; X-ultraposterior.

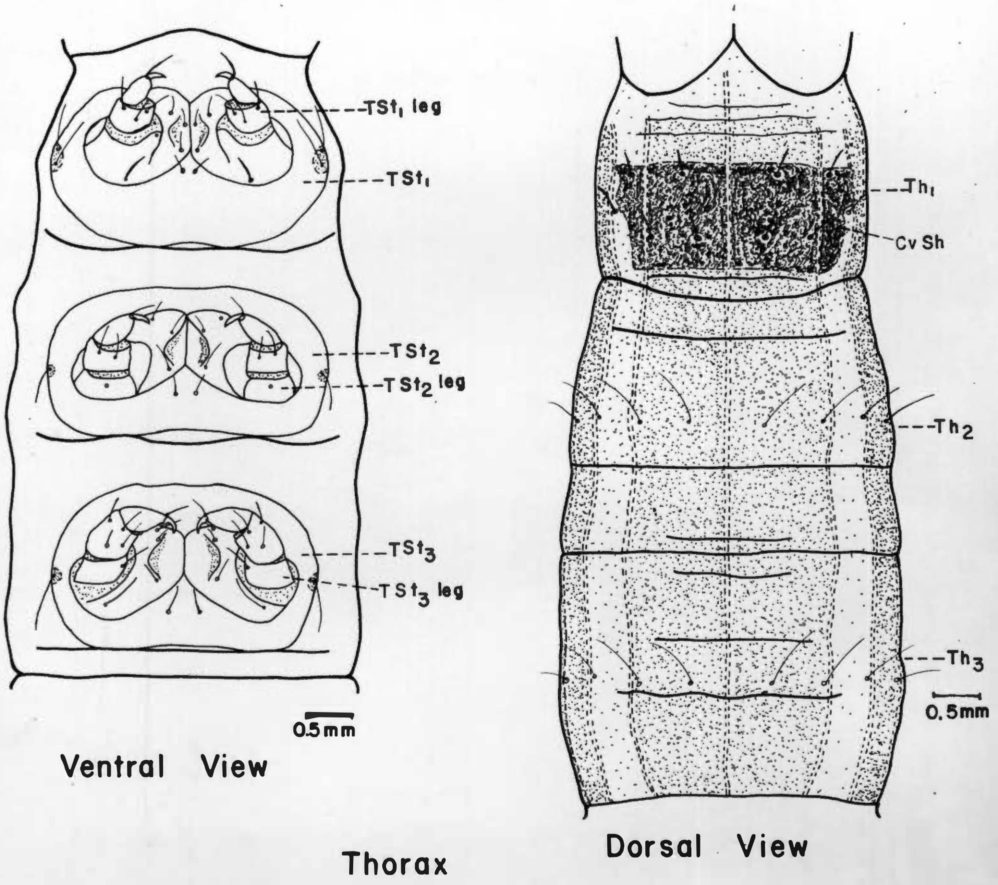


Figure 12. External features of the thorax of the sixth instar larva of Pseudaletia unipuncta. CvSh-cervical shield; Th_1-prothorax; Th_2-mesothorax; Th_3-metathorax; TSt-thoracic sternum.

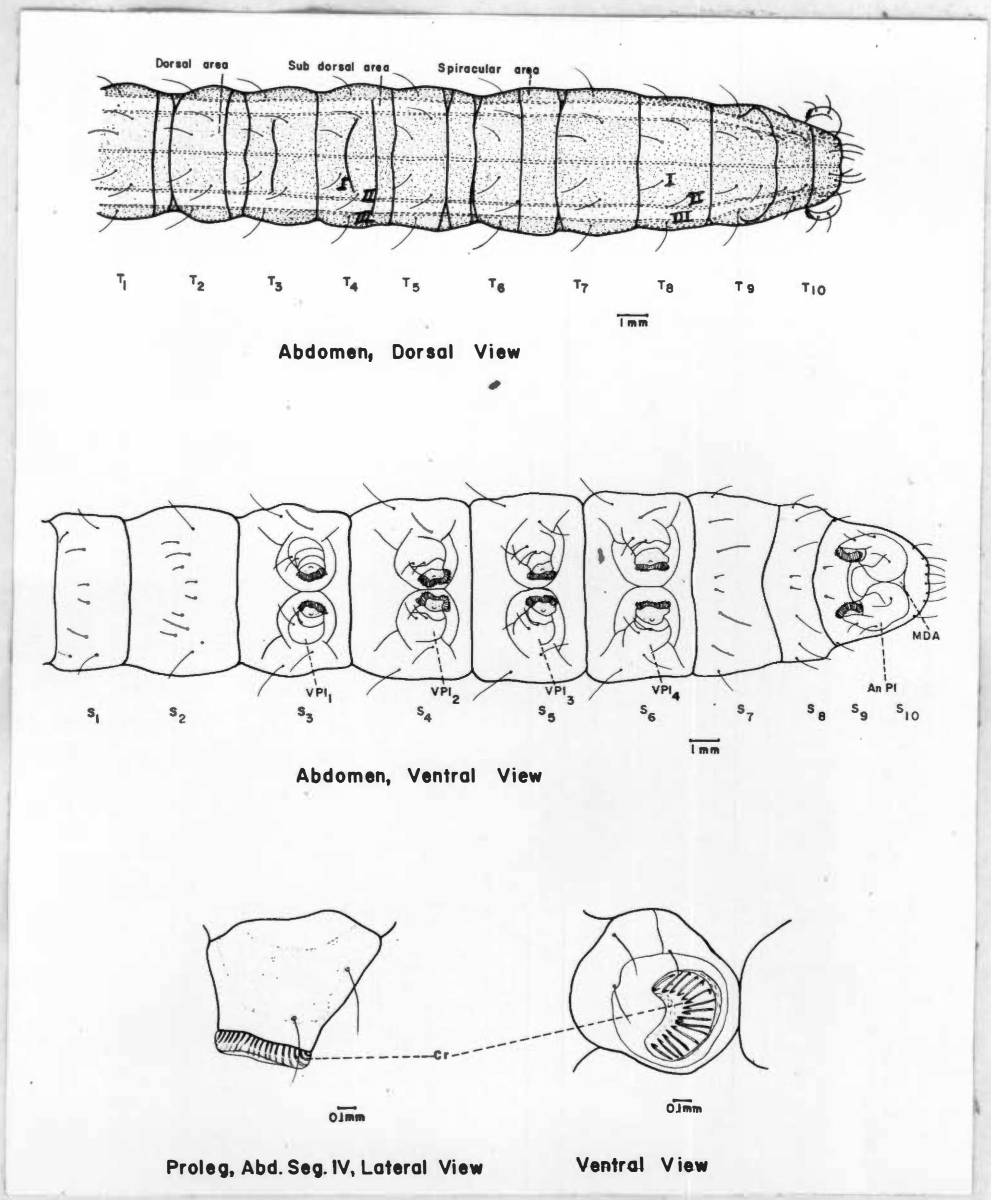


Figure 13. External features of the abdomen of the sixth instar larva of Pseudaletia unipuncta. AnPl-anal proleg; Cr-crochets; MDA-median depressed area; S_1-S_{10}-abdominal sterna 1 to 10; T_1 to T_{10}-abdominal terga 1 to 10; VPl-ventral proleg; I, II, III-setigerous tubercles I, II, and III.

<u>Description of Other Instars</u>

The newly hatched armyworm larva head capsule measurement averages .35 mm. in width; the body length averages 1.8 mm. The color is dull white except for the head which is brownish-black. The front two pairs of prolegs are underdeveloped.

The second instar larva head capsule averages .57 mm. in width; the body length averages 1.8 mm. Prominent color features are the medium yellow head with black ocelli and brown mandibles, and the yellowish-green tinge of the abdomen with very faint longitudinal lines more characteristic of later instars.

The third instar larva head capsule averages .94 mm. in width; the body length averages 7 mm. There is little color change from the preceding instar except in the increased prominence of the longitudinal stripes.

The fourth instar larva head capsule averages 1.5 mm. in width; the body length averages 11 mm. The head becomes a darker color, approaching brown, with reticulations so characteristic of the mature larva. The abdomen takes on a deeper grayish-green color and the cervical shield becomes more prominent. Other features and habits are those of the mature larva.

The fifth instar larva head capsule averages 2.3 mm. in width; the body length averages 18-20 mm. The general description fits that of the mature, sixth instar larva already given.

General Habits of the Larva

Upon hatching, the young worms devour the shells of the eggs from which they hatched and remain quiet for several hours thereafter. After this initial rest period, the larvae begin food-getting activities. They move with a looping motion resulting from the underdevelopment of the first two pairs of prolegs. First instar larvae are positively phototactic and because of this reaction they are commonly found at the uppermost part of plants shortly after hatching. This response is a useful one since the young larvae are dependent upon tender plant tissue such as that found at the growing tips. The first stage "worms" skeletonize the leaves on which they feed (figure 6). When disturbed, the young armyworm larva drops suspended from a silken thread which it spins. This habit undoubtedly serves to some extent in dispersion and as a means of escape. After dropping, the "worms" are seen to bend to the characteristic C-shaped curl of the cutworms, and remain motionless in that position for some time. The second instar larvae do not differ in habits from those of the first. The habit of looping and skeletonizing is lost in the third instar. Instead, the larvae crawl about with the venter in contact with the substrate and eat holes in the leaves from the edges inward to the mid-rib. When disturbed, larvae in this and subsequent instars fall to the ground without the benefit of the silken thread and assume the C-shaped curl. The third through sixth instars all have common habits. Larvae in these instars are active at dusk and dawn and do most of their feeding at night.

During the day they remain concealed under foliage of host plants or under debris in the field. This habit of concealment is one of the most important factors in the armyworm's ability to escape early detection. Not until the "worms" have matured and begun their gregarious march for additional food are they conspicuous. Another important factor in their escape from early detection is the relative amount of food consumed by the various instars. Davis and Satterthwait (1916) found that for a total of 108 individual armyworms, the average amount of foliage consumed per worm was 41.394 square inches and the average for the same individuals in the sixth instar alone was 34.128 square inches, the amount of foliage consumed by the sixth instar being 80 per cent of all foliage eaten during the entire larval period. This remarkable voracity of the armyworm in its last larval instar along with its concealment by day, helps to explain its sudden discovery in such enormous and destructive numbers only when it is nearly full-grown.

After the armyworm larva has consumed sufficient food, it crawls into the soil where the prepupa forms the pupal cell and molts to form the pupa.

The capacity of the armyworm for injury is enormous. Davis and Satterthwait (1916) state that according to feeding records, five armyworm larvae could devour two corn plants two feet high. These authors state that 8,890 corn plants to the acre would require 21,473 "worms" to destroy an acre of corn two feet high. This represents the potential progeny of not more than 40 moths.

Duration of Larval Life

The duration of larval life is influenced mainly by prevailing temperatures and availability of food. The period is greatly extended during winter months and much abbreviated during the warmer parts of the year. The writer has observed complete larval development from eclosion to pupation in as few as twenty days in June and July, while he has recorded an individual specimen remaining in a single instar, the fifth, for 130 days, during the winter months. Another specimen, observed from eclosion to pupation during winter months, had a larval development period of 118 days.

Aside from the overwintering brood, larval development was completed in from twenty to forty-eight days and averaged about twenty-eight days.

During June and July, 1957, close records were kept on the length of the various instars for several groups of larvae, two hundred in each group. The total larvae completing an instar on a particular day was recorded, and when 80 per cent of a group had completed an instar by a certain date, that date was taken as the date of completion of the instar for the group. All larvae were supplied with surplus quantities of food daily. The records of five such groups are given in table 16.

The sixth instar is always the longest in duration during the summer months; however, among overwintering larvae, the middle instars are usually the longest, since the late instars are present toward spring when the weather is warmer.

TABLE XVI

DURATION OF THE VARIOUS INSTARS AND LENGTH OF LARVAL LIFE
IN FIVE GROUPS OF Pseudaletia unipuncta
JUNE 12, 1957 THROUGH JULY 12, 1957

	Length of Instar in Days				
	Group				
Instar	I	II	III	IV	V
First	2	3	3	3	3
Second	2	3	3	2	3
Third	4	2	3	3	2
Fourth	2	3	2	3	3
Fifth	5	4	4	4	5
Sixth	10	7	7	10	10
Total All Instars	25	22	22	25	26

Inasmuch as the species does significant damage only in the late instars, the total larval developmental period is of more consequence than the length of time in the various instars. The expected time of the appearance of mature larvae in the field is a factor of considerable importance. During each of the four full broods of 1957, the writer recorded the minimum and maximum periods of larval development on every group of insectary-reared armyworms, and from these data determined the rate of larval development for each brood. The results are presented in table 17. From the data in this table it can be seen that the minimum period of time required for completion of larval life, twenty days, was observed in early summer and the maximum period, forty-eight days, was observed in fall. The average duration of larval life varied from 23.1 days in early summer to 34.6 days in spring. Comparison of data on duration of larval life and the mean temperature for the period shows the effect of temperature on development. These data might be useful in computing the minimum time required for mature larvae to appear in an area after a flight of moths has been detected. The length of larval life among overwintering specimens was determined in the fall and winter of 1956 and 1957 and that information is given in the section dealing with winter studies.

Annual Broods

The number of annual broods varies with the climate. Knight (1916) reports two broods for New York, while Slingerland (1897) reports at least three for that state. Gibson (1915) gives two as the number

TABLE XVII

DURATION OF LARVAL LIFE OF Pseudaletia unipuncta IN EACH OF THE FOUR FULL BROODS IN TENNESSEE, 1957

Brood Number	Period of Observations	Number of Groups	Mean Temperature*	Duration of Larval Development in Days** Range	Ave.	St. Error
I	Mar. 28-May 20	8	66.5	24-42	34.6	± 2.80
II	June 14-July 15	19	79.2	20-30	23.1	± 0.51
III	July 24-Aug. 29	11	79.2	22-28	25.0	± 0.74
IV	Sept. 2-Nov. 2	12	65.6	22-48	33.7	± 3.11
Totals		50	--	20-48	27.9	± 1.13

*In °F.

**From eclosion to pupation.

of annual broods in eastern Canada. Howard (1894) states that there are two or three broods in the northern states and perhaps six in the South. Knutson (1944) lists two to three for Minnesota. Walkden (1950) gives three for the Central Great Plains and Riley (1883) gives a like number for the Ohio River area, the Great Lakes, and north to central New York. Walkden and Packard (1940) list three as the general number of broods without respect to locality.

During each of the past three years, 1955, 1956, and 1957, Tennessee has had five broods of the armyworm. Studies in 1956 indicate that the fifth brood overwinters as partly grown larvae. The dates for the various broods are given in the section dealing with the seasonal cycle.

Outbreaks

Armyworms are present every year and are among the more numerous of the cutworm-like species. When present in only ordinary numbers, they feed singly in grassy areas and attract only little attention. However, under a certain set of conditions not yet fully understood, they become so numerous as to devour all of their breeding area food before they attain full growth. An outbreak results. When this occurs the larvae are forced to move to new areas for food. Unlike many insects under such circumstances, they exhibit a gregarious habit and move en masse. This migrating habit gives the species its common name. Such circumstances do not occur often, perhaps not more often than once each ten years or even less in a particular area. The gregarious habit contributes largely to the fact that the species is

hardly ever destructive in successive years, for when the larvae become so numerous, they have the serious problem of traveling great distances for food and they expose themselves to wholesale destruction by predators, parasites, and infectious diseases. By this same habit, they likewise expose themselves to easier destruction by the farmer. In Tennessee in 1956 and 1957, a survey revealed 32.3 and 42.5 per cent parasitism respectively and in 1957, a virus disease almost completely destroyed the armyworm population in several fields in Monroe, Lincoln, and Franklin counties, and was always a threat to insectary colonies. The effects of natural enemies of the armyworm are more fully discussed in a later section of this work.

A review of past armyworm outbreaks shows the irregular intervals of their occurrence. Even though not validly in our nomenclature until 1810, the armyworm has been known as a serious pest since early colonial times. The outbreak of 1743 over all of the present North Atlantic States is considered to be the first authentic report of widespread armyworm damage in the United States. A severe outbreak occurred in 1861 in the eastern United States, in 1881 in the Midwest, and in 1914 there was a general outbreak in the entire agricultural region west of the Rocky Mountains and north of the Gulf States. Serious outbreaks occurred in Canada in 1861, 1865, 1881, 1896, and 1914.

In recent years localized outbreaks have become more numerous. The recent increase in frequency of localized outbreaks might be due to the greater use of insecticides which kill off large numbers of parasites which normally hold the species in check.

Other Noctuid Larvae with the Armyworm Habit

Certain species of Noctuid larvae, other than *P. unipuncta*, sometimes exhibit the armyworm habit of gregarious dispersal, and owing to this habit have been called armyworms. The true armyworm may be distinguished from these others by a combination of the general description given on page 63, by the fact that it usually is found feeding on grasses, and by the time of its appearance in a given area. Crumb (1927) described and keyed all species of Noctuids known to assume the armyworm habit. A summary of information on the armyworm species, taken from Crumb's article, is given in table 18. The reader is referred to the original article for detailed descriptions and a systematic key to the various species.

The species most likely to be confused with *Pseudaletia unipuncta* in Tennessee are *P. phragmatidicola* and *P. pseudargyria*. *Laphygma frugiperda*, the fall armyworm, might be confused with the true armyworm, not so much for its morphological resemblance as for its frequent appearance in armyworm populations. The writer has prepared a key to separate these four species, since the three of the genus *Pseudaletia* are likely to be confused even by trained workers, and the fall armyworm is added because of its occasional appearance along with the true armyworm in late season outbreaks. Terminology used in this key conforms to that of figures 11, 12, and 13.

TABLE XVIII

THE SPECIES OF NOCTUID LARVAE EXHIBITING THE ARMYWORM HABIT[1]

Species	Common Name	Food Plants	Distribution
Chorizagrotis auxillaris Grote	Army cutworm	General	West of Miss. River
Feltia gladaria Morrison	Clay-backed cutworm	Field and garden crops	East of Rocky Mountains
Feltia ducens Walker	Dingy cutworm	Field and garden crops	Northern U. S. and Canada for entire longitude
Pseudaletia unipuncta Haworth	Armyworm	Primarily grasses	East of Rocky Mountains
Pseudaletia phragmatidicola Guen.	Yellow armyworm	Primarily grasses	East of Rocky Mountains
Pseudaletia pseudargyria Guen.	Brown armyworm	Primarily grasses	East of Rockies, more northern
Neleucania albidinea Huebner	Wheat-headed armyworm	Primarily grasses	North of latitude of Ohio River, east of Rockies, also in Ky., Ariz., N. M., and Texas
Agrotis c-nigrum Linnaeus	Spotted cutworm	Field and garden crops	Northern U. S., including Tenn.
Peridroma margaritosa Haworth	Variegated cutworm	Field and garden crops	Entire U. S.
Laphygma frugiperda Smith & Abbot	Fall armyworm	Cereals and grasses, but will attack many others.	U. S. west to Nebr., Kans., Tex., & N. M.
Prodenia eridania Cramer	Semitropical armyworm	Field and garden crops	Southern U. S. north to Tenn.
Prodenia ornithogalli Guen.	Yellow-striped armyworm	Field and garden crops	Common only in South, but occurs from N. Y. to Fla. & westward to Minn., Nebr., N. M., Ariz., & Calif.

1 Compiled from Crumb (1927)

Key to the Larvae of Four Noctuid Species Likely to be Taken for the True Armyworm in Tennessee

1. Skin pavement granulose; each mandible with five distinct teeth; no dark longitudinal stripe on the abdomen through setigerous tubercle II .... *Laphygma frugiperda*

   Skin smooth; each mandible with but two obscure teeth; with a dark longitudinal stripe on the abdomen through setigerous tubercle II 2

2. With a pale longitudinal stripe between setigerous tubercles I and II; spiracles entirely black; setigerous tubercles II on abdominal segment 8 further apart than tubercles I ... *Pseudaletia unipuncta*

   With not more than a pale line between setigerous tubercles I and II; spiracles yellowish or gray with black rim; setigerous tubercles II on abdominal segment 8 not further apart than tubercles I ... 3

3. Spiracular area strongly infuscated or black, much darker than supraspiracular area; spiracles pale yellowish with black rims .... *Pseudaletia phragmatidicola*

   Spiracular area but slightly infuscated or black, but little darker than supraspiracular area; spiracles yellowish to dark gray with black rims .... *Pseudaletia pseudargyria*

The Pupa

General Description (figure 6)

The pupa of *Pseudaletia unipuncta* is a typical Noctuid pupa. Both sexes measure from 13 to 17 mm., and average about 14.5 mm. in length, and from 5.0 to 6.0 mm. broad. There are two stiff, converging, black thorns (cremasters) at the anal end, each with a fine curled hook. The color is a light amber at pupation, but darkens to a shiny mahogany brown with age. Figure 14 shows the sexual differences of the male and female pupa.

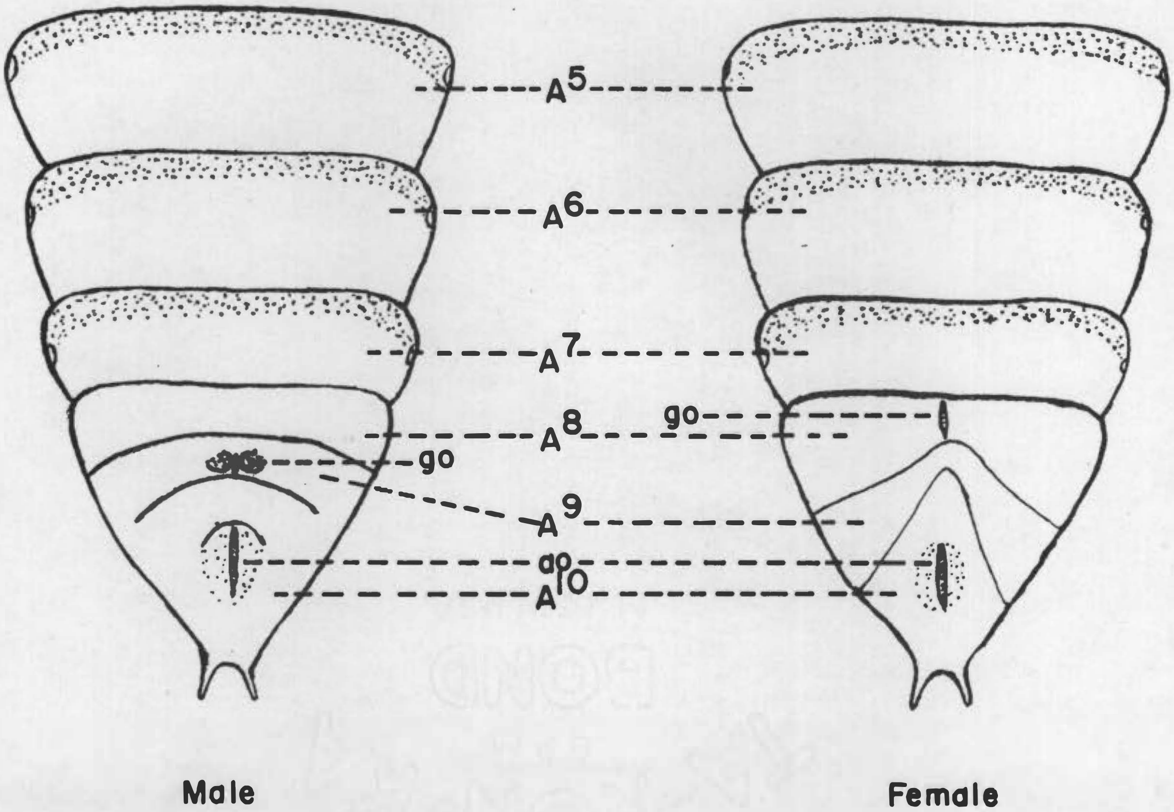


Figure 14. Terminal segments of the male and female pupa of Pseudaletia unipuncta to show sex differences. A^5 to A^{10}- abdominal segments 5 to 10; ao-anus; go-gonopore.

Place of Pupation

Pupation normally occurs in the soil to a depth varying from one inch to three inches depending upon texture of the soil and presence or absence of cracks suitable for larval burrowing prior to pupation. Pupae in the field are normally found beneath dead foliage, clods of dirt, or cracks in the soil. In field experiments and observations the writer has never observed the pupa to be exposed on the surface of the ground. In most cases, the pupa is contained within a little earthen pocket formed around the slightly spun silken case made by the prepupa. However, this pocket is not necessary since successful pupation will occur even on the floor of an open rearing jar where no soil or debris is available.

Duration of the Pupal Stage

Temperature greatly affects the length of the pupal stage of the armyworm as it does the length of the egg and larval stages. The amount of humidity does not appear to be an important factor in determining the length of the pupal stage. Pupae kept in moist sand do not have pupal lengths differing from those maintained in dry containers when both types of containers are kept under the same temperature conditions.

When temperature conditions are right, the moths emerge, regardless of the season of the year. This relationship is an important factor in the failure of the species to overwinter in this stage, for the moths are quickly killed upon the return of cold weather after they have emerged from the pupa during a warm spell of winter.

Observations on the length of the pupal period were made during each of the four full broods of 1957. These records show a range of seven to forty days in the pupal stage and an overall average of 15.1 days. The results of each of the broods are given in table 19. Duration of the stage during the winter months is discussed under the winter studies section of this work.

TABLE XIX

DURATION OF PUPAL LIFE OF *Pseudaletia unipuncta* IN EACH OF THE FOUR FULL BROODS IN TENNESSEE, 1957

Brood Number	Period of Observations	Number of Groups	Duration of Pupal Life in Days		
			Range	Ave.	St. Error
I	May 14-June 10	10	10-17	13.6	± 0.37
II	July 5-July 27	11	7-13	9.8	± 0.44
III	Aug. 14-Sept. 12	15	8-14	11.3	± 0.42
IV	Sept. 28-Nov. 16	8	24-40	31.6	± 0.74
Totals		44	7-40	15.1	± 1.76

SEASONAL STUDIES

Seasonal Cycle in Tennessee

During the course of this study, March, 1956, through November, 1957, the writer has been able to observe the armyworm for two complete seasons. By combining information obtained from direct field observations, insectary rearings under near natural conditions, and light trap data, the seasonal cycle of the species in the state has been elucidated.

In early March, 1956, overwintering forms began to produce a few adults, but from a population standpoint the active spring flight period of the first 1956 moths began the first week in April, reached its peak the middle of April, and continued through the first week of May. This flight of moths deposited the eggs which hatched into the first 1956 brood of armyworms. In mid-May, a survey by the writer of several East Tennessee counties from Knox to Johnson, revealed the quite general presence of immature armyworm larvae in grain fields throughout the area. These larvae reached the sixth and final instar by the third week of May and appeared in destructive numbers of outbreak proportions on several farms in the survey area, as well as in the Sweetwater Valley of Monroe County. The general outbreak culminated in early June producing adults which were the parents of the second 1956 brood. The second flight reached its peak in mid-June and accounted for second-brood mature larvae in mid-July, which produced adults of the third brood in late July. By late August, the third brood

larvae were mature and adults issued in mid-September, which were the parents of the fourth brood. These fourth-brood larvae matured toward mid-October and produced the fifth flight of moths in early November. These moths deposited eggs which hatched and developed into the fifth brood worms which overwintered and produced the first 1957 flight of moths the following spring.

The first 1957 moths issued from pupated overwintering larvae, from early March to early May, but reached their peak in mid-April as did their 1956 counterparts. The 1957 moths deposited the eggs which gave rise to the first brood larvae of 1957 which matured in late May and from which the second flight of moths resulted in early June. These moths produced the second brood larvae which matured in early July and which produced the third flight of moths in late July and early August. The larvae from this flight, the third brood, matured in late August and produced the fourth flight of moths in mid-September. The fourth brood larvae resulting from this flight matured in mid-October and produced the fifth flight moths in early November. These moths deposited eggs which hatched to produce the fifth brood larvae which are destined to overwinter and produce the first 1958 flight of armyworm moths.

By comparing the account of the 1956 and 1957 seasonal cycles, the reader can see the close correlation of the cycle in the state for those two years. The cycle for the 1956 season is represented in figure 15.

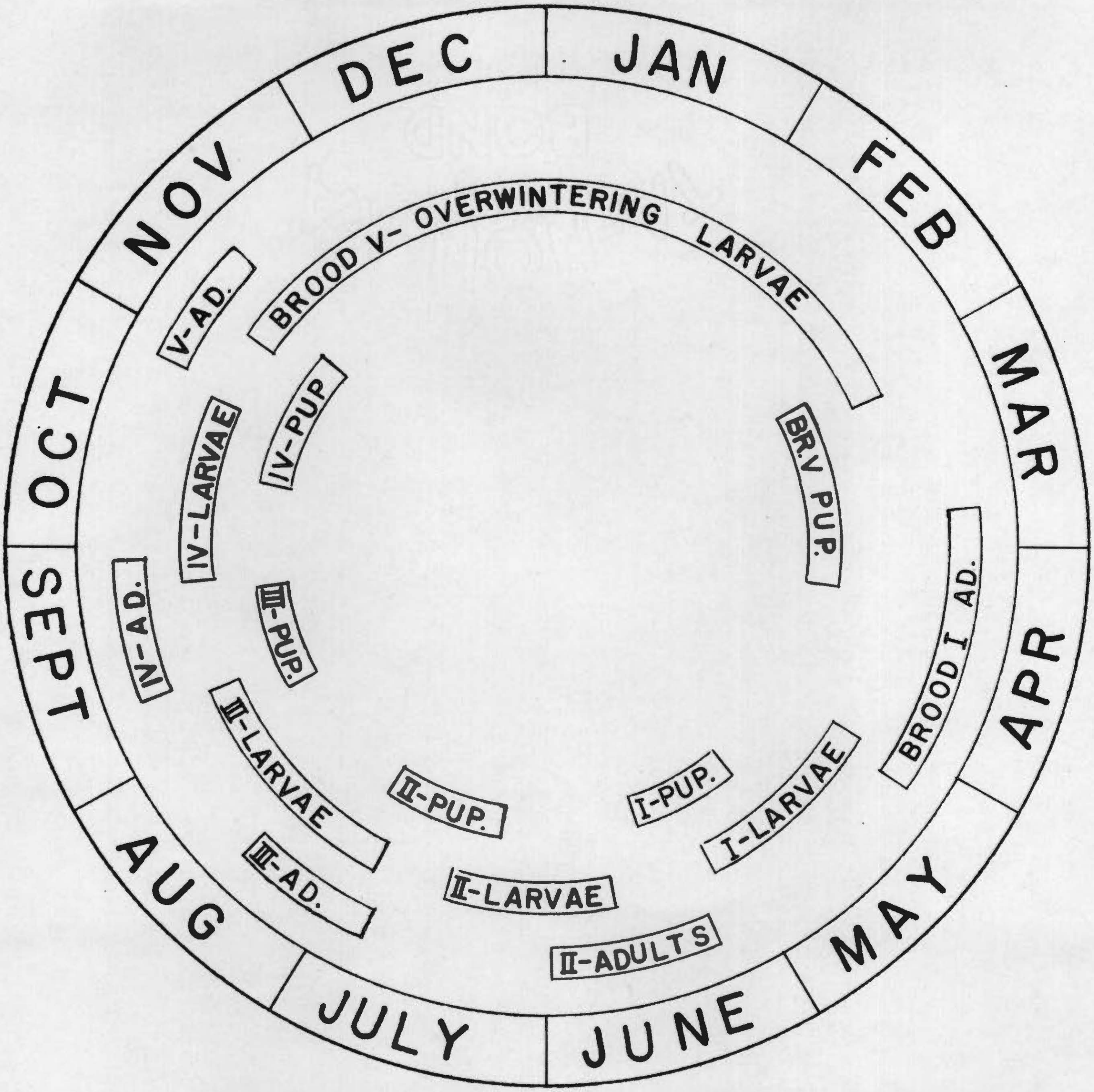


Figure 15. Graphic representation of the seasonal cycle of *Pseudaletia unipuncta* in Tennessee.

Winter Studies, 1956-57

A cloak of confusion has hung over the winter activities of the armyworm because most studies have dealt with the species only during outbreak periods of major outbreak years. Adding to the confusion is the fall armyworm, Laphygma frugiperda, which is preserved as a permanent resident only in the warmer parts of the South, passing the winter in the United States in that region included in the tropical life zone. This insect becomes redistributed each year by migrations of the moths over most of the austral region (Luginbill, 1928). Because of the similarity of the fall armyworm to the true armyworm, P. unipuncta, in structure, gregariousness, and common name, this migratory habit has often been attributed to the true armyworm in explanation of its sudden appearance in the spring. To help clarify this situation and to elucidate the real overwintering status of the true armyworm in temperate regions, a three-phase study of the winter habits of the species was conducted in the fall and winter of 1956-57, the methods and results of which are herewith presented.

Winter Study Number One

This phase of the winter study was conducted to determine the ability of the armyworm to overwinter in Tennessee under natural conditions. On October 18, 1956, 40 sixth-instar armyworm larvae from the insectary colony were released, 20 each, in two cylindrical screen-wire baskets, 18 inches tall and 12 inches in diameter, open at one end. These containers had previously been partly filled to a depth of several inches with soil and grass removed from a likely looking army-

worm habitat (figure 16). Each container was then placed in a hole from which the soil had been removed. A portable plastic screen cage, 6 feet by 6 feet by 6 feet, open at the bottom and with a zipper opening on one side, was placed over the area where the baskets were located. The frame of the cage was of one-half inch iron pipe, the four corners driven into the ground and packed with soil in a fold of the screen (figure 17). Larvae of instars other than the sixth developed in the insectary colony in late December, 1956, and by January 7, 1957, larvae of the first five instars had been similarly released. Twenty specimens each of the first, second, third, and fourth larval instars were released into clay flower pots of 4-, 5-, 6-, and 8-inch top diameters respectively. Fifth instar larvae were released into wire baskets of the same dimensions as the one previously described for sixth-instar specimens. All containers were manipulated as already described. Observations of the contents of each container were made at irregular intervals throughout the fall and winter, with daily observations as spring neared. Soil temperatures were taken at frequent intervals, for the most part daily, throughout the period of study (table 20). As pupation approached, cheese-cloth was tied around the top of containers to prevent the escape of emerging adults. On March 25, 1957, the specimens, after having obviously withstood the winter, were removed from each container to individual metal salve boxes and kept at outside temperatures until development was completed.

Figure 16. Containers used for releasing armyworm larvae under natural field conditions.

Figure 17. Portable screen cage used for confining armyworms under natural conditions.

TABLE XX

SOIL TEMPERATURES IN WINTER FIELD CAGE, 1956-57

Date of Readings*	Temperature in °F.**
1956: Oct. 18	66
22	64
24	65
29	61
Nov. 5	63
7	63
9	51
1957: Jan. 5	43
7	45
8	41
9	49
10	48
11	41
14	43
15	40
16	38
17	32
18	21
19	21
21	25
22	38
23	35
24	31
25	37
28	39
29	53
30	42
31	44
Feb. 2	38
4	40
5	48
6	51
7	54
1957: Feb. 8	54
9	53
11	41
12	31
13	34
14	34
15	29
16	40
18	27
19	41
20	29
21	29
22	32
23	32
25	38
26	50
27	48
Mar. 1	37
2	34
4	30
5	40
6	40
8	32
9	30
11	30
12	50
13	42
14	45
15	50
16	34
18	36
19	49
20	42
21	31
22	42

* Readings at midday

** At the soil surface just below mat of covering vegetation

With one exception, all surviving sixth instar larvae, released on October 17, 1956, had pupated by October 29, 1956, and adults had emerged in December, 1956. This coincided with the presence of adults in the greenhouse light trap during December, 1956, from which were obtained colony "worms" which had been released into baskets in the first week of January, 1957. The one exception among the sixth instar "worms" released on October 17, 1956, was a specimen which was still a sixth instar larva on February 21, 1957, and which pupated on March 11, 1957, with the adult emerging on or before March 21, 1957. A total of 128 days had been spent as a mature larva and prepupa, as compared to an average of about ten days for other members of the same batch under the same conditions. This exception might be due to the specimen's doing little or no feeding, with consequently an arresting development long enough for later low temperatures to produce their effect.

The first five instars, released during the first week of January, 1957, had varying degrees of success in overwintering, and a portion of all of these instars successfully withstood the winter and emerged as adults during March, April, and May, 1957, the normal months for the first flight of moths each spring, as indicated by light trap collections. Of the 100 larvae in the first five instars released in early January, 1957, 55 became pupae between early March and mid-May, 1957, and 50 successfully emerged. Adults of all groups were successfully mated and produced offspring. It might be added that the coldest temperatures of the winter came in January after all larvae had been released (see table 20). A summary of the foregoing data is given in table 21.

TABLE XXI

RECORDS OF ALL INSTARS OF Pseudaletia unipuncta LARVAE RELEASED INTO FIELD CAGES DURING THE FALL AND WINTER OF 1956-57, KNOXVILLE, TENNESSEE

Cage Number	Source of Specimens	Larval Instar	Date Released	Number Released	Pupating No.	Pupating Pd.	Adult Emergence No.	Adult Emergence Pd.	Fertile Eggs
1*	F.C. 523	VI	Oct. 17, '56	40	26	Oct. 22-29	10	Dec., '56	**
2	F.C. 536c	I	Jan. 3, '57	20	12	Apr. 18-May 1	12	May 13-	Yes
3	F.C. 536b	II	Jan. 3, '57	20	8	Apr. 22-26	6	May 7-11	Yes
4	F.C. 536a	III	Jan. 3, '57	20	11	Apr. 18-21	10	Apr. 21-26	Yes
5	F.C. 536a	IV	Jan. 3, '57	20	7	Apr. 3-18	7	Apr. 26-30	Yes
6	F.C. 536a	V	Jan. 7, '57	20	17	Early March	15	Mid-March Apr. 29	Yes

* Two cages combined

** Moths emerged and dead before discovered

Winter Study Number Two

To augment the study discussed above and to prove that the armyworm not only can, but does overwinter in Tennessee, field searches were made for overwintering larvae at various intervals throughout the winter months from October, 1956, through February, 1957. Overwintering larvae were found at three localities; namely, the Cherokee peach orchard on the University of Tennessee farm, where the field tests already described were conducted, thus enhancing the value of that area as a testing site; the Highland Rim Experiment Station, Springfield, Tennessee; and the Lee Price farm, near Dandridge, Tennessee. The latter locality provided the majority of the specimens and served as a collecting area throughout the winter.

In all cases, the larvae were found only after diligent searching beneath thick mats of grassy vegetation. Forty-two specimens in various stadia from five collections, one collection for each month from October, 1956, through February, 1957, were used in the study. The specimens were collected alive in the field, taken to the insectary immediately, and isolated in two-ounce metal salve boxes which in turn were placed in a one-gallon syrup can with a tight-fitting lid. This larger can was sunk in the ground outside the insectary in an effort to match as nearly as possible prevailing soil temperatures, at the same time affording the specimens protection from excess moisture, predaceous ground beetles, etc. Observations were made at frequent intervals, usually daily, of each specimen concerning its stadium, physical

condition, and amount of feeding. At each observation, the larvae were given grass for food in surplus quantities and the temperature in the large container and in the surrounding soil just below the mat of covering vegetation was recorded (table 22).

Of the forty-two specimens used in this study, fifteen completed development to the adult stage. Three of these fifteen moths proved not to be P. unipuncta, but a closely related species, P. pragmatidicola. Because of the presence of P. phragmatidicola, the records on all specimens which failed to produce adult moths are unreliable. Consequently, only those twelve specimens positively known to be P. unipuncta are included in this analysis. This mistaken identity of field collected larvae led the writer to construct the key given on page 78.

A summary of the development of each of the twelve specimens culminating in the adult stage is given in table 23 and is shown graphically in figure 18.

Data from this study show that the development of the armyworm is arrested in the several larval stages thus extending the duration of development through the winter months. Consider specimen number one of table 23. This specimen spent virtually the entire fall and winter season in the third and fourth instars. It was captured as a third-instar larva on October 26, 1956, and remained in that stage until January 4, 1957, when it molted to the fourth instar in which it remained until March 18, 1957, for a total of 143 days in these two instars. The same specimen required a total of 209 days, nearly seven months, to complete its development from the third instar to adult.

TABLE XXII

SOIL AND CONTAINER TEMPERATURES ASSOCIATED WITH WINTER STUDIES TWO AND THREE

Date of Reading*			Soil Temperature in °F.	Container Temperature in °F.
1956:	Oct.	26	-	60
		29	-	60
	Nov.	5	-	55
		12	-	65
		15	-	56
		23	-	41
	Dec.	3	-	51
		10	-	50
		17	-	56
1957:	Jan.	4	42	41
		5	42	42
		7	44	44
		8	40	40
		9	51	51
		10	49	48
		11	36	36
		12	40	40
		14	37	36
		15	34	35
		16	32	33
		17	21	24
		18	25	30
		19	23	27
		21	40	41
		22	46	46
		23	44	44
		24	34	36
		25	40	40
		26	41	41
		28	48	49
		29	62	60
		30	42	44
		31	46	47

* Readings at 8:00 A. M.

TABLE XXII (Continued)

SOIL AND CONTAINER TEMPERATURES ASSOCIATED
WITH WINTER STUDIES TWO AND THREE

Date of Reading*	Soil Temperature in °F.	Container Temperature in °F.
1957: Feb. 1	53	54
2	40	42
4	57	56
5	50	51
6	54	54
7	56	56
8	56	55
9	55	55
11	46	48
12	37	40
13	40	44
14	40	44
15	35	38
16	44	47
18	36	40
19	42	45
20	30	33
21	34	36
22	38	41
23	40	40
25	52	52
26	54	54
27	52	52
28	50	50
Mar. 1	44	44
2	45	46
4	38	42
5	45	46
6	46	46
7	48	48
8	41	42
9	37	39
11	42	44
12	52	54
13	48	50
14	52	52
15	53	53
16	45	47
18	50	51
19	52	54
20	46	46

TABLE XXIII

DEVELOPMENT RECORDS OF THE TWELVE SPECIMENS OF WINTER STUDY NUMBER TWO COMPLETING GROWTH TO ADULT

Specimen Number	Date of Collection	Instar Isolated	Date Molted to Stadium						
			III	IV	V	VI	VII	P	AD
1	Oct. 26, '56	Third	-	1-4	3-18	4-8	4-25	5-13	5-23
			70*	73	21	17	18	10	
2	Nov. 9, '56	Fourth	-	-	1-23	2-11	-	3-2	3-22
				75	19	21	-	20	
3	Dec. 4, '56	Third		12-10	12-17	1-4	1-15	2-25	3-24
			6	7	18	11	41	28	
4	Dec. 4, '56	Fifth	-	-	-	4-14	-	5-13	5-29
			-	-	130	29	-	16	
5	Jan. 9, '57	Fourth	-	-	1-12	1-24	2-11	3-25	5-2
				3	12	18	43	40	
6	Jan. 9, '57	Fourth	-	-	2-1	2-18	-	3-26	5-3
				23	17	37	-	38	
7	Feb. 18, '57	Fourth	-	-	2-25	3-18	-	4-10	5-6
				7	22	23	-	26	
8	Feb. 18, '57	Fourth	-	-	3-4	4-4	-	4-26	5-20
				15	31	22	-	24	
9	Feb. 18, '57	Fifth	-	-	-	2-26	-	4-2	5-2
					8	36	-	30	
10	Feb. 18, '57	Fifth	-	-	-	2-20	-	4-1	5-3
					2	41	-	32	
11	Feb. 18, '57	Fifth	-	-	-	2-27	-	4-24	5-22
					9	57	-	28	
12	Feb. 18, '57	Sixth	-	-	-	-	-	3-16	4-29
						27	-	44	

* Number of days in instar

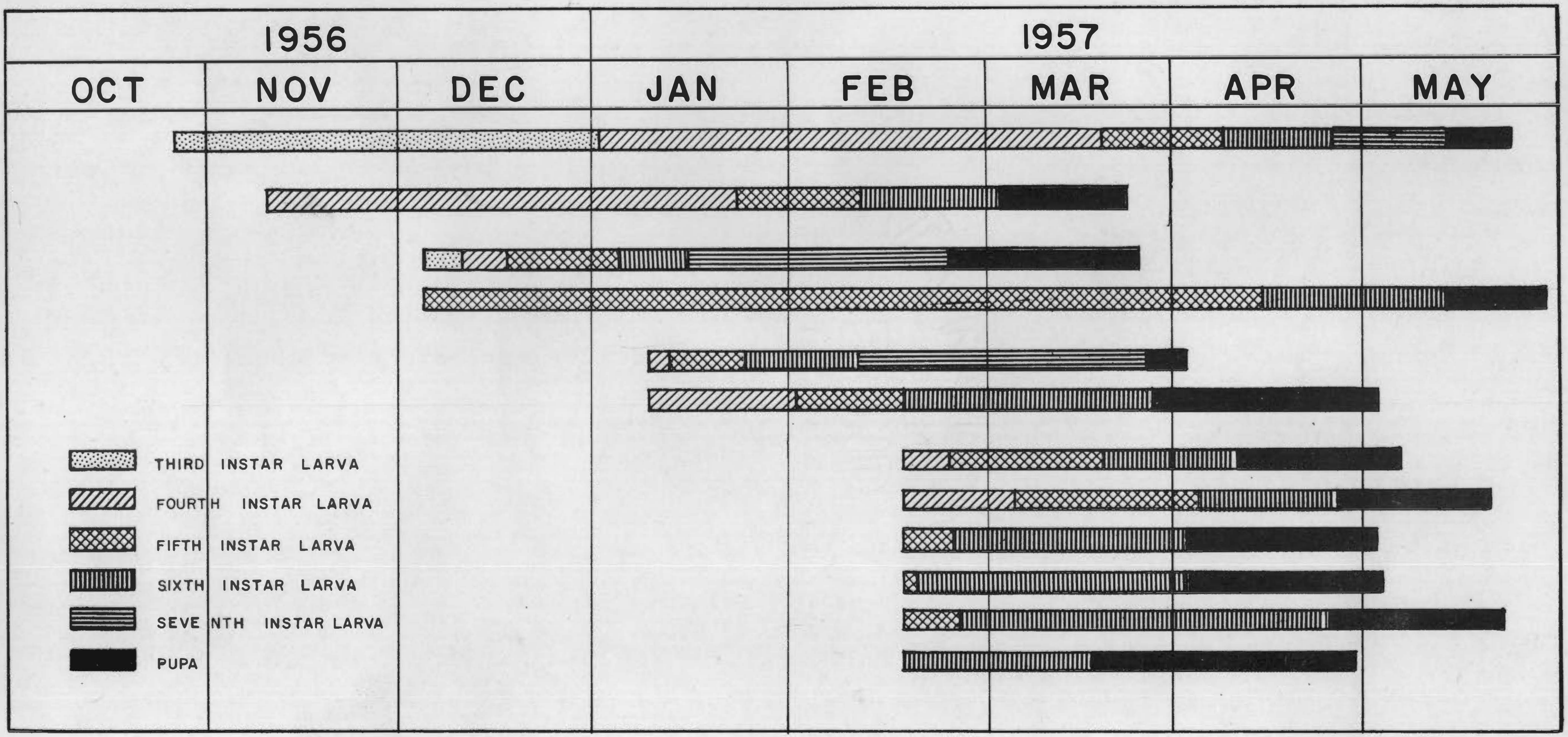


Figure 18. Graph showing the winter development records of twelve field collected armyworms under natural temperature conditions in Tennessee, 1956-57.

The greatest length of time spent in any one instar was by specimen number four which remained in the fifth instar for a total of 130 days after its capture in that stage.

In no case did overwintering larvae show evidence of a true diapause. Their development was arrested and there was no movement or feeding on colder days. However, on warmer days of winter, specimens resumed activity and began to crawl and feed, sometimes voraciously. More exact records of overwintering larvae are discussed in part three of this study which follows.

Winter Study Number Three

This study was conducted in order to obtain records of the relative abilities of the various larval instars to withstand Tennessee winter temperatures, to provide information on the developmental time of the armyworm when released under natural temperature conditions, and to supplement data of winter studies one and two.

During the early part of January, 1957, a total of 96 larvae was isolated, one each according to instar into metal salve boxes. These boxes were in turn placed in larger syrup cans as already described. Further procedure was identical to that of winter study two. This study differs from winter study one in that larvae of that group were grouped and exposed to natural field conditions, while those of this study were isolated and exposed only to natural temperatures. It differs from winter study two in that larvae of that study were collected in the field from natural overwintering areas before being isolated whereas these larvae were insectary reared before being isolated. Specimens in

this study were isolated as follows: January 2, 1957, 10 third-instar specimens; January 3, 1957, 50 first-instar specimens; January 5, 1957, 10 second-instar specimens and 10 fourth-instar specimens; January 7, 1957, 10 fifth-instar specimens; and January 12, 1957, 6 sixth-instar specimens.

The data of table 24 show that first instar larvae had little success in surviving winter temperatures. Only one specimen of the original fifty completed development and only three lived for as long as the third instar. It seems that the species is destined to failure if eggs are deposited and hatch immediately preceding a killing frost. The remaining five instars were able to survive the cold temperatures satisfactorily.

As this study progressed, it became apparent that the armyworm was capable of adding extra instars to its normal developmental stages. The one first-stage larva which succeeded in developing to the adult stage had seven larval instars; seven of the larvae released in the second instar had seven larval instars; nine of those released as thirds had seven instars, six had eight instars, and one had nine instars; of those released as fourths, nine had seven instars and nine had eight instars; of those released as fifths, all had at least seven instars, and two had eight instars; of those released as sixths, none had additional instars. This adding of extra instars could be a valuable mechanism for the armyworm for the survival of a long winter.

TABLE XXIV

SURVIVAL RECORDS OF *Pseudaletia unipuncta* LARVAE OF VARIOUS INSTARS DURING THE WINTER OF 1957 IN TENNESSEE

Group Number	Date Isolated	Instar	Number in Group	Number Reaching Stadium I	II	III	IV	V	VI	P	AD
1	Jan. 3	First	50	50	3	3	1	1	1	1	1
2	Jan. 5	Second	10	-	10	9	9	9	9	9	9
3	Jan. 2	Third	10	-	-	10	10	10	10	9	9
4	Jan. 5	Fourth	10	-	-	-	10	10	10	8	7
5	Jan. 7	Fifth	10	-	-	-	-	10	10	10	10
6	Jan. 12	Sixth	6	-	-	-	-	-	6	6	5

Table 25 gives the gross developmental time of all specimens which reached the pupal stage in this study. It also shows the number completing development in each group and the periods of adult emergence. From these data it can be seen that duration of development from the starting point of the various instars occurs in an orderly manner, taking the shortest time from the sixth instar and the longest from the first, with all intermediate instars in between. These data offer convincing evidence of the ability of the armyworm to extend developmental time by alternate periods of activity and inanition during the winter months. In this connection it is interesting to note that an extended warm period in January, 1957, resulted in much feeding and molting in all instar groups. The data also shed some light on the reasons for the long spring flight of moths which results from the various stages of larvae present when the cold weather begins in the fall. All groups of moths of the second through sixth instar groups were mated and produced fertile eggs.

Figure 19 shows graphically the development records of the specimens given in table 25.

TABLE XXV

GROSS DEVELOPMENT RECORDS OF ARMYWORM LARVAE OF VARIOUS INSTARS REARED DURING THE WINTER OF 1957 IN TENNESSEE

Instar Isolated	Date Isolated	No. of Specimens	No. Days to Complete Larval Development: Range	No. Days to Complete Larval Development: Ave.	Number Reaching: Pupae	Number Reaching: Adult	Period of Emergence
First	Jan. 3	50	123	123	1	1	May 22
Second	Jan. 5	10	94-101	98	9	9	May 8-13
Third	Jan. 2	10	93-111	97	9	9	May 6-14
Fourth	Jan. 5	10	84-87	85	8	7	May 3-6
Fifth	Jan. 7	10	64-69	66	10	10	Apr.29-May 1
Sixth	Jan. 12	6	33-46	42	6	5	Apr.23-26

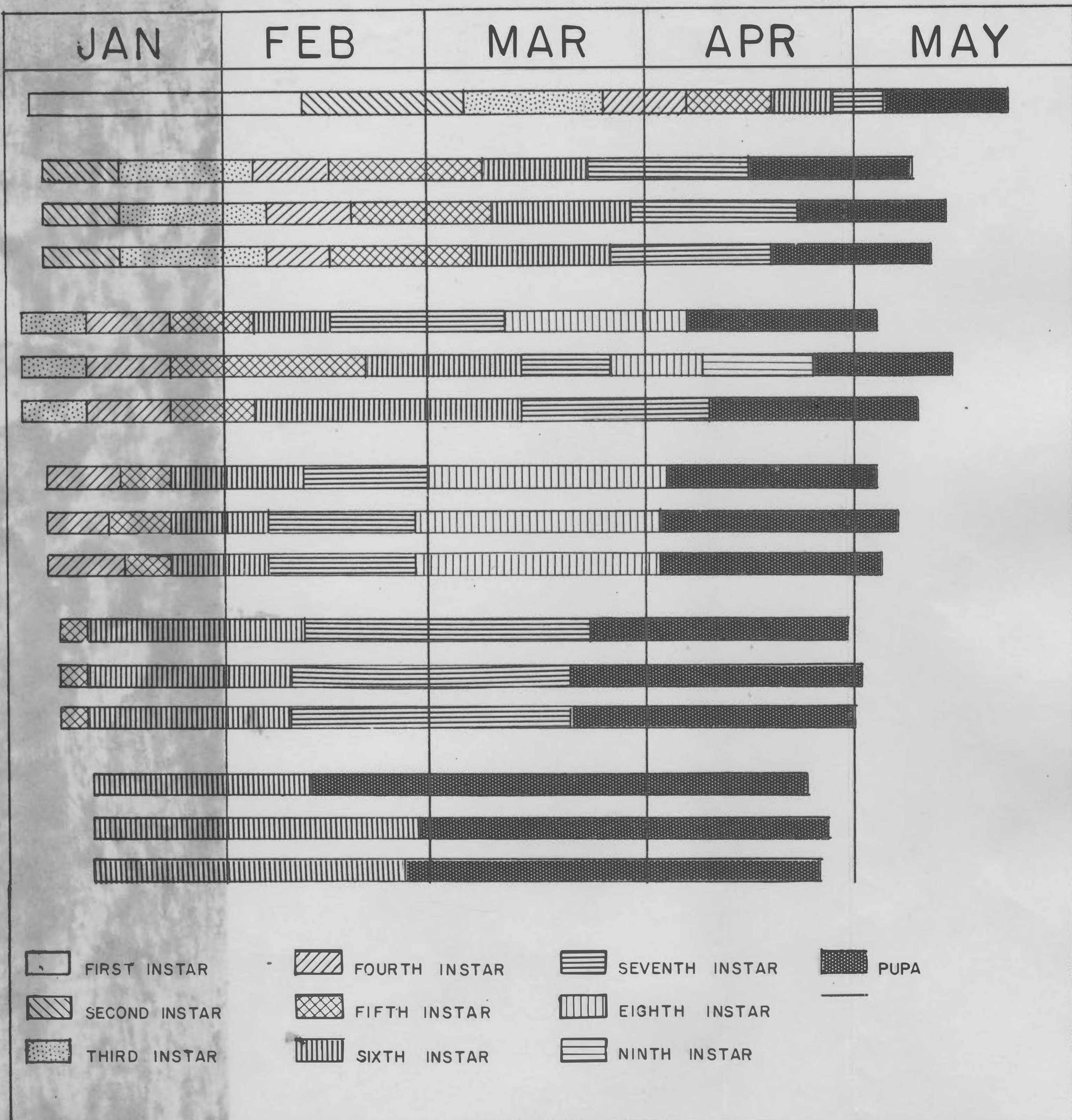


Figure 19. Graph showing the winter development records of the various larval instars of *Pseudaletia unipuncta*.

NATURAL ENEMIES OF THE ARMYWORM

Armyworms are almost never damaging in the same locality in two successive generations. Under pressing hunger, the species exhibits a gregarious habit, and instead of dispersing separately, the larvae move together in a definite direction, exposing themselves to wholesale destruction by parasites, predators, and infectious diseases. Thus the population is reduced sometimes beyond recovery during the outbreak generation.

During this study, extensive rearings of field-collected armyworms were made in an effort to determine the natural enemy complex and its effect upon the species. In addition to rearings, observations of those parasites present were made in the field during outbreak periods. Predators were not seriously studied except for occasional collections of predatory insects when they were conspicuously present. For this reason, information on predators in this section is taken largely from the literature.

Parasites

Thompson (1945) edited a catalogue of the parasites and predators of insect pests which had been recorded in the literature at that time. The parasites, but not the predators, of *Pseudaletia unipuncta* are included. This list is reproduced here and is arranged according to the families of the parasites. The reader is referred to the citation for authorities of the entries. Those species which have been reared from the armyworm by the writer are denoted with an asterisk (*).

Diptera: Tachinidae

*Achaetoneura aletiae Riley - U. S. A.

*Achaetoneura archippivora Will. - Hawaii

Actia nigritula Mall. - Australia

Archytas analis F. - U. S. A.

Archytas piliventris Wulp - U. S. A.

*Belvosia unifasciata R. -D. - Canada, U. S. A.

Carcelia kockiana Tns. - Siam

Chaetogaedia monticola Big. - Hawaii

Compsilura concinnata Mg. - U. S. A.

Compsilura concinnata sumatrensis Tns. - Australia

Cuphocera pilosa Mall. - Australia

Cuphocera varia F. - Australia

Exorista civiloides Bar. - Siam

Gaediogonia jacobsoni Tns. - Siam

Linnaemyia nigripalpus Tryon - Australia

Nemorilla anomala Vill. - Siam

Peletieria robusta Wd. - U. S. A.

Phorocera claripennis Macq. - Canada, U. S. A.

Phorocera leucaniae Coq. - U. S. A.

Phryxe vulgaris Fall. - Canada, U. S. A.

Plagiomima spinosula Big. - U. S. A.

Prosopaea paradoxa B. B. - Siam

Sturmia albifrons Walk. - Canada

Sturmia inconspicua Mg. - Fiji

Sturmia inconspicuoides Bar. - Australia

Tritaxys heterocera Macq. - Australia

Wagneria carbonaria Panz. - U. S. A.

Wagneria sequax Will. - Canada

Winthemia quadripustulata F. - N. America

**Winthemia rufopicta* Big. - U. S. A.

Hymenoptera: Braconidae

Apanteles sp. - Fiji, Canada, U. S. A., Australia

Apanteles belliger Wilkn. - Mauritius

Apanteles flaviconchae Riley - U. S. A.

Apanteles forbesi Vier. - U. S. A.

Apanteles laeviceps Ashm. - N. America

Apanteles limenitidis Riley - Canada

Apanteles marginiventris Cress. - U. S. A.

**Apanteles militaris* Walsh - Argentina, N. America

Apanteles ruficrus Hal. - China, Australia

Apanteles rufocoxalis Riley - N. America

**Meteorus autographae* Mues. - U. S. A.

Meteorus communis Cress. - Canada, U. S. A.

Meteorus laphygmae Vier. - U. S. A.

Microplitis melianae Vier. - N. America

Microplitis varicolor Vier. - N. America

Rogas atricornis Cress. - U. S. A.

**Rogas terminalis* Cress. - U. S. A.

Hymenoptera: Ichneumonidae

Amblyteles brevipennis Cress. - U. S. A.

*Enicospilus sp. - Australia

Enicospilus purgatus Say - Canada, U. S. A.

Enicospilus skeltoni Kirby - Australia

Exephanes leucaniae Tryon - Australia

Hyposoter exiguae Vier. - Hawaii

Ichneumon brevipennis Cress. - U. S. A.

Ichneumon jucundus Br. - Canada

Ichneumon koebelei Sw. - Hawaii

Ichneumon laetus Brulle - Canada

Ichneumon leucaniae Fitch - Canada

Lissopimpla semipunctata Kirby - New Zealand

Melanichneumon leucaniae Uch. - Japan

Mesochorus vitreus Walsh - Canada

Mesostenus albopictus Smith - New Zealand

Paniscus sp. - Australia

Paniscus geminatus Say - Canada

Paniscus productus Brulle - Australia

Pimpla pedalis Cress. - N. America

Theronia rufipes Tryon - Australia

Hymenoptera: Eulophidae

*Euplectrus platyhypenae How. - Hawaii

Hymenoptera: Eurytomidae

Eurytoma striatifacies Gir. - Australia

Hymenoptera: Pteromalidae

Eupteromalus sp. - Canada

Hymenoptera: Scelionidae

Telenomus sp. - U. S. A.

The effect of parasitism on a population of armyworms may be shown by an observation made in a heavily infested nine-acre field of wheat by the author in Monroe County, Tennessee, June 1, 1956. On this day, armyworms were at their peak and pupation had already begun. The field of wheat had virtually been destroyed and the armyworms had begun their march toward a field of oats. The writer with the help of Mr. Ray Stamey, Monroe County Agricultural Agent, pulled up six clusters of wheat stubble and made counts of organisms under each. The results are given in table 26. Assuming an average of two fly puparia to represent one armyworm, only 39 of 87 original armyworms would reach maturity in this sample. This would be a conservative estimate, since the pupae were not necessarily free of parasites and certainly not free of predatory attack.

More than one thousand armyworms from twenty-five field collections over a two-season period (1956-57) were individually reared by the writer and parasite data recorded (see tables 27 through 30). During 1956, 184 of 569 armyworms were parasitized (table 27), and in 1957, 199 of 479 showed parasitism (table 29). Populations for the two seasons were 32.3 and 41.5 per cent parasitized respectively (tables 27 and 29). A total of sixteen species of parasites were reared

TABLE XXVI

SUMMARY OF PARASITE CONDITIONS ASSOCIATED WITH SIX CLUSTERS OF WHEAT STUBBLE IN AN ARMYWORM INFESTED FIELD MONROE COUNTY, TENNESSEE, JUNE 1, 1956

Cluster Number	Armyworm Pupae	Masses of *Apanteles* Cocoons	Parasitized Armyworms (Tachinid Eggs)	Tachinid Puparia	*Enicospilus* Cocoons
1	5	3	2	4	0
2	9	5	0	7	0
3	4	2	3	3	1
4	10	1	1	8	0
5	3	6	0	6	3
6	8	3	1	6	0
Total	39	20	7	34	4

TABLE XXVII

SUMMARY OF EXTENT OF PARASITISM IN ELEVEN GROUPS OF FIELD-COLLECTED ARMYWORMS, *Pseudaletia unipuncta*, 1956

Collection Number	Date	Location	Number of Host Specimens	Number Parasitized	Percent Parasitized
508	May 21	Monroe Co., Tenn.	18	3	16.7
509	May 21	Monroe Co., Tenn.	296	95	32.1
510	May 22	Blount Co., Tenn.	28	6	21.4
511	May 30	Blount Co., Tenn.	31	11	35.4
512	May 30	Blount Co., Tenn.	29	18	62.3
513	June 1	Monroe Co., Tenn.	24	10	41.7
514	June 1	Monroe Co., Tenn.	21	8	38.2
515	June 1	Monroe Co., Tenn.	29	9	31.0
516	June 1	Monroe Co., Tenn.	24	3	12.6
521	July 20	Hablen Co., Tenn.	6	4	66.6
526 *	Aug. 9	Lincoln, Nebraska	63	17	27.0
Total, All Collections			569	184	32.3

* Collection sent to writer by L. W. Anderson, University of Nebraska.

TABLE XXVIII

RELATIVE NUMBERS AND PERCENTAGES OF PARASITES REARED FROM THE ARMYWORM DURING 1956

Species	Number of Armyworms Parasitized by	Per Cent of Total
Diptera:		
Larvaevoridae		
Undetermined Larvaevoridae	56	30.44
Winthemia rufopicta	22	11.96
Archytas apicifer	7	3.80
Achaetoneura aletia	3	1.63
Wagneria laevigata	3	1.63
Belvosia unifasciata	2	1.09
Achaetoneura archippivora	1	.54
Blepharigena cineria	1	.54
Encelatoria rubentis	1	.54
Total Larvaevoridae	96	52.17
Total Diptera	96	52.17
Hymenoptera:		
Braconidae		
Apanteles militaris*	50	27.17
Rogas terminalis	10	5.44
Meteorus autographae	6	3.26
Total Braconidae	66	35.87
Eulophidae		
Euplectrus plathypenae	4	2.18
Total Eulophidae	4	2.18
Ichneumonidae		
Enicospilus sp.	17	9.24
Campoletis oxylus	1	.54
Total Ichneumonidae	18	9.78
Total Hymenoptera	88	47.83
Total Diptera and Hymenoptera	184	100.00

*Two groups of Apanteles militaris were parasitized by the hyper-parasite, Mesochorus discitergus.

TABLE XXIX

SUMMARY OF EXTENT OF PARASITISM IN FOURTEEN GROUPS OF FIELD COLLECTED ARMYWORMS, *Pseudaletia unipuncta*, 1957

Collection No.	Date	Location	Number of Host Larvae	Number Parasitized	Per Cent Parasitized
581	May 3	Blount Co., Tenn.	28	12	42.9
582	May 3	Lincoln Co.	30	9	30.0
583*	May 3	Lincoln-Franklin Co.	100	60	60.0
584	May 6	Monroe Co.	22	15	68.2
585	May 6	Monroe Co.	45	27	60.0
586	May 6	Monroe Co.	27	7	26.0
587	May 9	Monroe Co.	20	5	25.0
589	May 9	Monroe Co.	14	6	42.9
590	May 7	Rutherford Co.	35	19	54.3
591	May 16	Blount Co.	25	6	24.0
592	May 17	Monroe Co.	25	14	56.0
593*	May 21	Monroe Co.	38	5	13.2
594*	May 21	Monroe Co.	30	8	26.7
595	May 21	Monroe Co.	40	6	15.0
Total of All Collections			479	199	41.5

* Collections 100 per cent infected with a virus disease. Parasites listed emerged before the virus produced death of the host. All non-parasitized armyworms in these collections died from the virus as mature larvae.

TABLE XXX

RELATIVE NUMBERS AND PERCENTAGES OF PARASITES
REARED FROM THE ARMYWORM DURING 1957

Species	Number of Armyworms Parasitized by	Per Cent of Total
Diptera:		
Larvaevoridae		
Undetermined Larvaevoridae	11	5.6
Winthemia rufopicta	3	1.5
Archytas apicifer	2	1.0
Total Larvaevoridae	16	8.1
Total Diptera	16	8.1
Hymenoptera:		
Braconidae		
Apanteles militaris	72	36.1
Rogas terminalis*	45	22.6
Meteorus autographae	11	5.6
Rogas aciculatus	1	0.5
Total Braconidae	129	64.8
Ichneumonidae		
Hyposoter sp.	39	19.6
Enicospilus sp.	9	4.5
Campoletes sp.	6	3.0
Total Ichneumonidae	54	27.1
Total Hymenoptera	183	91.9
Total Diptera and Hymenoptera	199	100.0

* One specimen of Rogas terminalis was parasitized by the hyperparasite, Mesochorus sp.

(see tables 28 and 30), eight of which were dipterous and a like number hymenopterous. The two orders were nearly equally represented in 1956, 52.17 per cent of all parasites being Diptera and 47.83 per cent Hymenoptera (table 28); however, in 1957 hymenopterous parasites made up nearly 92 per cent of the total (table 30). Flies were numerous in the field during 1957, and many eggs were seen on larvae of the armyworm; but a virus disease took a heavy toll of the "worms," and the earlier development of the hymenopterous parasites, before the worms died of disease, undoubtedly accounted for this great difference, since the flies had insufficient time to develop.

The braconid, *Apanteles militaris* Walsh, was the predominant species among the hymenopterous insects, accounting for 27 per cent of all parasitism in 1956 and 36 per cent in 1957. Among the flies, *Winthemia rufopicta* Big., a larvaevorid (Tachinidae), dominated with 12 per cent of the total 1956 parasites, and was heavily represented among armyworm populations in 1957, though records indicated only 7.1 per cent. The low percentage of Diptera in 1957 was undoubtedly due to the early death of armyworm hosts from a virus infection.

A discussion of each parasite reared from the armyworm by the writer follows.

Hymenoptera: Braconidae

Apanteles militaris Walsh. Of all the parasites of *P. unipuncta*, the most effective, as previously stated, is *Apanteles militaris* Walsh (figures 20, 21, and 22), which was reared from 11.7 per cent of all

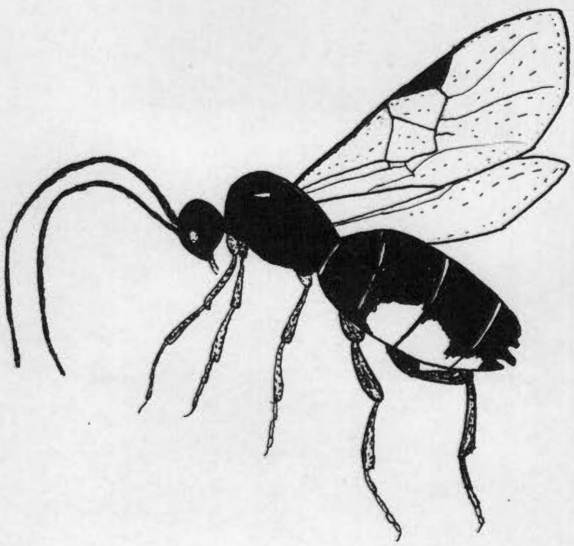


Figure 20. Apanteles militaris, an important parasite of the armyworm. Greatly enlarged. Drawing by S. Marcovitch.

Figure 21. Larvae of Apanteles militaris emerging from an armyworm host. Slightly enlarged.

Figure 22. Cocoons of Apanteles militaris. Natural size.

armyworms collected over a two-season period and which accounted for approximately 32 per cent of total parasites reared from the armyworm during the same period.

Tower (1916) states that armyworms parasitized by A. militaris eat approximately half as much as do non-parasitized larvae during the same period, and that it seems conclusive that parasitism by this species is beneficial in the generation attacked. The parasite ultimately kills its host, thereby being beneficial also in preventing many worms from maturing and beginning a new generation.

Armyworms parasitized by A. militaris show no signs of their plight until nearly mature when they become sluggish, and death comes only after the parasite larvae have emerged and spun their cocoons. Emergence of the A. militaris larvae from the armyworm host takes place with all larvae coming out at essentially the same time (figure 21). Cocoon spinning begins immediately after emergence from the host and is completed within a few hours time. The parasites emerge in large numbers from full grown or nearly full grown armyworms and spin white silken cocoons in a mass side by side. The cocoons average about 3.0 mm. in length and 1.3 mm. in width. Figure 22 shows a typical mass of cocoons. The number of cocoons spun from each of 49 armyworm larvae during 1956 ranged from 6 to 101 and averaged 49.

In the presence of adults of A. militaris, armyworms exhibit a nervous behavior. The female parasite attacks the armyworm almost immediately upon contact, and is capable of depositing several scores of eggs with one quick thrust of the ovipositor in any available part

of the armyworm host. The whole act of oviposition is a matter of seconds. The victim turns upon being attacked and spits, sometimes drowning the assailant in a large bubble of dark green fluid. The writer has observed a large armyworm destroy an adult _Apanteles_ in flight. The female parasite will attack any size armyworm, but the third and fourth stages seem to be the most vulnerable to their attacks in so far as success of the parasite is concerned. Extremely small armyworms are killed by the initial attack, and larger larvae being tough skinned, are more resistant, as well as too near maturity to allow time for _Apanteles_ development.

In the early summer of 1957, four generations of _A. militaris_ were reared by the writer. These rearings show that the time from oviposition to cocoon spinning ranges from ten to twenty-one days and averages thirteen days, and adults issue in from four to six days, for an average of five days after cocoon spinning for a total development time averaging eighteen days. These records are given in table 31.

That _A. militaris_ is capable of overwintering in the larva of the armyworm is evidenced by two such occurrences during the winter of 1957. Two armyworms from a batch of larvae collected on January 9, 1957, near Dandridge, Tennessee, were parasitized by _A. militaris_. One of these armyworms, collected as a sixth instar larva, died February 20, 1957, and dissection yielded sixty-eight living larvae of _A. militaris_. The other specimen was collected as a fourth instar larva, moulted twice during the winter, and yielded seven _A. militaris_ larvae which successfully

TABLE XXXI

DURATION OF LARVAL AND COCOON STAGES IN FOUR GENERATIONS OF *Apanteles militaris* DURING THE SUMMER OF 1957

Date of			Duration in Days	
Oviposition	Cocoons	Adults	Larvae	Pupae
May 14	June 4	June 8	21	4
June 8	June 18	June 24	10	6
June 24	July 5	July 10	11	5
July 10	July 21	July 26	11	5
Average of Four			13.2	5.0

spun cocoons on April 1, 1957. Thus, in this latter specimen, the parasitic larvae lived for a minimum of two and one-half months. The host worm died on April 6, 1957, six days after emergence of the parasitic larvae.

The biology of A. militaris has been studied and reported on by Tower (1916).

Meteorus autographae Mues. This parasite was reared from six armyworm specimens in 1956 and from eleven specimens in 1957, thereby accounting for 3.2 per cent and 5.6 per cent of all reared parasites for those two seasons respectively. The species has been collected only during the month of May in Tennessee, but was reared from an August collection of Nebraska worms sent to the writer by L. W. Anderson of the University of Nebraska.

The female of M. autographae apparently oviposits in the early larval stages of the armyworm and the solitary larva of the parasite emerges from the armyworm in the fifth instar. The larva of the parasite spins a golden-brown, oval cocoon about 5 mm. in length and 1.7 mm. broad, which is attached to the host plant or other object by a silken thread. Rearing records of four specimens show that the cocoon stage lasts from three to eleven days.

The adult and cocoon of this species is shown in figure 23.

Rogas terminalis Cress. This parasite represented 5.4 per cent of all parasites reared during the 1956 season and 22.6 per cent during the 1957 season. According to Pennington (1916), the parasite copulates immediately upon emergence with oviposition following rapidly.

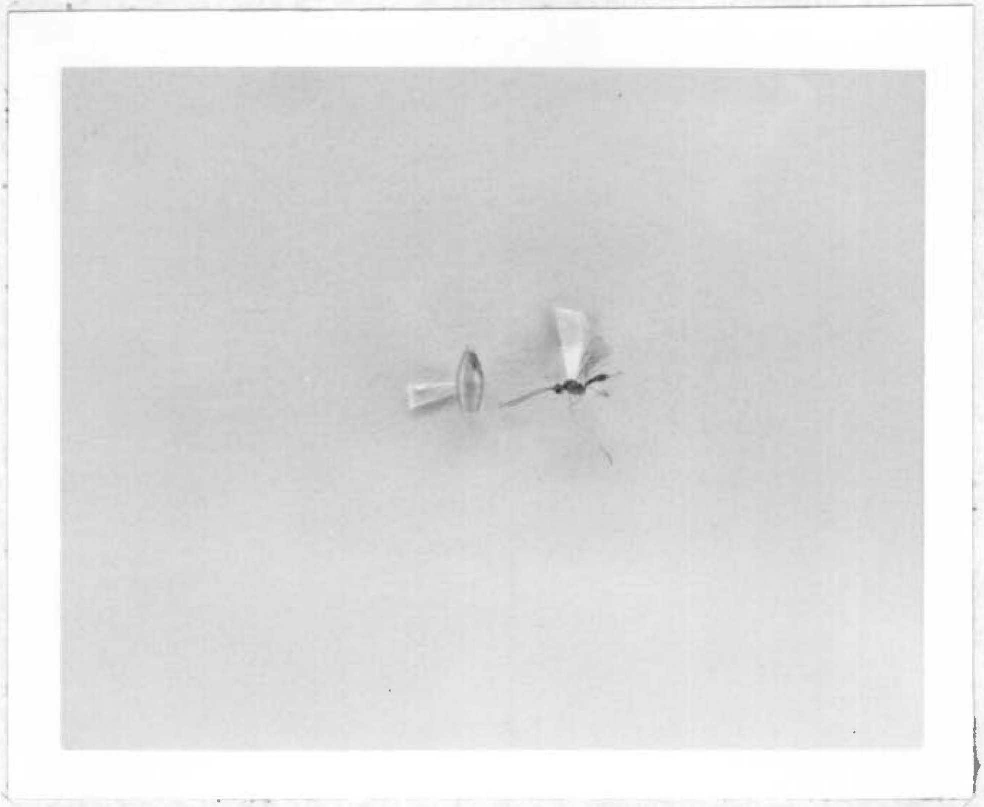


Figure 23. Cocoon and adult of Meteorus autographae. About twice natural size.

The white egg is elongate oval with the sides nearly parallel and measures .18 mm. in length and .09 mm. in diameter. Apparently only one egg is deposited. The cocoon of the species (figure 24) is made of the transformed and reinforced larval skin of the host. The shape is fusiform with the ventral surface flattened and affixed to the object on which it rests by a black exudation. The surface of the cocoon is turgid, almost obliterating the segmentation of the host larval skin, and is deep reddish-brown to black. The length measures from 9 to 10 mm. and the width about 3 mm. The adult parasite emerges by gnawing an irregular hole caudad in the dorsum of the host skin.

Records of twenty reared specimens show that the length of time spent in the cocoon ranges from six to fourteen days and averages ten days. Pennington (1916) states that the parasite hibernates in the pupal stage.

The adult and cocoon of R. terminalis are shown in figure 24.

Rogas aciculatus Cress. This species was reared from only one host armyworm captured May 16, 1957, in Blount County, Tennessee. It forms a cocoon similar to that of R. terminalis but somewhat smaller and a lighter brown color. The specimen formed its cocoon on May 30, 1957, and the adult parasite issued on June 3, 1957, after a total of fourteen days in the pupal stage.

Hymenoptera: Ichneumonidae

Enicospilus sp. A total of twenty-six specimens of a large ichneumonid parasite was reared during the two-year course of this study. The specimens were identified by the U. S. National Museum personnel as

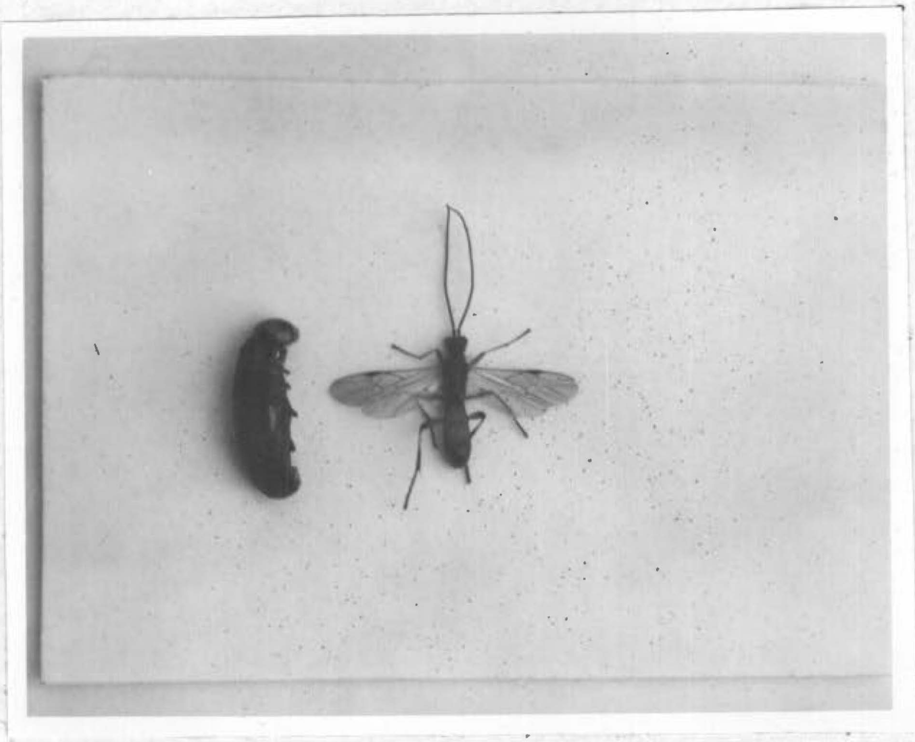


Figure 24. Cocoon and adult of <u>Rogas terminalis</u>. About twice natural size.

Enicospilus sp. Members of this genus are noted as being parasitic on larvae of the family Noctuidae. During 1956, Enicospilus parasites were reared from seventeen specimens, accounting for 9.24 per cent of all parasites, and in 1957 they were reared from nine specimens representing 4.5 per cent of all parasites.

This parasite was observed always to kill the armyworm host in the sixth instar. The parasitic larva, upon emergence from the host, spins a large golden to dark brown cocoon measuring about 10.0 mm. in length and 5.0 mm. in width. The duration of the cocoon stage in two specimens successfully reared to adult was eight and seventeen days respectively during June of 1956. The parasite apparently undergoes one and at the most two generations per year.

Campoletis oxylus (Cress.). This parasite was reared from only seven specimens of the armyworm, one in 1956 and six in 1957. The cocoon is of a medium brown color and measures 6.5 mm. in length and 2.5 mm. in width. No biological data were obtained on the species.

The adult and cocoon are shown in figure 25.

Hyposoter sp. This species was not recovered in 1956, but was one of the more abundant ones during 1957 when it accounted for 19.6 per cent of all parasites reared. It was found throughout the month of May in nearly all fields examined. The solitary larva emerges from the armyworm host and spins a white cocoon with an irregular black band at either end. The cocoon measures 6.0 mm. in length and 2.5 mm. in width. The adult issues from the cocoon in from three to fourteen days. The cocoon and adult are pictured in figure 26.

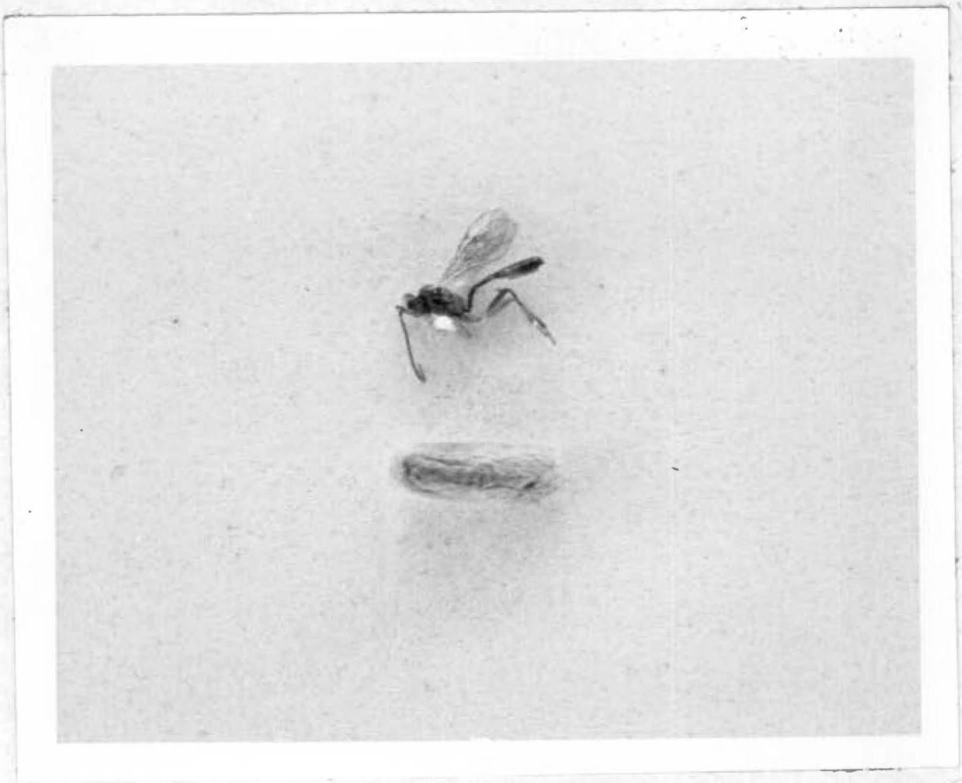


Figure 25. Cocoon and adult of Campoletis oxylus. About three times natural size.

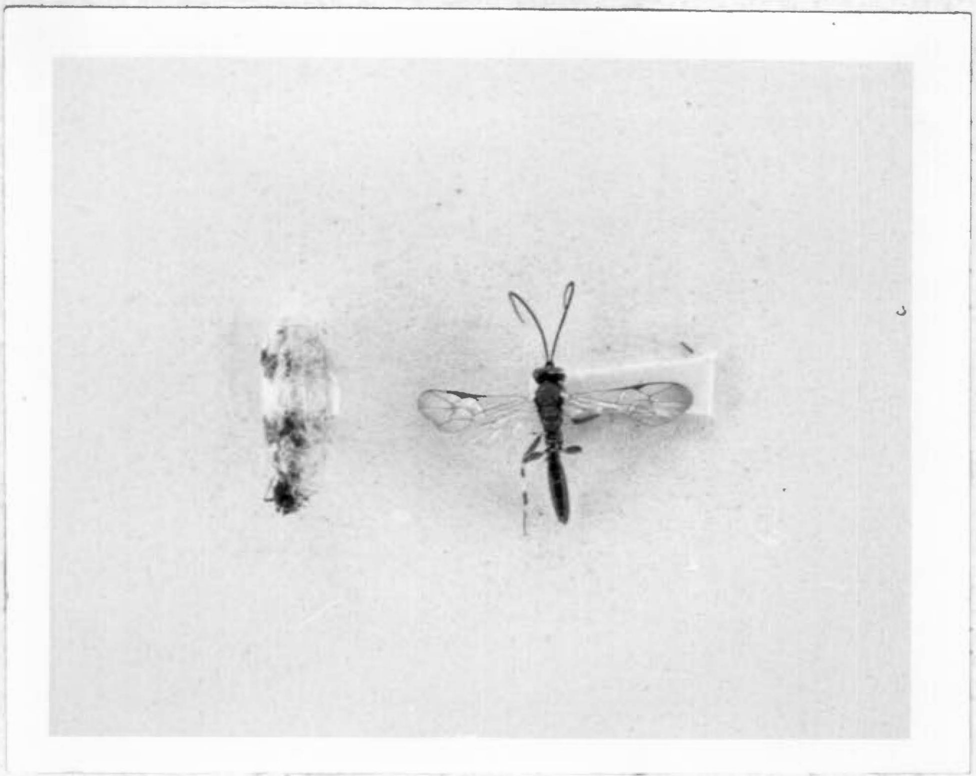


Figure 26. Cocoon and adult of <u>Hyposoter</u> sp. About three times natural size.

Hymenoptera: Eulophidae

Euplectrus plathypenae Howard. This parasite was reared from four armyworms collected July 20, 1956, from Hamblen County, Tennessee. A total of seven females and five males was reared from the four armyworms. One of the parasites was collected in the egg stage. The eggs hatched in three days. The larval developmental time was three days and the pupal period was nine days for a total developmental time of fifteen days. The larvae of this species feed in a cluster externally on the host worm. They finally destroy the host and spin their cocoons in a row under the outstreatched skin of the dead host.

Diptera: Larvaevoridae (Tachinidae)

Tachinid flies have always played a large role in the parasitic destruction of armyworms during outbreaks. A brief review of the literature will serve to establish their importance. Riley (1883) states that "the worms never abound or travel from one field to another but they are accompanied by a number of two-winged flies, which are often so numerous that their buzzing reminds one of that of a swarm of bees." Howard (1896) says "hundreds and thousands of these flies (tachinid flies) are usually seen buzzing about a field infested by the armyworm." The same author is quoted below.

> In 1880 we visited a large tract of land planted in timothy grass in the vicinity of Portsmouth, Virginia. A search for hours during the hot part of the day failed to show a single worm which did not bear tachinid eggs.

Knight (1916) stated that two species of parasitic flies, *Winthemia quadripustulata* Kabr. and *Goniomima unifasciata* Desv.

parasitized from 50 to 60 per cent of the worms in certain fields in New York during 1914.

Shermon (1915) working in North Carolina, collected 534 armyworms with a total of 1,313 parasite eggs. A total of only 18 adult armyworm moths was obtained from this group and 296 parasitic flies were reared.

The writer has observed the buzzing flight of these parasitic flies on two occasions on the farm of Tinsley Allen in Monroe County, Tennessee, on May 21, 1956, and May 17, 1957. On the former date, hundreds of armyworms were examined, practically all of which had tachinid eggs.

During 1956, 52.17 per cent of all parasites reared from 569 field-collected armyworms was parasitized by flies of this family. During 1957 accurate records could not be obtained since rearings were made difficult by the presence of a virus disease among field-collected specimens.

It is unfortunate that tachinid parasites do not attack the host until the latter is nearly mature and thus has accomplished its most destructive work. In spite of this fact, these parasites of the armyworm function efficiently by destroying large numbers of a given generation of larvae and thus greatly reduce succeeding generations.

Winthemia rufopicta Big. (figure 27). The most important of eight tachinid fly species reared during the two-season study of the writer was *Winthemia rufopicta* Big. This species is discussed in detail, but other species were so infrequent that only brief notes are given. This fly oviposits on larvae of the fifth and sixth instars.

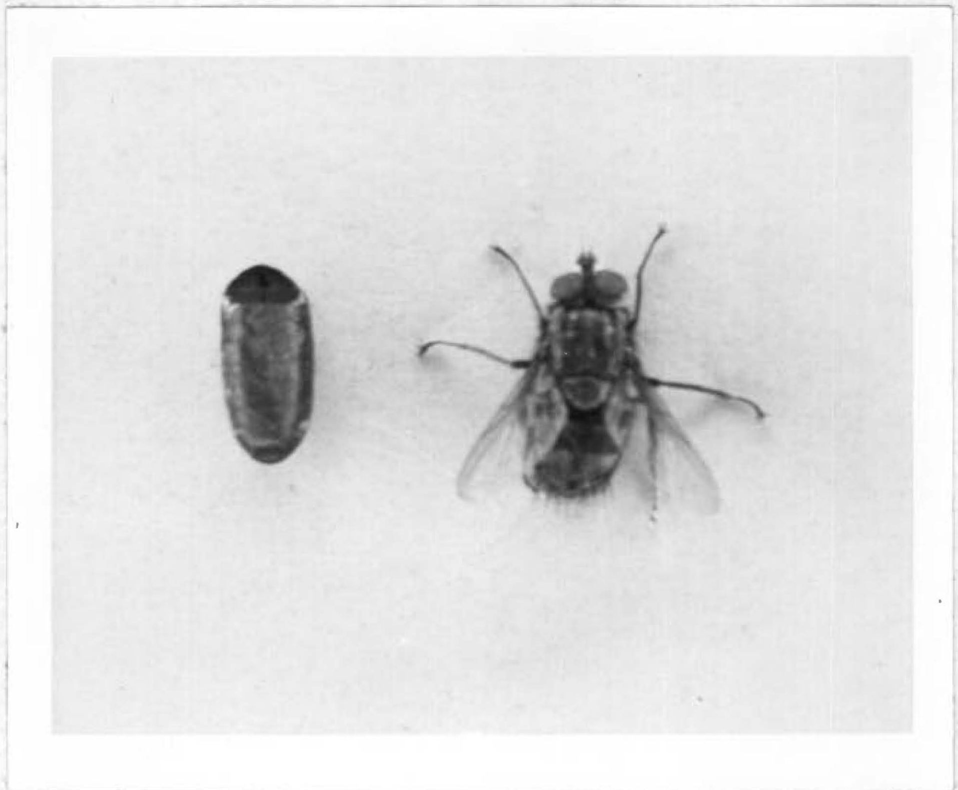


Figure 27. Puparium and adult of Winthemia rufopicta, an important parasite of the armyworm. About four times natural size.

Eggs are attached tightly to the dorsum of the thoracic segments of the host. The number of eggs placed on one larva is usually two or three; however, the writer on one occasion found thirteen eggs on one individual.

The egg hatches almost immediately upon deposition. The tachinid larva emerges from the side of the egg next to the worm, and bores directly through the body wall of the host. The victim is active during most of the time the maggot is feeding, but dies before the parasite emerges. Usually more than one fly larva develops in the host armyworm. The number of fly puparia of this species obtained from twenty-one host armyworms ranged from one to nine and averaged 2.3 per host. Figure 28 shows developing larvae of this species in a dead armyworm host.

It is interesting that this fly always deposits eggs on nearly mature larvae. If the eggs were placed on young larvae, there would be a chance of the eggs being eliminated with the exuvium before they had a chance to hatch.

A review of table 26 will show the effectiveness of tachinid flies in the control of an armyworm population.

Archytas apicifer Wlk. This species was reared from seven armyworm specimens during the 1956 season and from two during the 1957 season. In all cases, the host armyworm completed development to the pupal stage and the adult parasite emerged. A normal puparium is formed inside the host pupa, and only one parasite develops per armyworm. The only accurate records obtained by the writer on the duration of development of this species are those from pupation of the armyworm to the emergence of the parasitic fly. This varied from eighteen to twenty-two

Figure 28. Larvae of Winthemia rufopicta emerging from host armyworm. Note white egg shells of the fly attached to the armyworm skin just posterior to the head. Slightly enlarged.

days for six specimens between August 13 and September 4, 1956. This fly is illustrated in figure 29.

Other Larvaevoridae (Tachinidae). Aside from Winthemia rufopicta and Archytas apicifer, tachinid flies were scarce in number, though six other species were reared from the armyworm by the writer, all during the 1956 season. Three specimens each of Achaetoneura aletia (Riley) and Wagneria laevigata (Wulp) were reared. The former species was reared in May and June from a Monroe County, Tennessee, collection and the latter during the same months from a Blount County, Tennessee, collection.

Two of the three specimens of A. aletia emerged from the armyworm pupa, while the other formed a puparium after the mature armyworm larva had died. The duration of the pupal stage of the other specimen of A. aletia observed was eight days, that is, from May 31, 1956, to June 8, 1956.

All specimens of W. laevigata formed puparia after the host armyworms had died, two in the sixth instar and one in the fifth. Eight adult flies were obtained from the three armyworm specimens. The pupal periods of the flies ranged from five to nine days.

Two specimens of the tachinid parasite, Belvosia unifasciata R. D., both from Monroe County, Tennessee, from armyworm pupae were reared during June of 1956, and in each case ten days elapsed between pupation of the armyworm host and emergence of the adult fly.

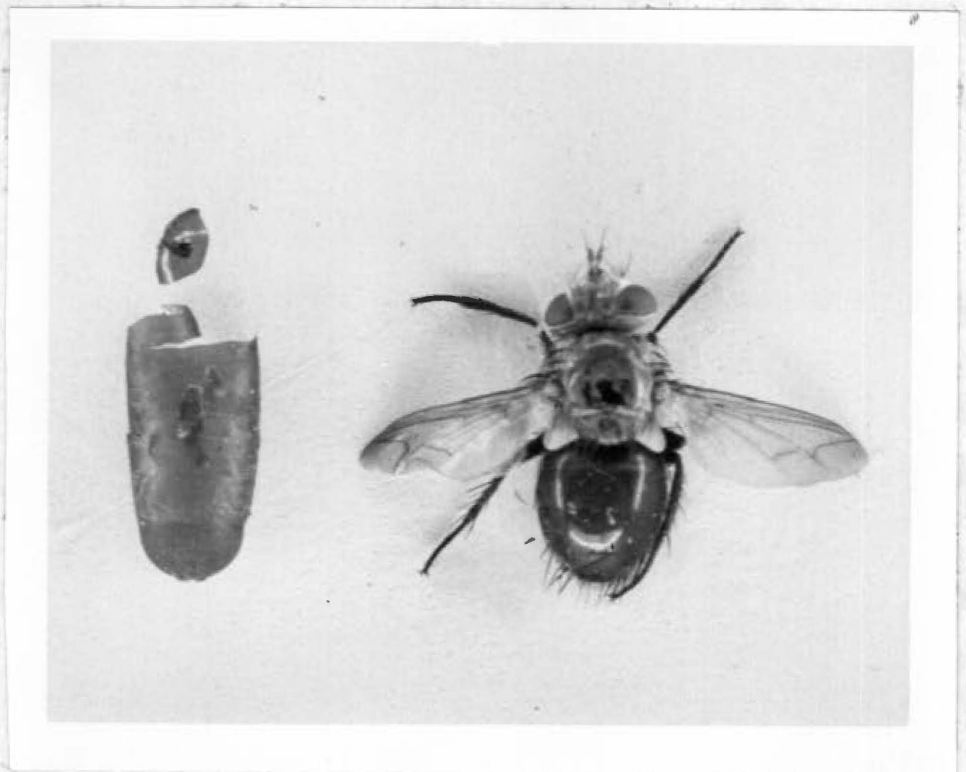


Figure 29. Puparium and adult of Archytas apicifer. Greatly enlarged.

The parasite, Achaetoneura archippivora Will. was reared from one armyworm sent to the writer by L. W. Anderson, of the University of Nebraska, from a Lincoln, Nebraska, collection. The host armyworm was isolated on August 9, 1956, and pupated on August 16, 1956. On August 21, 1956, the puparium was formed and on September 9, 1956, the adult emerged.

One specimen of Encelatoria rubentis (Coq.) was reared from an armyworm collected May 30, 1956, in Blount County, Tennessee. No biological records were obtained on this species.

Blepharigena cinerea (Coq.) was reared from a specimen from L. W. Anderson, Lincoln, Nebraska. The armyworm was isolated, in its sixth instar, on August 9, 1956. On August 13, 1956, the puparium was formed and on August 29, 1956, the fly emerged.

Predacious Enemies

The writer made no special study of armyworm predators. However, two species of carabid beetles, Calosoma calidum and C. scrutator were consistently found in relatively large numbers in fields moderately to heavily infested with armyworms.

Since predaceous animals form a large segment of the natural enemy complex of the armyworm, the writer has reviewed the literature and compiled pertinent information on known predators of the insect. This information is presented below according to the various animal groups to which the predators belong.

Insects

Coleoptera. Always in fields heavily infested with the armyworm, a large number of predaceous beetles gather and feed extensively upon the worms. Riley (1883) lists fourteen species, namely: Cicindela repanda Dej., Elaphrus ruscarius Say, Calosoma extermum Say, C. scrutator (Fabr.), C. calidum (Fabr.), C. wilcoxi Lec., Pasimachus elongatus Lec., Amara angustata Say, Harpalus caliginosus (Fabr.), H. pennsylvanicus (Dej.), Pterostichus sculptus Lec., Anisodactylus rusticus Dej., Cratacanthus dubius (Beauv.), and Selenophorus pedicularius (Dej.).

Tryon (1921) lists Calosoma australis as a predator in Queensland.

Knight (1916) reports Calosoma calidum as the most conspicuous predaceous beetle in the New York outbreak of 1914, other beetles of importance in this outbreak being Pterostichus lucublandus Say, Harpalus calignosus Fabr., and H. pennsylvanicus (Dej.).

King and Barber (1921) reports that Calosoma chinense Kirby destroyed large numbers of first generation armyworm larvae in a Russian outbreak of 1926.

Annand (1947) reports that Calosoma argentinense Csiki was introduced from Argentina against P. unipuncta in Florida.

Engel'hardt (1929) reports that Calosoma chinense Kirby destroyed large numbers of first generation armyworm larvae in a Russian outbreak of 1926.

Hemiptera. Riley (1883) lists the thick-thighed Metopodius femorata (Fabr.), a large true bug, common in the South as a predaceous enemy of the armyworm.

Luginbill (1928) states that the bug, Apateticus maculiventris Say, probably ranks next to Calosoma beetles as a predatory enemy of the fall armyworm, Laphygma frugiperda, that it is a common enemy of other lepidopterous insects and is considered to be the most useful of our predaceous Hemiptera.

Hu and Tse (1936) list the following pentatomids as predaceous enemies of the armyworm in China: Andrallus spinidens F., Nezara viridula var. torquata F., Menida histrio F., Piezodorus hybneri Gmel. (rubrofasciatus F.), and Scotinophora lurida, Burm. These same authors list the coreid, Cletus punctiger Dall.

Amphibians

Toads are mentioned by several authors as destroying large numbers of armyworm larvae (Gibson, 1915; Severin, 1920; King and Barber, 1921; Bell, 1936; Lever, 1939). According to Bell (1936) the toad, Bufo marinus, was introduced from Hawaii into Queensland, successfully bred in confinement, and liberated for armyworm control. Lever (1939) states that the same species of toad was greatly responsible for reducing an armyworm population in Fiji.

Birds

Riley (1883) states that all of the insectivorous birds feed upon the "worms." He says that the most prominent bird is the bobolink

(Dolichonx oryzivorus), which has been known to become so numerous in southern Illinois during armyworm years, that it has received the popular name of "armyworm bird." The same author mentions chickens and turkeys as important armyworm predators. King and Barber (1921) also give considerable credit to the bobolink, and Knight (1916) states that poultry were very useful for destroying armyworms in the 1914 New York outbreak. Knight reported that in one field turkeys destroyed the pests so fast that the armyworms had no chance to migrate to adjoining grain fields. Other birds listed in the literature as armyworm predators include: the robin, bluebird, blackbird, meadow lark, and pigeon woodpecker (Flagg and Field, 1896); the swallow, fly catcher, crow, catbird, thrush, sandpiper, screech owl, and sparrow hawk (Warren, 1896); the blue jay, golden-winged woodpecker, and chickadee (Soule, 1897); the starling (Kalmback and Gabrielson, 1921); the mynah bird, English sparrow, and the golden plover in Hawaii (Swezey, 1908); and the duck in China (Hu and Tse, 1936).

Of the birds listed, some are due special mention. Criddle (1914) states that crows are great destroyers of cutworms and armyworms, and Kalmbach (1918) says that noctuid larvae, including armyworms, are among the first items supplied to newly hatched young of the crow. Kalmbach and Gabrielson (1921) state that the starling has few equals among the bird population of the northeastern United States as an effective destroyer of terrestrial insects which compose 41.55 per cent of its food. They further state that Lepidoptera, chiefly cutworms, are attractive

to nestlings, forming 38.1 per cent of the food of young starlings. According to Swezey (1908) the mynah bird was introduced into Hawaii from India in the late nineteenth century to be used as predators against armyworms and cutworms. Swezey reports this bird to be one of the best checks against these insects in Hawaii.

Mammals

Hogs are reported by Riley (1883) to be important armyworm predators, sometimes to the extent that they die in consequence. The skunk is mentioned by several authors as being predaceous on the armyworm (Warren, 1896; Gibson, 1915; Severin, 1920; Lever, 1939).

Diseases

Virus Diseases

During the summer of 1956 the writer lost a considerable portion of his insectary colony of armyworms from a virus disease, but finally managed to bring the infection under control by dividing the colony into smaller units and applying strict cleanliness. In November of 1956, several hundred apparently healthy "worms" were released into an outdoor cage only to be completely wiped out by the disease within a three-day period. On May 3, 1957, Mr. W. W. Stanley, University of Tennessee Experiment Station Entomologist, brought a large collection of armyworms to the laboratory from Lincoln and Franklin counties, Tennessee, and reported that worms were numerous in that area. This collection was virtually 100 per cent infected with the same virus disease that had

been in laboratory colonies the previous year. On May 7, 1957, Mr. R. P. Mullett, University of Tennessee Extension Entomologist brought in a collection of armyworms from Rutherford County, Tennessee; this, too, proved to be nearly 100 per cent diseased. The author made collections throughout the month of May, 1957, in the east Tennessee area, and all collections were very heavily diseased.

In all of these cases, original observations showed an unusually large number of early season armyworms which were preceded by the highest moth catches at light traps for the first generation since the 1953 outbreak. Subsequent observations, a week or two later, in the same areas examined earlier by Mr. Stanley, Mr. Mullett, and the writer respectively, showed a tremendous decrease in the armyworm population, and no outbreak occurred in any area of the state. The author and his colleagues are convinced that the widespread presence of the virus was of great importance in the destruction of early season armyworm populations in Tennessee in 1957. The disease reappeared in colony worms and persistent care was necessary to prevent the destruction of the colony. It might be noted that the writer's predecessor, Mr. B. K. Dozier, also had a colony of armyworms completely wiped out by the disease in the summer of 1955. Therefore, the disease has been present for three continuous years in Tennessee, 1955-57.

During the 1957 season, the writer sent a container of several specimens showing the symptoms of the virus disease to the U. S. Department of Agriculture Insect Pathology Laboratory, Beltsville, Maryland,

for identification of the pathogen. This sample showed the presence of polyhedrosis virus. According to Dr. S. R. Dutky (in litt.) an excess of nine billion polyhedra was recovered from the specimens submitted for identification.

Terminal stages of the disease are characterized by liquefaction and disintegration of tissues. The symptoms are first apparent when the armyworm becomes listless and begins to discolor, a condition which is rapidly followed by the terminal one. Stages of the disease are shown in figure 30. Tests at the Beltsville laboratory, according to Dr. Dutky, show that the larvae are much more susceptible to infection in the first instar.

The disease was described by Chapman and Glaser (1915) from whose work I quote.

Clinical Picture

> The wilt is characterized by the formation in the bodies of infected caterpillars of polyhedral-shaped, highly refractive, angular bodies, which have their origin in the nuclei of the trachel matrix, hypodermal cells, fat cells and blood corpuscles. Later some of these burst and the polyhedra are set free in the blood. When death results they make up a great part of the saponified body tissues of the caterpillars. The caterpillars hang by their prolegs, become flaccid and their skin disrupts at the slightest touch. An examination immediately after death reveals few or no bacteria and no bad odor. The wilt appears in nature in both a chronic and an acute form. If, however, a dead caterpillar, on microscopic examination, shows no polyhedra it does not have wilt, even though all the gross symptoms may be present.

These authors report the disease from an armyworm outbreak in Long Island, Boston Harbor; Nantasket, Massachusetts; Hagerstown, Maryland; and Norfolk, Virginia. They also refer to the presence of the disease in North Carolina in 1914 and in Illinois and Oklahoma

Figure 30. Progressive symptoms of the polyhedral virus disease of the armyworm. Note the complete disintegration in specimen at the right.

during the same year. This was a prominent armyworm year in the United States.

Glaser and Chapman (1916) state that several forms of polyhedral disease can be distinguished, each characterized by a special type of polyhedra caused by a virus which disintegrates nuclear material of certain tissue cells in such a way that polyhedral bodies are synthesized from the disintegrating proteins. They further state that the polyhedra are therefore not living organisms which are responsible for the disease.

Tanada (1956) reports a virus epizootic which almost exterminated a localized population of the armyworm in Hawaii in 1954. The same author studied some factors that might affect the susceptibility of *P. unipuncta* to this virus and another, a granulosis virus, for which Tanada must be given credit for the first record from the armyworm (1955). In his 1956 paper, Tanada states that resistance of the armyworm to virus infections increased directly with the age of the larvae. The first and second instar larvae were highly susceptible to both viruses, whereas the last four instars were much more resistant. He also made the point that the two diseases, polyhedrosis and granulosis, had a synergystic relationship in his tests, resulting in increased virulence of the pathogens.

Aside from the polyhedrosis and granulosis diseases discussed above, another virus, *Morator nudus* Wasser was described from *P. unipuncta* by Wasser (1952). Wasser believes this to be the first demonstration of a noninclusion type virus which has been verified by means of infectivity tests.

Bacterial Diseases

Gibson (1915) states that large numbers of armyworms were destroyed by a bacterial disease in Ontario in 1914.

In the specimens sent to the U. S. Department of Agriculture, Beltsville, Maryland, by the writer for pathogen identification, three of the diseased specimens were negative for polyhedra but had a heavy bacterial count. It is assumed that these specimens had died from the bacterial infection.

Fungus Diseases

The writer has observed a fungus of the genus *Empusa* from a collection of armyworm larvae collected near Morristown, Tennessee, in August, 1956. The fungus, *Metarrhizium anisopliae* (Metsch) was reported from *P. unipuncta* by Williams (1931) and Walkden (1950).

DISCUSSION

Outbreaks of the armyworm are the cause of heavy financial losses to our agriculture, and any practical means that can be devised to prevent their occurrence warrants investigation. Lack of good chemical control measures against the species is not the problem, since several insecticides now on the market give excellent control once an outbreak is discovered. The crux of the armyworm outbreak problem is the element of surprise. A potential outbreak population goes unnoticed since the individuals remain concealed by day and do little feeding until the final larval instar when they begin to feed voraciously as an army of "worms". One can imagine the consequences of a lack of vigilance during the critical "maturing" period of a field of these "worms". If a field harboring a large population of armyworms goes unobserved for a period of several days after the major portion of the armyworm larvae have matured, the application of an insecticide would be virtually useless in so far as that particular field is concerned.

The sporadic nature of armyworm outbreaks is evidenced by the history of the species. Invasions have always come at irregular intervals and no pattern has been set. For example, between 1861 and 1952, the armyworm appeared in Tennessee at intervals varying from one year to thirty-eight years. Thus, if history repeats itself, armyworm outbreaks cannot be expected to occur every year, or at regular intervals in the same area. There is, at present, insufficient information on causes of outbreaks to allow their being predicted on the basis of causative factors.

Until we have information that may be relied upon as a basis for forecasting outbreaks, how can we defend our fields against such unpredictable invasions? The answer seems to lie in a thorough knowledge of the life history of the species with reference to its seasonal cycle in an area. The author is of the opinion that losses from the armyworm may be minimized by a simple application of life history knowledge in the proper season each year. A timely warning would do much to prevent armyworm damage in a region, and it is believed that a workable warning system can be developed with a minimum effort once the life history and seasonal cycle of the species is known.

A study of the armyworm has shown that the first brood is the only one which does damage in Tennessee. Knowing this, we need only to determine the time of this flight for the grain-growing regions of the state and calculate the minimum time required for development to the mature larval stage. The minimum expected time in days could be added to the date of the first flight of moths and the resulting date would be the very earliest time that armyworms could be expected to make an appearance. The maximum developmental time could also be calculated from the end of the first flight, and the latest date of expected outbreaks could be ascertained from life history knowledge. Although a prediction that an armyworm outbreak is inevitable is not possible from such information, limiting dates can be set. In other words, a statement could be prepared to the effect that "if armyworm damage is to occur this season, it will come between May 15 and June 5."

From this information, the county agent could warn all grain farmers in his county to search for developing armyworms in his fields at periodic intervals from the week of May 8, through June 5. Along with the warning statement, details of survey methods should be included as well as instructions for evaluation of the survey results, e. g., in a field where three or more immature "worms" per square foot are found, immediate control measures should be taken. This timing of application would prevent major damage, since it is established that only mature worms are capable of inflicting serious losses. Such a system would require a breakdown of the state into natural climatic areas. In Tennessee, for example, probably West Tennessee, Middle Tennessee, lower East Tennessee (low altitudes), and upper East Tennessee (higher altitudes) would be sufficient division. However, the final division would be subject to a review of long-time weather data. Once this has been done, light traps should be placed in operation in early March in the larger grain-growing areas of each climatic division. The date of the first moth flight could then be determined for each area, the minimal developmental time calculated from that area, and the warning system put into effect.

Let us consider a test case for the application of such a system from data available in this work. From the data in table 5, page 37, it is seen that the first heavy flight of moths came in lower East Tennessee (Knox, Blount, and Monroe counties) by the week ending April 22, 1957, so that April 15 is the earliest date of heavy moth activity in the area, and April 29 is the latest date. Therefore, egg

deposition could not have begun before April 15 and must have been completed by May 7 (tables 5, page 37, and 12, page 57). From this knowledge, the following calculations can be made.

We know from table 14, page 60, that a minimum of three and a maximum of fifteen days are required for egg hatching during this period. From table 16, page 71, we know that a minimum of fifteen and a maximum of sixteen days are required for larval development to the sixth instar. Therefore, from April 15, the earliest date of adult activity, a minimum of eighteen days can be expected before mature armyworms could appear in the field, and from May 7, the latest date of adult activity, a maximum of thirty-one days can be expected until all larval damage must have been done. Therefore, a statement might be made as follows: "If the armyworm is to occur this season, it will be between May 3, and June 8." On the strength of this statement, searches should be made from April 26 through June 8. A look at table 29, page 113, will show that the first armyworms were found on May 3, 1957, in Blount County, on May 6 in Monroe County. If the Monroe County agent had been told to warn his farmers to search for armyworms beginning with the week of April 23, 1957, and his advice had been followed, then incipient outbreaks would have been detected in ample time for control measures to be applied where necessary. Also, after June 8, 1957, no searching would have been necessary, since the critical period had subsided by that time. The same technique could be employed in other areas of the state and in other states.

It is hoped that this discussion will serve to show the value of life history and seasonal cycle knowledge of this species. The same type of knowledge might also prove useful in the control of other species of insect pests. The fact that the armyworm seldom, if ever, is destructive for two successive generations in an area suggests the advisability of widespread use of such a warning system. Only the damaging brood and fundamental life history knowledge for that brood need to be known for the successful application of the system in an area.

An armyworm outbreak is evidently an unnatural occurrence and appears to be disadvantageous to the species. When the biotic system of which the armyworm is a part is in equilibrium, the population remains approximately stationary over a considerable period of time and the individuals making up the population behave as do other solitary noctuids. Only when environmental resistance is low does the species reach enough of its potential to produce outbreaks.

If we consider the total resistance to be made up of physical resistance (climate) and biotic resistance (natural enemies), the role of natural enemies might be discussed in a more favorable light. It must be assumed that when an armyworm outbreak occurs, either total resistance, physical resistance, or biological resistance is low. Therefore, if biotic resistance could be determined by natural enemy surveys and physical resistance by past conditions associated with outbreaks, and put on a quantitative basis, there might be a basis on

which to attack the problem of causative factors of outbreaks. At present this information is not available and the effect of the natural enemy complex on the population in respect to outbreak cause cannot be determined, since it cannot be distinguished from physical resistance. Two important things, however, are known--that parasites lag behind the armyworm and that only larval stages are affected. Therefore, an outbreak must be initiated as a result of lowered physical resistance to the moth which deposits a maximum of eggs of which a large percentage must hatch. If physical resistance to the larvae were high, then no outbreak could occur, even though egg production were high, nor could parasites build up without a maximum number of hosts. Thus, we must conclude that an outbreak must begin in an environment of low physical resistance. It appears then, that natural enemies cannot prevent an outbreak, and that their role must be one of minimizing damage during an outbreak and reducing the armyworm population once again to equilibrium which, after all, is favorable to the host and consequently to the parasite itself. The major parasites, tachinid flies and braconid wasps, fit nicely into this picture. Neither can build a large population except when armyworms are numerous. The braconid wasps deposit their eggs in young armyworm larvae, but reach maturity only after the armyworms are nearly grown. Thus they cannot appear in sufficient numbers to be an important factor in controlling the armyworm until a major amount of damage has already been done by the host. It has been shown, however, by Tower (1916) that armyworms parasitized by the braconid, *Apanteles militaris*, eat approximately one-half as much food as do

non-parasitized worms. Thus, this species serves to minimize damage during the outbreak period and the large numbers of adults, as many as one-hundred from a single host, help to reduce the armyworm population in the succeeding generation. The tachinid flies attack, for the most part, only nearly full grown armyworm larvae and are therefore of little benefit against the generation attacked. However, the host is inevitably killed so that the parasite is effective in cutting off a subsequent brood of armyworms.

Infectious diseases and predators seem to have a similar role in their effect upon an armyworm population, that of maintaining stability when the armyworm, by lowered physical resistance, becomes so numerous that an outbreak results.

SUMMARY

The purpose of this dissertation is to report findings on the fundamental biology of the armyworm, Pseudaletia unipuncta (Haworth), based on a two-season study in Tennessee (1956-57).

Data were obtained from a combination of direct field observations, detailed insectary colony rearings, extensive light trap operations, and several controlled laboratory experiments.

Background material for the study is presented and includes a review of the literature, both the general and systematic histories of the species, geographical distribution, and known host plants.

The general life-history is given for Tennessee along with a general description of the various life history stages and detailed biological data associated with those stages.

A key is presented for separating closely related species in Tennessee. All noctuid species which sometimes assume the armyworm habit are listed with their host plants and distribution.

A detailed account is given of the seasonal cycle of the armyworm in Tennessee with emphasis on the overwintering status of the species in the state.

A section is included on the natural enemies of P. unipuncta in which all known parasites are listed and notes are included on those species reared by the writer. A summary of known predators and diseases of the armyworm is included.

The principal results of this study are as follows:

1. There are five annual broods of the armyworm in Tennessee of which only the first brood is likely to be damaging.

2. Any damage resulting from the armyworm in Tennessee is likely to occur not later than the first week of June of a given year.

3. The fifth brood enters the winter in the partially grown larval stage and is capable of surviving Tennessee's winter conditions.

4. Larvae which enter the winter season in their middle instars have the best chance of overwintering in Tennessee.

5. The armyworm is able to arrest development during extended cold periods, resuming normal activities during warm periods of winter, thereby extending developmental time which results in successful overwintering.

6. Overwintering larvae produced adults in early spring which matured and produced fertile eggs in as few as six days after emergence.

7. Overwintering larvae frequently add extra instars to the normal six. This mechanism is valuable to the species inasmuch as it extends development time.

8. Two species of parasites, Apanteles militaris and Meteorus autographae, were found to overwinter successfully as larvae in host armyworms.

9. The female moth was found to be capable of depositing a much larger number of eggs than was previously thought possible. One specimen deposited 1,759 eggs, all fertile and from only one mating.

10. Parasite-caused mortality of natural populations in Tennessee was 32.3 and 41.5 per cent, respectively, in 1956 and 1957.

11. The most important parasites of P. unipuncta in Tennessee are the braconid wasp, Apanteles militaris Walsh and the tachinid fly, Winthemia rufopicta Big.

12. A polyhedral virus disease takes a heavy toll of armyworms in Tennessee and is known to have been present in the state for three successive years, 1955-57.

13. A mass-rearing technique was developed from which as many as twenty thousand eggs were obtained from one cage of fifty moths in one week.

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LITERATURE CITED

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APPENDIX

COMPREHENSIVE BIBLIOGRAPHY OF LITERATURE DEALING WITH THE ARMYWORM, *Pseudaletia unipuncta*

As a prerequisite to a basic biological study of an insect so widely known as the armyworm, *Pseudaletia unipuncta* (Haworth), the author deemed it necessary to make a rather complete survey of the literature. It was realized that much previous work had been reported on this popular insect and that a comprehensive review of the literature would be required to reveal the areas of investigation which had not been adequately covered.

Since considerable time and effort went into the preparation of a bibliography of the literature on the armyworm, it would seem wasteful not to make it available to other workers. For that reason, it is herewith included.

The bibliography which follows is, of course, not entirely complete, for the very nature of such a task makes its accomplishment almost an impossibility for one individual with limited facilities and time. However, the author has made an effort to choose those bibliographic tools which would yield best results for the time expended. The following bibliographic sources were used in this survey.

1. Bibliography of Agriculture (1943-1956)
2. Biological Abstracts (1926-1956)
3. Review of Applied Entomology (1913-1952)
4. Index to the Literature of American Economic Entomology (1905-1954)
5. Experiment Station Record (1889-1946)

For references prior to 1883, the reader is referred to the lengthy bibliography of Riley (1883).

This bibliography is virtually complete to the extent that indexed references included in the above bibliographic publications for the dates indicated are included. On rare occasions a reference was not included which obviously did not contribute to the knowledge of the species.

The coverage outlined above extends back to and includes the year 1889, which is the date of the first edition of the Experiment Station Record.

References are complete in so far as possible. Those in Part Two from the Index to the Literature of American Economic Entomology, are listed by author and source only, since titles are not given in that publication.

The bibliography is divided into two parts as follows: (1) by author or agency with title and source of publication and (2) by author and source of publication but without title.

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