Biology and population ecology of parasites of the green cloverworm, Plathypena scabra (F.) (Lepidoptera: Noctuidae) in Iowa

by

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TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

INTRODUCTION

Within the past decade, some of mankind's more pressing problems have now converged at a single focal point. The dilemma of producing food, shelter and clothing for a burgeoning population while attempting to reduce the contamination of our environment is now the concern of people in many walks of life. The problems of providing even adequate nutrition for the less fortunate of this nation, as well as millions throughout the world, have, even in recent months, become more severe. The rising costs of living have removed from many tables some of the principal sources of protein.

One of the alternate sources of utilizable protein which has made its way to the supermarket shelves is soybean. In addition to its value as an oil crop, various soybean products are now, through much research and promotion, considered some of the leading substitutes for meat protein.

Soybean production has increased tremendously in recent years. Adverse weather conditions have, in recent months, caused the loss of many 1973 crops and have forced thousands of farmers to replant lost acreages to soybean. In spite of increased acreages, market prices for soybean continue to increase and have almost doubled in recent months. The demand for this valuable crop, both at home and in foreign markets, will undoubtedly continue to increase.

In spite of increased acreages and more widespread planting of this crop, the soybean has been, until now, relatively free of insect pests. Outbreaks of pests of soybean have occasionally occurred in localized

areas. Whether this relatively pest free status will continue in soybean remains to be seen.

One of the few insects considered of importance in the soybean ecosystem is the defoliator, the green cloverworm, Plathypena scabra. This "occasional pest" of soybean (Pedigo 1972) has received more attention in recent years than most other insects associated with soybean.

The renaissance of insect control by ecologically based decisions, known more commonly as pest management, demands that those making the decisions be firmly grounded in ecological principles and thoroughly familiar with the population dynamics of the pest to be controlled (Rabb 1970). The very success of this management approach depends largely on the degree to which the integration of actions is guided by an understanding of these principles and knowledge of the dynamics of pest populations (Rabb and Guthrie 1970).

Clark (1970) proposed a 3-phased approach to the study of pest situations. Phase 1 of this approach seeks a knowledge of the pest's life system, including the components inimical to the pest species.

The studies presented herein were embarked upon with the primary objective of achieving a better understanding of the importance and possible roles of parasites in the life system of the green cloverworm. Secondarily, a better understanding of the population dynamics of the green cloverworm was sought. To acquire this understanding and knowledge, the following studies were carried out to achieve the specified objectives.

Extensive sampling programs were conducted within the state of

Iowa during 1970 and 1971 with the following objectives:

1) To identify the parasites of the green cloverworm.
2) To determine the distribution and seasonal occurrence of these parasites.
3) To determine the incidence of parasitism, both collectively and individually, by these parasites through space and time.
4) To determine various host-parasite relationships, i.e., stage of host attacked, whether parasitism is solitary or gregarious, and host stages in which parasite development occurs.
5) To identify the hyperparasites associated with the green cloverworm.
6) To determine the incidence of parasitism, distribution, seasonal occurrence and host associations of these hyperparasites.
7) To determine characteristics of green cloverworm larval populations, i.e., relative abundance, adult sex ratio, incidence of disease and other mortality factors.

An egg parasite study was undertaken with the following objectives:

1) To identify egg parasites of the green cloverworm.
2) To determine the incidence of egg parasitism and its possible role in population regulation.

An intensive sampling program was conducted near Ames in 1971 with the following objectives:

1) To determine, on a weekly basis, any changes in the incidence of parasitism by individual and groups of parasite species within field populations of green cloverworms.

2) To determine possible reasons for changes observed in the incidence of parasitism.

3) To determine the seasonal occurrence and abundance of individual parasite species in 2 ecosystems.

4) To determine differences in the incidence of total parasitism in 2 ecosystems.

5) To define more precisely the host-parasite relationships.

6) To determine any density-related responses by prominent parasite species to the host population.

7) To determine more precisely, the characteristics of the host population.

Biological studies were conducted in the laboratory on the 2 prominent parasite species, Rogas nolophanae and Winthemia sinuata, with the following objectives:

1) To observe and record basic biological phenomena, i.e., mating, oviposition, development, etc.

2) To determine stadia of various life stages.

3) To observe and describe selected life stages of the parasite species.

REVIEW OF LITERATURE

The Green Cloverworm, Plathypena scabra (Fab.)

According to Balduf (1923), the green cloverworm is the worst potential enemy of soybean. The adult green cloverworm was first described by Fabricius (1794) as Hyblaea scabra. Walker (1859) placed this name into junior synonomy under Hypena scabralis and, in the same paper, presented a description of Hypena erectalis Guenee (1854). Almost 15 years later, Lintner (1873) discovered that all specimens of Hypena scabra Fab. he was studying were males and all specimens of Hypena erectalis Guenee were females. He concluded that both were sexual dimorphs of a single species. He related this fact to Grote who subsequently erected the genus Plathypena with Fabricius' scabra as the type species (Grote 1873).

Smith (1895) redescribed the genus, reviewed early taxonomic literature of the species and presented the most complete technical description of the species to date. Hill (1925) gave a complete quotation of the adult description by Smith (1895). Less technical descriptions and illustrations of these brown, snout-nosed, deltoid moths have been provided by Chittenden (1901), Holland (1903), Britton (1909, 1920), Hill (1918, 1925), Sherman and Leiby (1920), Hawley (1922), Balduf (1923), and Pedigo, Stone, and Lentz (1973). The synonomy of the species was presented by Holland (1903) and Barnes and McDunnough (1917). The classification of this species within the family Noctuidae was given by Crumb (1956).

The distribution of Plathypena scabra is limited almost exclusively

to the Nearctic regior E of ca. 103° W long. (Pedigo et al. 1973). A notable exception is the collection of a single male adult taken in England in 1956 (Bradley 1960, Bruce 1961). The earliest distribution of P. scabra was given by Walker (1859) as the United States and Nova Scotia. Several authors presented modifications of this distribution (Grote 1872, Riley 1885, Smith 1895, and Holland 1903). Hill (1918, 1925) gave distribution maps for the species and reported it as being present throughout the United States and southern Canada E of 98° W long., excepting portions of Florida and the Gulf coast. The extension of the distribution into new areas, as discussed by Pedigo et al. (1973), could be: 1) actual movement of the species, 2) the result of more extensive collection and better reporting, or 3) both.

The larvae of the green cloverworm probably feed on leguminous crops in general (Hill 1925). Hill (1925) examined the feeding response of larvae to several host plants and presented a list of those which had previously been reported as host plants of the species. Prior to 1900, larvae had been reported feeding on approximately 5 plant species (Riley 1880, Coquillett 1881, and Riley 1885). In the next quarter century, almost 20 additional plant species were added to the list of host plants with soybean appearing often in research reports (Hill 1918, Smith 1919, Sherman and Leiby 1920, Britton 1920, Hawley 1922, and Balduf 1923). Pedigo et al. (1973) compiled a list of 34 plant species which serve as host plants.

Although it is a common insect in alfalfa and clover fields, (Comstock 1879, Coquillett 1881, Hill 1918, Smith 1956, and Smith and

Franklin 1961), severe outbreaks of the green cloverworm have seldom occurred. The most serious and widespread outbreak of this "occasional" pest of soybean (Pedigo 1972) and other economic legumes (Stirrett 1931) appears to have occurred in 1919 (Smith 1919, Sherman and Leiby 1920, Britton 1920) throughout the Atlantic Coastal Plain (Smith 1919) to Ontario, Canada (Stirrett 1931). Another outbreak of this defoliator occurred in 1931 in Iowa, Nebraska, North Carolina, Virginia and Tennessee (Stirrett 1931). Considerable injury to soybean was reported from Minnesota in 1944 (Kretzschmar 1948); Ontario, Canada, in 1955 (MacNay 1955); Maryland in 1957 (Ratcliffe, Bissell, and Bickley 1960); and Iowa in 1966 and 1968 (Gunderson, Stockdale, and Peters 1967, Gunderson 1968). Outbreak history of the green cloverworm in soybean was reviewed by Pedigo et al. (1972a).

The causes of outbreaks of green cloverworms are unknown. Hawley (1922) hypothesized that above average numbers of insects emerging in the spring of 1919 was due to the mild winter of 1918-19 in which temperatures averaged 11° F higher during the months of Dec.-Feb. Balduf (1923) expressed the belief that periodic outbreaks were due to several factors, one of which was favorable weather during the winter. In Canada, Stirrett (1931) believed 2 mild winters in succession may have allowed the species to increase to outbreak proportions by the season of 1931.

Aspects of the life history of the green cloverworm have been studied to differing degrees, but most completely by Hill (1925), Smith and Franklin (1961), and Pedigo et al. (1973). The adult moths emerge

in the spring of the year and lay eggs on available host plants. Mating of green cloverworms was described by Pedigo et al. (1973) and oviposition by Hill (1925) and Pedigo (1971).

The reported fecundity of the green cloverworm is quite variable. In his 1st report, Hill (1918) reported 200-600 eggs/♀ and in 1925 gave 60-670 eggs/♀, the latter study having a mean of 201.2 eggs/♀. Smith and Franklin (1961) reported a mean of 230 eggs/♀. The average number of eggs/♀ (38.8) found by Pedigo et al. (1973) in an oviposition study was believed exceptionally low because counts of larvae in other observations gave a mean realized fertility of 96.3 larvae/♀.

The definite existence of a preoviposition period ranging from 10 or 11 days (Smith and Franklin 1961, Hill 1925), a wk or more (Sherman 1920), to 4-5 days (Pedigo et al. 1973) has been recognized. The ovipositional response of the green cloverworm was characterized by Pedigo (1971). His studies with selected natural and artificial surfaces indicated that surface texture, namely pubescence, had the most stimulating effect.

In the spring, when oviposition begins, eggs are laid singly on available host crops (Hill 1918, 1925; Frost 1955; Laster 1962; Pedigo et al. 1973). On alfalfa, the eggs are laid on the underside of leaflets (Hill 1918, 1925), but later in the season, when soybean leaflets are available for oviposition, no preference is shown for either surface (Sherman 1920, Sherman and Leiby 1920, and Pedigo 1971).

The translucent green eggs, measuring ca. 0.5 mm in diam x 0.35 mm high, have been described or illustrated by several authors (Coquillett

1881, Chittenden 1901; Britton 1909, 1920; Hill 1918, 1925; Sherman and Leiby 1920; Balduf 1923; and Pedigo et al. 1973). Development of the larva within the egg and changes in the egg appearance were described by Pedigo et al. (1973). Eggs begin hatching in ca. 4-6 days (Coquillett 1881; Hill 1918, 1925; Sherman 1920, Sherman and Leiby 1920; Smith and Franklin 1961; and Pedigo et al. 1973) or as much as 9.4 days in the spring (Hill 1925). Eclosion from the egg was described by Hill (1925) and Pedigo et al. (1973).

The first description of the green cloverworm larva was presented by Comstock (1879) and is as follows:

> "Length when full grown 16 mm. Color, dark yellow-green, with a narrow subdorsal and lateral whitish line. Head, prothoracic and anal plates of the same color as the body, but glassy. Whole body with sparse dark hairs, longer on anal plate. Spiracles dark-brown; tips of prolegs and mouth parts brown. Sides subparallel; greatest width 2.6 mm."

Riley (1880) also gave a description of the larva and included the important fact that the larva has only 3 pairs of abdominal prolegs, a characteristic which distinguishes it from other green larvae found in similar habitats. Coquillett (1881) described 2 larval molts, after which, markings and color remained the same. He noted the larval length at maturity was ca. 1 in. Detailed molting behavior was described by Stone (1970) and Pedigo et al. (1973).

It is now recognized that, during the period of larval development, there are 6 larval stages, with 7 occurring occasionally (Hill 1925, Smith and Franklin 1961, and Stone and Pedigo 1972). The latter found that 7 stages occurred in 24.2% of the larvae reared on soybean.

Descriptions and illustrations of the 6 larval instars were presented by Hill (1925). Less detailed descriptions or illustrations of varying detail are given by other authors (Britton 1909, 1920; Hill 1918; Smith 1919; Sherman and Leiby 1920; Balduf 1923; Crumb 1956; and Pedigo et al. 1973).

Upon hatching, the larva almost immediately begins searching for food (Hill 1925, Stone 1970). The egg chorion is not eaten by the newly hatched larva (Pedigo et al. 1973). The new larva, ca. 1/8 in. long (Hill 1918, Sherman and Leiby 1920), feeds on the underside of the leaflets. Young larvae, stages 1-3, can often be seen hanging from the leaflet by a silken thread (Britton 1920, Sherman 1920, Hawley 1922, and Pedigo et al. 1973).

Larval stages 1 and 2 usually eat all but the upper epidermis of the leaf, leaving a window-like appearance on the leaves (Pedigo et al. 1973). Sherman (1920) reported that, within 3 days, the larvae eat through soybean leaves. Hill (1925) stated that, on alfalfa, this type of feeding is characteristic of the first 3 instars (7.66 days). Smith and Franklin (1961) reported feeding behavior similar to Sherman's account but that the second instar begins to eat through alfalfa leaflets. Stone (1970) observed larvae of the first 4 stages feeding completely through soybean leaflets. Larger larvae are voracious feeders, eating entirely through the leaf (Sherman 1920, Hawley 1922, and Pedigo et al. 1973).

Hill (1925) measured leaf consumption by green cloverworm larvae on alfalfa and found that larvae consumed 3.78 $in.^2$. Stone and Pedigo

(1972) found larvae consume 16.31 $in.^2$ of soybean leaf tissue with over 90% being consumed during stages 5-7.

Little is known of the relationship of green cloverworm larval feeding and crop losses caused by this insect. Stone and Pedigo (1972) developed theoretical economic injury levels on soybean by utilizing larval food consumption data and agronomists' data from defoliation-yield reduction studies. Results of their studies indicated that presently recommended economic injury levels should probably be revised upward.

Burbutis and Kelsey (1970) found on lima beans in Delaware, that infestations up to 8 larvae/plant/wk had no significant effect on lima bean yield. Also, no significant reduction in yield occurred in any of the treatments where 10, 50, and 75% of the small pods were removed by hand at weekly intervals.

Larval feeding on blossoms of soybean was reported by Smith (1919) and on pods by Britton (1909, 1920), Hawley (1922), Stirrett (1931), and Burbutis and Kelsey (1970). Pedigo et al. (1973) reported that, under conditions of stress and after a period of starvation, larvae would feed on pods, flowers, cotyledons and stems.

Several authors have reported on the stratification of the larvae within the plant canopy. A distinct preference of the larvae for the young upper leaves of the plant was reported by Smith (1919), Sherman and Leiby (1920), Balduf (1923) and Kretzschmar (1948). Pedigo et al. (1973) found that stages 1-4 showed no preference for any of 3 levels

in the plant canopy but large larvae were found most frequently in the upper 3rd of the plants.

The reported length of developmental time of the green cloverworm has varied from worker to worker, most probably due to different environmental conditions at different locations. Coquillett (1881), in Illinois, reported a mean stadium of 25 days; Hill (1918, 1925), in Tennessee, 4 wk and 22.84 days respectively; Sherman and Leiby (1920), in North Carolina, ca. 25 days; Smith and Franklin (1961), in Kansas, 21.5 days. Stone and Pedigo (1972) reported stadia of 19.9, 19.0, and 18.0 days for 3 groups of larvae reared in environmental chambers.

During the course of feeding on the plants, green cloverworm larvae, if disturbed, exhibit a violent flipping and wriggling action which often dislodges them from plants (Britton 1920, Sherman 1920, Sherman and Leiby 1920, Hawley 1922, Balduf 1923, and Pedigo et al. 1973), an action which the latter authors suggest is a mechanism of defense against predators and also serves to disperse larvae among the plants.

At the cessation of feeding, the 6th (or 7th) stage larva moves to a suitable pupation site where it spins a fine silken cocoon and begins its transformation into a pupa. During this transformation, described by Hill (1925) and Pedigo et al. (1973), the larva goes through a prepupal stage which was first recognized and described by Chittenden (1901). Pedigo et al. (1973) reported that larvae about to enter the prepupal stage produce 2-3 gold to orange fecal pellets in amber fluid. The prepupal stage lasts 1.2 to ca. 2 days (Hill 1925, Smith and Franklin 1961, and Stone and Pedigo 1972), but late in the season, as the weather cools,

the prepupal stadium may last up to 10.8 days (Smith and Franklin 1961).

Riley (1880) reported finding green cloverworm pupae under tree bark, while Britton (1909, 1920) found larvae in rolled leaves. Pedigo et al. (1972b) reported that 10.4% of larvae studied pupated in the plant canopy. However, most authors report pupae were found in or under vegetative material on the soil surface or just under the soil surface in cracks and crevices in the ground where cocoons were webbed with particles of soil (Chittenden 1901; Britton 1909, 1920; Hill 1918, 1925; Sherman 1920; Sherman and Leiby 1920; Hawley 1922; Balduf 1923; Stirrett 1931; Laster 1962; and Pedigo et al. 1972b).

Most authors report the pupal stadium to be, on the average, ca. 10-14 days. Hill (1918) reported a pupal stadium of ca. 8 days during a normal summer, but he found it was quite prolonged in cold weather. Smith and Franklin (1961) stated that, late in the season, the pupal stage could last up to 28 days in Kansas. Eclosion from the pupa was described by Pedigo et al. (1973).

Green cloverworm moths are seldom seen in daylight hours (Chittenden 1901, Balduf 1923, and Hill 1925). Moths were reported hiding on the undersides of leaves, in tree tops or around buildings and haystacks where their dark brown color allows them to go unnoticed (Hill 1918, 1925; Sherman and Leiby 1920; and Balduf 1923). If driven from their hiding places, the moths make a quick appearance (Balduf 1923), fly in a zigzag and undulating manner for a few paces (Hill 1925), and then quickly dart to the underside of leaves or other objects (Balduf 1923, Hill 1925). If pursued, moths frequently fly higher than housetops for

a distance of 50 to 100 yd and then quickly alight (Hill 1925).

Feral adults have been reported feeding on the nectar of blossoms of host plants (Hill 1925) and cultured moths on molasses (Sherman 1920) and water or 1% sugar solution (Pedigo et al. 1973).

Mean longevity of the adult stage has been reported as 7.3 days (Hill 1925); 9.0 days (Smith and Franklin 1961); 7.9-11.1 days (Stone and Pedigo 1972), and 22.4 days (Pedigo et al. 1973). These latter workers found that females live significantly longer under greenhouse conditions than do males.

Like many other noctuids, moth activity begins at dusk and continues into the night. Pedigo et al. (1973) observed flight to begin at ca. 3 ft-c of light and increased 3-fold (15-52 moths flying) at < 1 ft-c, during a 10-min period. Moth activity, as measured by black-light trap catches, was shown by Pedigo et al. (1973) to occur between 8:00 PM and 2:00 AM CDT.

The use of light traps to measure seasonal moth activity in Ontario, Canada, was reported by Stirrett (1931). No moths were caught in the trap between June 15 and 30, but were caught, however, between July 5 and Oct. 3 with peak moth activity between July 13 and Aug. 3. In Minnesota, moth activity was measured and reported by Knutson (1944). He collected moths as early as the 1st wk of May with heaviest flights occurring the last 3 wk of July. Pedigo et al. (1973), in Iowa, also found heaviest numbers occurring in July but reported numbers to drop substantially on Sept. 11. These latter workers reported catches to be quite erratic, though, and found no clear generation or seasonal pattern.

Sex ratios of moths from Knutson's studies (1944) indicated a 1.3♂♂:1♀ ratio. Pedigo et al. (1973), however, found light trap collections to be extremely biased toward males (6.6♂♂:1♀), because natural larval populations showed a 1:1 sex ratio.

The number of generations of this insect occurring during the growing season varies from location to location and probably depends on the length of the growing season. Comstock (1879) reported the presence of 2 generations with perhaps a 3rd occurring in the Washington, D.C. area. However, Chittenden (1901) observed 3 well-defined generations in the same area. In the Woodstock, Ill., area, Coquillett (1881) found that only 2 generations occurred. At approximately the same latitude, but further W, Pedigo et al. (1973) reported the occurrence of 3 prominent generations of the species in alfalfa and one in soybean. However, the latter authors noted a great overlap of generations.

Hawley (1922), at Ithaca, N.Y., stated that 2 generations were present with a partial 3rd occurring in longer growing seasons. Balduf (1923) expressed the belief that, at Marietta, Ohio, 3 broods were likely to occur since the 2nd was present in mid-summer. Hill (1925) observed 4 generations at Knoxville, Tenn., in 1916.

The overwintering stage of the green cloverworm is a point of considerable disagreement among researchers. Comstock (1879) concluded that the moth overwinters in the South because of the numbers of moths sent to him for determination during the winter months. Riley (1880) reported the adult to overwinter over its entire range but because of

the presence of pupae under bark in Missouri during the winter, he felt it probably overwintered in the South as both a moth and a pupa. Because of the faded and worn condition of a gravid female moth he had collected, Coquillett (1881) believed the adult to be the overwintering stage. Chittenden (1901) stated that the green cloverworm moth was one of the latest and earliest species active near Washington, D.C. The moth was commonly found in buildings as late as the 1st wk of Dec. and as early as Mar. 10. Because of this late and early appearance, he believed the adult was the overwintering form. During the winter of 1878-79, moth flight was observed by him on warm sunny days. Britton (1920), Sherman (1920), and Hawley (1922) all reported the adult to be the overwintering stage.

In addition to Riley (1880), other authors (Hill 1918, 1925; Sherman and Leiby 1920; Balduf 1923; Frost 1955; Smith and Franklin 1961; and Laster 1962) have reported both the moth and pupa to overwinter. Sherman and Leiby (1920) noted that some pupae do overwinter and hypothesized that "perhaps only those which winter as pupae and emerge as moths in spring can reproduce."

Nettles, Smith and Thomas (1970) also suggested that only pupae can pass the winter and emerge as moths to oviposit in the spring. The overwintering stage in Iowa remains an unresolved question (Pedigo et al. 1973).

Parasites of the Green Cloverworm

The first reported parasite of the green cloverworm was Euplectrus platyhypenae (sic) Howard (1885) which was reared from larvae collected

in the District of Columbia in 1882 and named for the genus from which it was reared. Chittenden (1901) reared the second parasite from the green cloverworm on Sept. 7, 1899, which was identified by Coquillett as the tachinid fly, Exorista (= Eusisyropa) blanda Osten Sacken.

In rather intensive studies of the green cloverworm at 2 locations in North Carolina, Sherman (1920) found that approximately 50% of the green cloverworm eggs examined were parasitized by a "very important egg parasite," the minute wasp, Trichogramma pretiosa Riley (= T. minutum Riley). Seventeen specimens of the next most abundant parasite, a tachinid fly, Phorocera (= Euphorocera) claripennis Macquart were reared from the green cloverworm. Sherman noted that P. claripennis was also the second most prevalent parasite of the true armyworm in North Carolina during 1919 when the armyworm " ... was in evidence where these studies were made." Two specimens of the fly, Exorista (= Eusisyropa) boarmiae Coquillett (one from each location) were also reported. In addition, Sherman and his assistant also reared from the green cloverworm single specimens of a wasp, "a Campoplegine apparently new species and new genus" and the flies Frontina (= Lespesia) aletiae Riley, Euphorocera floridensis Townsend, Sarcophaga (= Boettcheria) climbicis Townsend and Anthrax (= Villa) lateralis Say. Sherman reported a greater incidence of pupal parasitism at Terra Ceia, N. C., than at Elizabeth City.

Hawley (1922), in New York, reared two hymenopterous parasites from the green cloverworm. A single specimen of Aleiodes intermedius Cresson [= Rogas stigmator (Say)] was reared from a larva collected in 1919 and

8 specimens of Rhyssalus loxoteniae Ashmead [= Oncophanes americanus (Weed)] emerged from the sole larva found in 1920.

At Marietta, Ohio, Balduf (1923) also found Aleiodes intermedius attacking small larvae "to a slight entent." However, the chief internal parasite was "the Red-tailed Tachina (Winthemia quadripustulata Fabr.)" which was reared from nearly mature larvae.

A summary of all known parasites of the green cloverworm was presented by Hill (1925). A list of species, location of collection and the source of the report as given by Hill is shown in Table 1. Of the 10 species of parasites reared from larvae collected in Tennessee, Rogas nolophanae Ashmead was the most common at Nashville in 1914. In 1916, at Knoxville, Tenn., Trichophora (= Copecrypta) ruficauda Wulp was more abundant than any other parasite reared from this host.

In Minnesota, Kretzschmar (1948) found that "the green cloverworm was kept under control quite effectively by Voria ruralis (Fab.) and Apanteles flaviconchae (Riley)."

Smith and Franklin (1961) presented a report on the parasites associated with the green cloverworm in Kansas. Much of the work reported was conducted during 1921-6. The most common larval parasite was Winthemia quadripustulata F. The wasp, Rogas nolophanae, was reared many times from May to Aug. Other species of parasites reported included Phorocera claripennis, Euplectrus plathyhypenae Howard and Apanteles scitulus Riley. Descriptions of other unidentified parasites were presented as follows:

Table 1. Parasites of *Plathypena scabra* (F.)[a]

Parasite	Location	Source[b]
DIPTERA		
Bombyliidae		
Anthrax lateralis Say	N.C.	3
Sarcophagidae		
Sarcophaga cimbicis Townsend	N.C.	3
Tachinidae		
Compsilura concinnata Meigen	Mass.	6
Euphorocera floridensis Townsend	N.C.	3
Exorista amplexa Coquillett	Md.	6
E. blanda Osten Sacken	Washington, D.C.	2
E. boarmiae Coquillett	N.C.	3
Frontina aletiae Riley	N.C.	3
Hypochaeta eudryae Smith	Tenn.	6
H. longicornis Schiner	Miss.	6
Phorocera claripennis Macquart	Md.	6
P. flavicauda Wulp	Miss., Tenn.	6
Trichophora ruficauda Wulp	Mo., Miss., N.C., Tenn.	3,6
Winthemia quadripustulata F.	Mo., Tenn.	6
HYMENOPTERA		
Braconidae		
Apanteles harnedi Viereck	Tenn., Tex.	6
Meteorus sp.	Tenn.	6
Microgaster facetosa Weed	Tenn., Md.	5,6
Microplitis varicolor Viereck	Tenn.	6
(*Rhogas*) *Aleiodes intermedius* Cresson	N.Y.	4
Rhogas canadensis Cresson	Indiana	6
R. nolophanae Ashmead	Tenn.	6
Rhyssalus loxoteniae Ashmead	N.Y.	4
Ichneumonidae		
Hemiteles sp.	Indiana	6
Mesochorus sp.	Tenn.	6
A Campoplegine probably n. sp. n. gen.	N.C.	3

[a]From Hill (1925).

[b]1 = Howard (1885), 2 = Chittenden (1901), 3 = Sherman (1920), 4 = Hawley (1922), 5 = Muesebeck (1922), 6 = Hill (1925).

Table 1 (Continued)

Parasite	Location	Source
Trichogrammatidae		
Trichogramma pretiosa Riley	N.C.	3
Eulophidae		
Euplectrus comstockii Howard	S. Dak.	6
E. plathyhpenae Howard	Washington, D.C.	1

"An unidentified parasite larva emerged June 16, 1924, from a green cloverworm larva and pupated. This parasite pupa was ½ inch long and dark except for a large light green stripe running down its back, and two small, light green stripes, one on each side of the large stripe. This pupa was on the underside of an alfalfa leaf and was enclosed in a finely netted silken case. The adult parasite emerged June 21. It had a moth-like insect body about 3/8 inch long, and slender yellowish-white stripe on its back which divided and extended back on each wing. Another unidientified species of parasite came out of a green cloverworm June 16, 1924. It burst out of the larva and pupated. It lay crosswise of the host larva and had one end outside the larval skin but the other end remained within. It was about 3/16 inch long and 1/16 inch in diameter or about the same diameter as the host larva was when it died. The parasite had [illegible]etal projections at each end of the body. This parasite was quite unlike any other obtained from any other green cloverworm. Some larvae were parasitized by a large, unknown Hymenopterous parasite that pupated within the larval skin which turned brown. Another parasite spun a brown, wrinkled cocoon resembling a grain of wheat. The cocoon often was attached to the lid of the box. It was one of the small Hymenopterous parasites."

Smith and Franklin reared a series of 279 larvae collected May 30 to Sept. 17, 1921, and found ". . . 15 were parasitized by either Dipterous or Hymenopterous parasites and the host larvae died; 68 moths emerged;

34 died as pupae; 22 died as prepupae; 82 died as larvae; and 58 were killed during rearing, escaped, or were transferred to other series."

The insect parasite fauna associated with the green cloverworm in Delaware was reported by Whiteside, Burbutis, and Kelsey (1967). Studies conducted during the 1965 season resulted in 11 species of parasites (6 Hymenoptera, 5 Diptera) being reared from green cloverworm larvae collected from alfalfa, lima beans and soybean. Two additional known parasites of the green cloverworm were collected in sweep samples. Total parasitism for the season was 20.4% with the following 4 species predominating: R. nolophanae, 6.5%; Microgaster facetosa Weed, 2.8%; Winthemia sinuata Reinhard, 6.2%; and Apanteles marginiventris (Cresson), 4.1%. No parasitized larvae were collected June 7-30. The percent parasitism by all species averaged ca. 16% during most of July, dropped to 8% the 1st wk of Aug. and rose steadily from then to the 3rd wk of Sept. when 50% of the larvae collected were parasitized.

The following 4 of the 11 species reared were reported as parasites of the green cloverworm for the first time: Charops annulipes Ashmead and Isdromas lycaenae (Howard) (Hymenoptera) and Helicobia rapax (Walker) and an undescribed species of Chaetophlepsis (Diptera). In addition, 3 specimens of the wasp, Meteorus autographae Muesebeck and 1 and 2 specimens of the flies Compsilura concinnata (Meigen) and Euphorocera floridensis, respectively, were reared from the green cloverworm.

Based on previous studies (Hill 1925, Kretzschmar 1948) and their

own in Delaware, Whiteside et al. considered "R. nolophanae and W. sinuata the most effective parasites of the green cloverworm" in Delaware.

In Missouri, Barry (1970) found from collections made in 1969 that the 4 predominant species were the same as those reported from Delaware. The seasonal parasitism of the green cloverworm by each of the 4 was: R. nolophanae, 6.4%; Protomicroplitis (= Microgaster) facetosa, 5.0%; W. sinuata, 3.3%; and A. marginiventris, 2.7%. The total seasonal parasitism was ca. 19%. Weekly parasitism ranged 4-32.7%. In addition to the 4 predominant parasites reared, 4 other primary parasites were reared. These were as follows: Copecrypta ruficauda, Chaetophlepsis sp. (Diptera: Tachinidae), Meteorus autographe, Meteorus sp. (Hymenoptera: Braconidae).

Two species of hyperparasites were reared from primarily parasitized green cloverworms. Mesochorus discitergus (Say) was reared from both R. nolophanae and P. facetosa and Ceratosmicra meteori (Burks) from R. nolophanae. These were new host records for both hyperparasites.

In survivorship studies of the green cloverworm in Iowa in 1970, Pedigo et al. (1972b) found R. nolophanae, Apanteles sp., and Winthemia sp. parasitizing green cloverworms. More parasitized larvae were found during Aug. than July. In other 1970 Iowa studies, parasitism by Apanteles was less than 2.6%.

In a preliminary report of green cloverworm parasite studies in Iowa during 1970 and 1971, Lentz and Pedigo (1972) found at least 3

species of tachinid flies, 3 species of braconid wasps, 1 egg parasite and 3 hyperparasites associated with the green cloverworm. Total parasitism during the period June 17 through Aug. 31, 1971, was 30.7%. Parasitism by R. nolophanae alone was 19.6%.

The importance of parasites in regulating green cloverworm populations has been recognized by numerous workers. In Wisconsin, Russell and Morrison (1920) reported that a very large number of the larvae were found to be killed by parasites during the latter part of Aug. and early Sept. and, consequently, often held populations in check. Sherman and Leiby (1920) also referred to the ability of parasites to suppress populations in North Carolina.

Balduf (1923) hypothesized that the absence of parasites was 1 cause of outbreaks and that natural enemies constituted 1 of the effective factors in keeping the green cloverworm from developing to very serious numbers in Ohio. In Iowa, Harris (1954) stated that "the green cloverworm, P. scabra, regularly would be an important pest on clover if it were not for its natural enemies which keep its numbers down." The ability of parasites to effectively control the green cloverworm in Minnesota was referred to earlier (Kretzschmar 1948).

Whiteside et al. (1967) evaluated the importance of the green cloverworm parasites on the basis of host stage and seasonal occurrence. Not only was R. nolophanae the most abundant parasite, but it was also important in that it attacked the younger larval instars and killed them before they reached the serious defoliation stage. The importance of

W. sinuata was evaluated on the basis that the parasite lowers the reproductive potential by killing the host. M. facetosa, though parasitizing only 2.8% of the larvae during the season, "... appears to lower appreciably the number of late season larvae which ultimately would overwinter as adults."

Other workers have been less optimistic of the value of parasites. Hill (1918) stated that considerable numbers of larvae are killed each year in Tennessee by parasites, but he cautioned that they should not be relied upon to protect the crop. In writing of the outbreak of 1919 in Virginia, French (1920) pointed out that "during years of average weather conditions the green cloverworm has been kept in check by a number of insects which parasitize it, but our experience of the past season (1919) teaches us that in seasons like this one we cannot depend upon these natural enemies to prevent such outbreaks."

In Kansas, Dean and Smith (1935) were quite outspoken in that, although they often observed larvae to be heavily parasitized, they believed "... at no time (had) parasites been a dominating factor in the control of this insect."

Other Natural Population Regulators

In addition to the parasites which attack the green cloverworm, other biotic and abiotic factors in the environment function as regulators of larval populations.

One such element is the predaceous animals which feed on other

insects, in this case, those insects and other animals which consume green cloverworm larvae as a part of their diet. Sherman (1920) reported the capture of a paper-nest wasp (Polistes sp.) as it was feeding on a larva. Sherman and Leiby (1920) observed birds feeding upon the green cloverworm and, in addition, they commonly found many kinds of predaceous beetles and bugs in soybean fields during the outbreak of 1919.

Balduf (1923) also observed 1 of the social wasps, Polistes annularis (L.), consuming and carrying larvae from the field. However, the 2 most common predators were 2 species of robber flies (Deromyia umbrinus Loew and D. discolor Loew). These were often observed buzzing among the soybean plants searching for their prey and were reported to have eaten these larvae on the leaves where they were caught.

Hill (1925) found the slender gray bug, Nabis ferus L., exceedingly abundant in infested fields in Tennessee where 1st and 2nd instar nymphs were observed to attack and kill young larvae. Hill believed it aided considerably in the destruction of the caterpillars. Podisus maculiventris Say, the spined soldier bug, was also found commonly in infested fields and 1 bug found in the field had pierced a green cloverworm larva with its beak. Individuals reared in captivity fed readily on caterpillars.

Pedigo et al. (1972b) observed that predator species (Orius insidiosus (Say), Nabis sp., Chrysopa sp. and unknown species of spiders) generally fed on eggs and early-stage larvae. Mean numbers of the above

prominent predators were higher during Aug. than in July and generally increased throughout the period of the observations. Differences in the survivorship curves in screened and open field plots were believed to be due to predation by Nabis sp. and O. insidiosus.

Microbial pathogens appear to be quite important in the regulation of green cloverworm populations. Sherman (1920) observed that many larvae were killed by a bacterial disease and perhaps 25 had been seen infected with a fungus. Hill (1925) reported that many larvae were killed in the fall of the year at Knoxville and Nashville, Tenn., and at Hagerstown, Md., by the fungus, Botrytis rileyi Farl. Stirrett (1931) reported the above fungus "is now thought to be a species of the genus Spicaria."

Stirrett (1931) reported that on ca. Aug. 20, 1931, many larvae became sickly, died and later turned a blackish color. In 1 field, 18.7% of the larvae had died of the disease which was caused by Entomophthora sp. or Empusa sp. The epizootic existed generally over the entire district where the study was conducted.

During July, in Missouri, Barry (1970) found numerous dead and dying larvae which were infected with pathogenic microorganisms.

In Iowa, Pedigo et al. (1973) found the 3 primary pathogens of the green cloverworm were a granulosis virus, Metarrhizium sp., and Beauveria bassiana. The latter was an important factor in the collapse of outbreak populations in 1968.

Climatic factors, as well as natural enemies, have also been observed

to influence populations of green cloverworms. Hill (1918) reported that "caterpillars can stand a great deal of cool weather and even an occasional light frost, but continued frost will kill them in a few days." Hill (1925) observed on Nov. 14, at Greenwood, Miss., many dead larvae which had been killed by heavy frosts the previous 3 nights. A few larvae survived in protected places. At Nashville, Tenn., 8 larvae were caged on an alfalfa plant. The 1st night, 3 larvae died when the temperature reached 34° F. The next night, 2 more died when the temperature dropped to 31° F. The remaining 3 survived a 26° F night, 2 of these later pupating and 1 finally emerging as a moth.

Smith (1956) found that larvae may survive a short time when exposed to hot sun following cutting of alfalfa, but those surviving for a while eventually die of desiccation. Stage-4 larvae died in less than 3 min. when dropped on a soil surface of 55-56° C.

Pedigo et al. (1973) reported a mortality of 66.7% to the egg stage due to a severe thunderstorm in Iowa.

METHODS AND MATERIALS

1970 Extensive Sampling Program

The objectives outlined for the 1970 season were fulfilled by making extensive collections of larvae to be held for parasite emergence. These collections were made in conjunction with an ongoing extensive sampling program which was being conducted to monitor populations of soybean insects in Iowa. During the growing season, collecting trips were made to 4 distant areas of the state. Since green cloverworms were being collected from soybean as a part of faunistic studies and were subsequently killed, the author made separate collections from alfalfa and clover fields along the route. A summary of the collections made during these trips is presented in Table 2. The approximate locations of fields throughout the state from which collections were made are shown in Figure 1.

In addition to these distant collecting trips, collections were also made in the Ames area in Boone and Story counties. A summary of these collections is shown in Table 3. The location of fields from which these collections were made is shown in Figure 2.

Larvae were collected from the above fields with an 18-in.-diam muslin insect sweep net. The surveyor moved some distance into the field and then began sweeping in approximately 90° arcs along a transect which usually ran parallel to the length of the field. After several sweeps were made, the larvae were removed from the net and placed in a 1 qt ice cream carton with some of the host plant material.

Figure 1. Sites of extensive collections of green cloverworms for parasite rearings in Iowa. Summer 1970. Numbers are collection no. given in Table 2

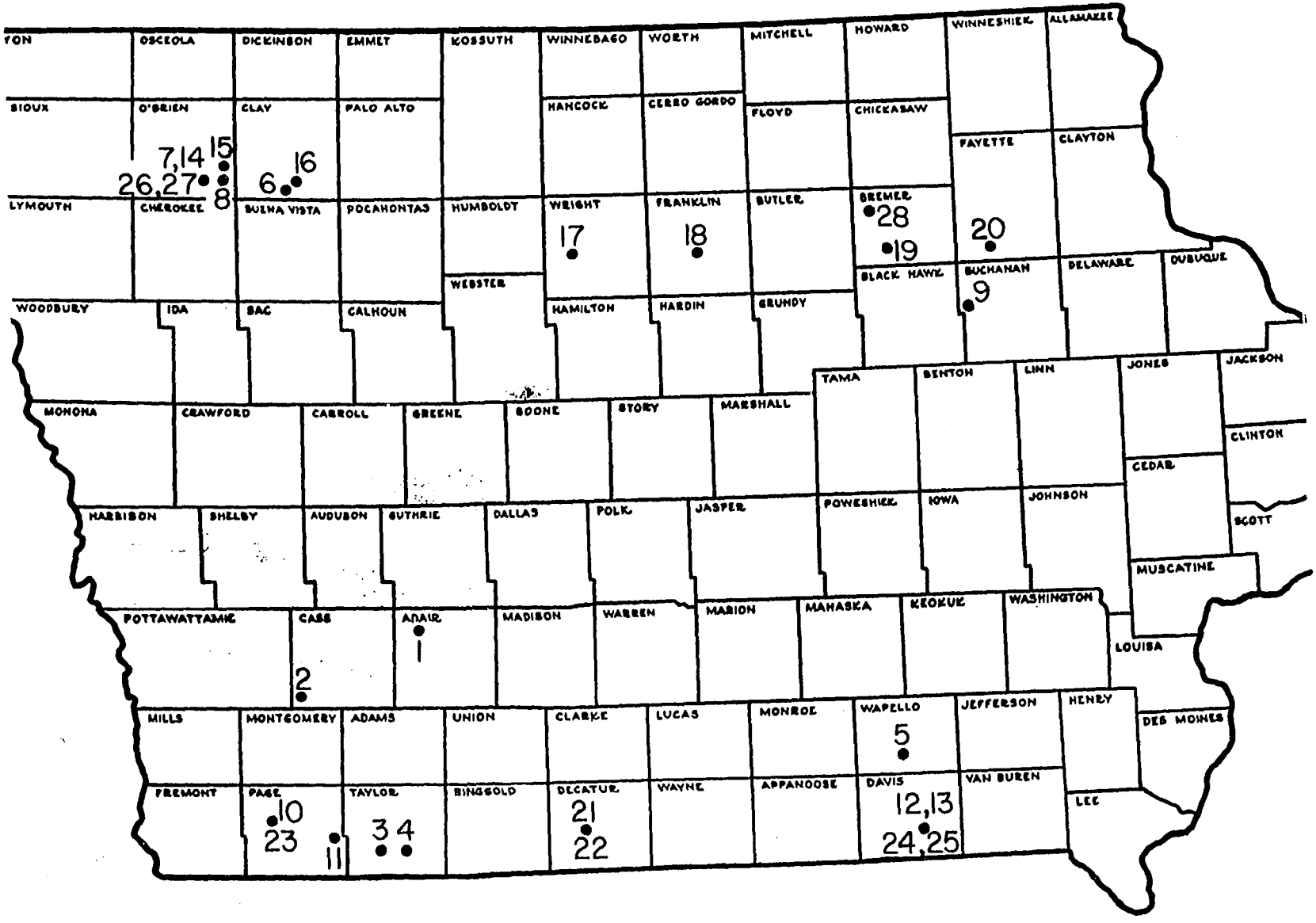

YON
OSCEOLA
DICKINSON
EMMET
KOSSUTH
WINNEBAGO
WORTH
MITCHELL
HOWARD
WINNESHIEK
ALLAMAKEE
SIOUX
O'BRIEN
CLAY
PALO ALTO
HANCOCK
CERRO GORDO
FLOYD
CHICKASAW
FAYETTE
CLAYTON
7,14 15
26,27
6
16
8
LYMOUTH
CHEROKEE
BUENA VISTA
POCAHONTAS
HUMBOLDT
WRIGHT
FRANKLIN
BUTLER
BREMER
28
19
17
18
20
BLACK HAWK
BUCHANAN
DELAWARE
DUBUQUE
9
WEBSTER
WOODBURY
IDA
SAC
CALHOUN
HAMILTON
HARDIN
GRUNDY
TAMA
BENTON
LINN
JONES
JACKSON
MONONA
CRAWFORD
CARROLL
GREENE
BOONE
STORY
MARSHALL
CLINTON
CEDAR
HARRISON
SHELBY
AUDUBON
GUTHRIE
DALLAS
POLK
JASPER
POWESHIEK
IOWA
JOHNSON
SCOTT
MUSCATINE
POTTAWATTAMIE
CASS
ADAIR
MADISON
WARREN
MARION
MAHASKA
KEOKUK
WASHINGTON
LOUISA
2
1
MILLS
MONTGOMERY
ADAMS
UNION
CLARKE
LUCAS
MONROE
WAPELLO
JEFFERSON
HENRY
DES MOINES
5
FREMONT
PAGE
TAYLOR
RINGGOLD
DECATUR
WAYNE
APPANOOSE
DAVIS
VAN BUREN
LEE
10
23
11
3 4
21
22
12,13
24,25

Table 2. Summary of extensive collections for green cloverworm parasite rearings. Iowa. Summer 1970

Date	Collection no.	County	No. sweeps	Host plant[a]
6/25	1	Adair	100	AC
"	2	Cass	200	C
"	3	Taylor	200	AC
"	4	"	200	AC
6/26	5	Wapello	200	A
6/29	6	Clay	200	AC
"	7	O'Brien	200	A
"	8	"	200	A
6/30	9	Buchanan	200	A
7/21	10	Page	250	AC
"	11	"	200	AC
"	12	Davis	350	AC
"	13	"	100	AC
7/23	14	O'Brien	300	A
"	15	"	100	A
"	16	Clay	200	A
"	17	Wright	300	A
"	18	Franklin	200	AC
"	19	Bremer	100	AC
"	20	Fayette	250	A
8/31	21	Decatur	250	AC
"	22	"	150	AC
"	23	Page	450	AC
"	24	Davis	340	AC
"	25	"	200	AC
9/1	26	O'Brien	200	A
"	27	"	350	A
9/-	28	Bremer	---	Legumes

[a]A = alfalfa; C = clover.

These larvae were subsequently returned to the laboratory where they were placed individually in cotton stoppered vials or 2-in. plastic zipper cases containing appropriate host plant material as the food source.

Figure 2. Locations of Ames area extensive sampling sites. Ames, Iowa. Summer 1970. Numbers are collection no. given in Table 3

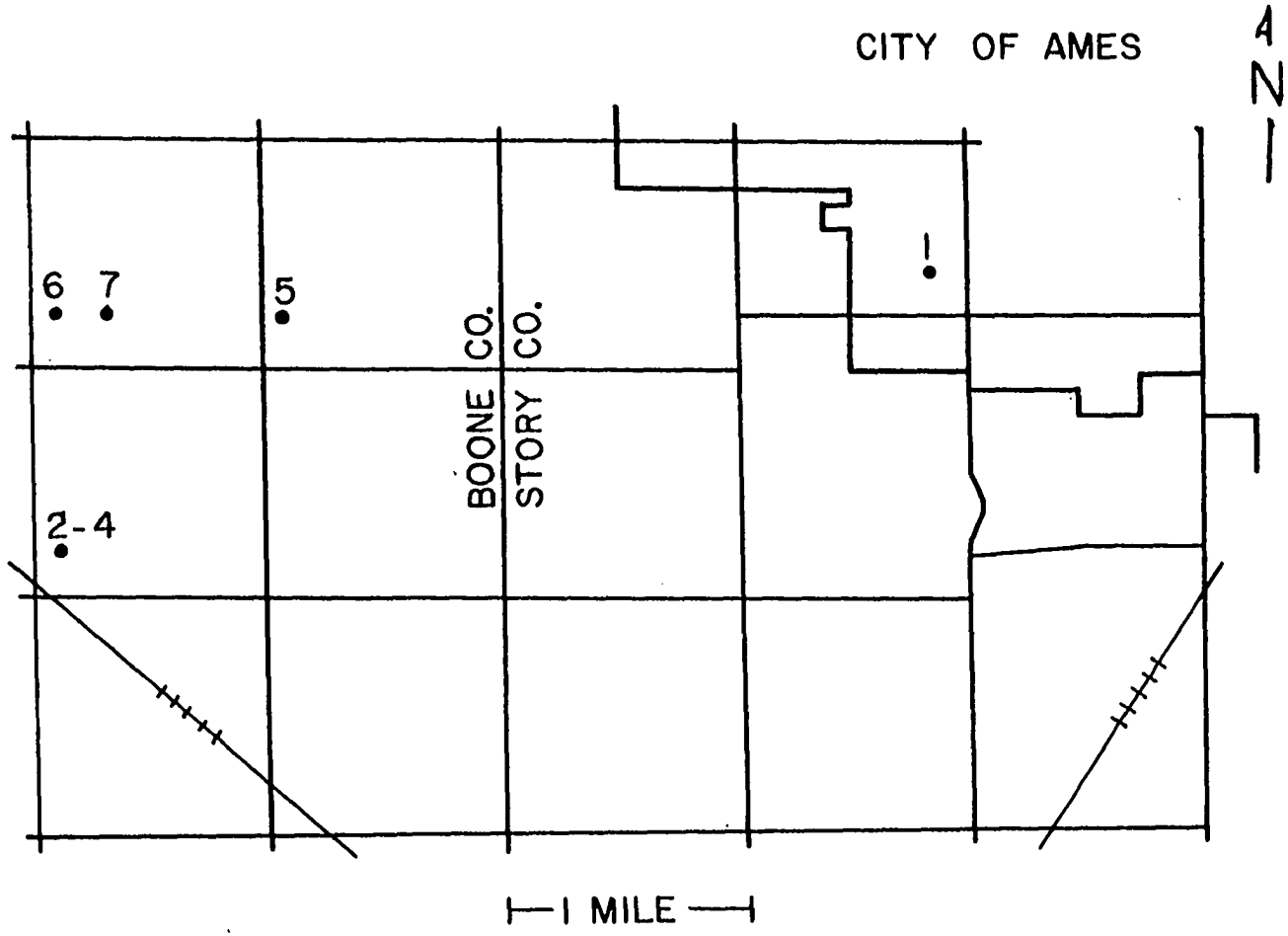

CITY OF AMES
N
1
6
7
5
2-4
BOONE CO.
STORY CO.
1 MILE

Table 3. Summary of Ames area extensive collections for green cloverworm parasite rearings. Ames, Iowa. Summer 1970

Date	Collection no.	No. sweeps	Host plant[a]
7/1	1	100	A
7/3	2	100	AC
"	3	100	AC
7/9	4	100	AC
7/13	5	100	AC
7/14	6	Unknown	AC
8/13	7	Unknown	S

[a]A = alfalfa; C = clover; S = soybean.

The larvae were held for parasite emergence and fed at least 3 times weekly. Larvae were held in the laboratory at approximately 24° C. As adult parasites emerged from cocoons, puparia or host larvae, they were killed, mounted and labelled with appropriate collection labels.

Egg Parasite Study

Field observations during mid-July, 1970, indicated an abundance of fecund green cloverworm adults. Sherman (1920) reported approximately 50% parasitism of the egg stage by Trichogramma pretiosa. Based on Sherman's report that egg parasitism can be a very important mortality factor, a study was conducted to measure the incidence of parasitism of green cloverworm eggs.

During the evening of July 18, clones of alfalfa and clover were removed from a university field which had been planted to a mixture of

alfalfa and red clover. This field, located approximately 2.5 miles west of Ames, Iowa, was the site where many moths had previously been observed in flight. Nine clones (4 alfalfa, 5 clover) were selected at 10-ft intervals along a transect across the field. These were removed with approximately 1 pint of soil and placed immediately into 1-qt plastic containers containing ½ pint of water.

The 9 clones were then taken to the laboratory and examined carefully for insect eggs. Any eggs found were removed. The "cleaned" plants were then placed in a 20 x 24 x 24 in. screened cage containing field- and light trap-collected moths. After approximately a 10-hr exposure to the moths, the plants, with the newly deposited eggs, were returned to their original locations in the field where they were planted in 1-pint containers. After a 72-hr exposure in the field, the plants were brought back to the laboratory where the leaflets containing green cloverworm eggs were removed and held individually in 1-oz jelly cups for parasite emergence. These leaflets in cups were kept in the laboratory at approximately 22° C.

1971 Extensive Sampling Program

The extensive sampling program for collection of green cloverworms for parasite rearing in 1971 was greatly expanded over the 1970 program. Two collecting trips were made into various areas of the state. Emphasis was placed on making collections in the 4 corners of the state, but additional collections were made during these trips as indicated in Tables 4 and 5. The approximate locations of fields from which collections

Table 4. Summary of extensive collections for green cloverworm parasite rearings. Southern Iowa. Summer 1971

Date	Field no.	County	No. samples[a]	Host plant[b]
7/15	1	Page	3	S
"	2	"	3	A
"	3	"	3	S
"	4	"	3	S
"	5	"	3	S
"	6	Taylor	2	C
"	7	Ringgold	2	S
"	8	Decatur	3	A
"	9	"	2	S
"	10	Davis	3	S
"	11	"	3	A
"	12	"	3	S
"	13	"	3	S
"	14	"	3	S
8/19	1	Page	3	S
"	3	"	3	S
"	5	"	3	S
"	10	Davis	3	S
"	12	"	3	S
"	13	"	3	S
"	14	"	3	S
"	15	Page	3	S
"	16	Wayne	4	S
"	17	Appanoose	4	S

[a]Each sample 100 sweeps.

[b]A = alfalfa, C = clover, S = soybean.

were made in 1971 are shown in Figure 3.

The sampling techniques for the 1971 season were modified in the following manner. Sample sizes in all host crops were standardized at 100 sweeps/sample. When collections were made in soybean fields, 20 sweeps were taken from a row in 5 different places in a field. These 5

Table 5. Summary of extensive collections for green cloverworm parasite rearings. Northern Iowa. Summer 1971

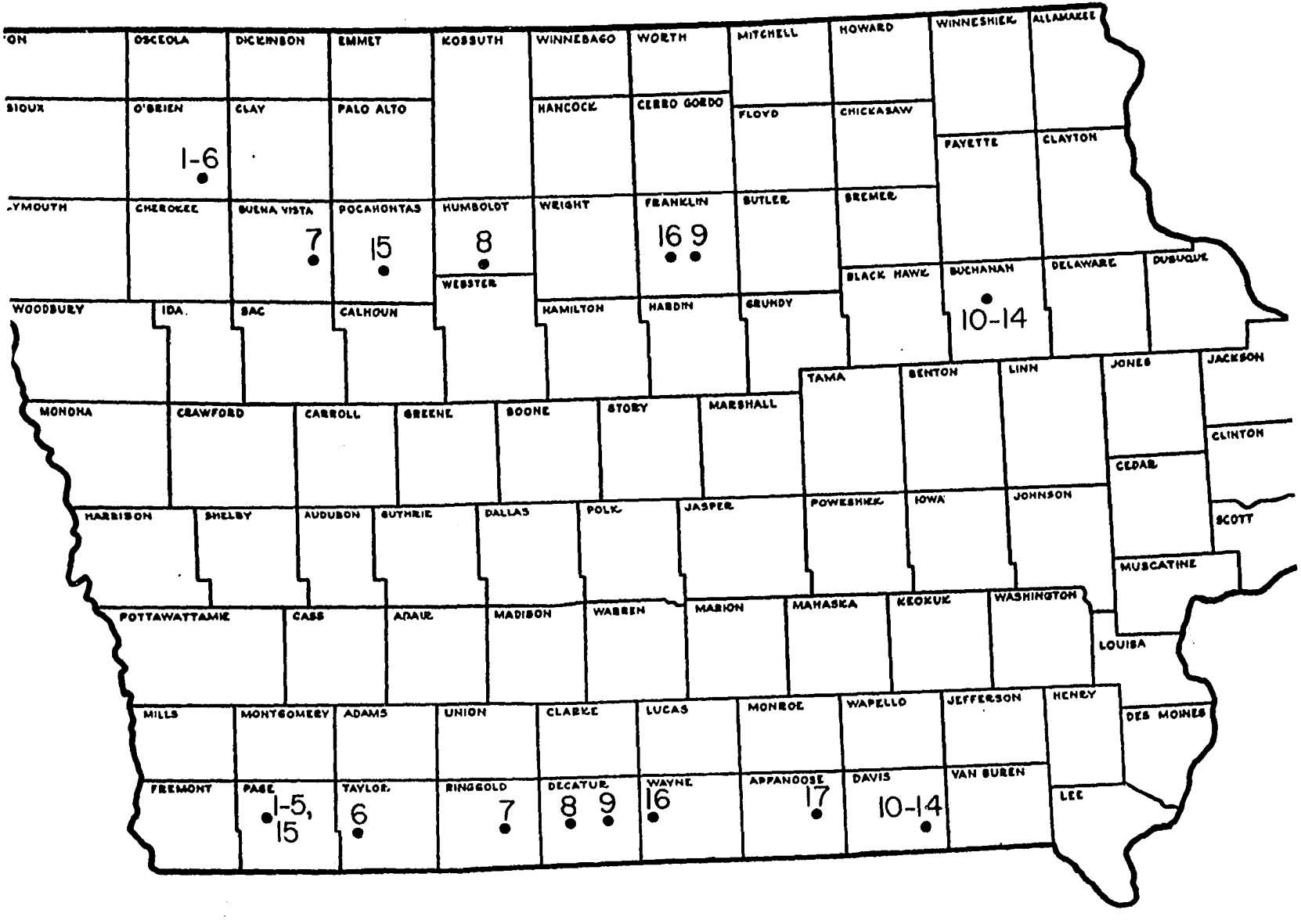
Date	Field no.	County	No. samples[a]	Host plant[b]
7/22	1	O'Brien	3	S
"	2	"	3	S
"	3	"	3	S
"	4	"	2	A
"	5	"	3	S
"	6	"	1	A
"	7	Buena Vista	2	A
"	8	Humboldt	2	S
"	9	Franklin	1	S
"	10	Buchanan	3	S
"	11	"	3	S
"	12	"	2	C
"	13	"	3	S
"	14	"	3	S
8/20	1	O'Brien	3	S
"	2	"	3	S
"	3	"	3	S
"	5	"	3	S
"	8	Humboldt	2	S
"	10	Buchanan	3	S
"	11	"	3	S
"	12	"	2	C
"	13	"	3	S
"	14	"	3	S
"	15	Pocahontas	2	S
"	16	Franklin	2	S

[a]Each sample 100 sweeps.

[b]A = alfalfa, C = clover, S = soybean.

subsamples were pooled and constituted 1 sample of 100 sweeps. When sweeps were taken in alfalfa and clover fields, the surveyor made 100 sweeps along a transect through the field.

Figure 3. Field locations for extensive collections for green cloverworm parasite rearings in Iowa. Summer 1971. Numbers are field no. given in Tables 4 and 5


OSCEOLA
DICKINSON
EMMET
KOSSUTH
WINNEBAGO
WORTH
MITCHELL
HOWARD
WINNESHIEK
ALLAMAKEE
SIOUX
O'BRIEN
1-6
CLAY
PALO ALTO
HANCOCK
CERRO GORDO
FLOYD
CHICKASAW
FAYETTE
CLAYTON
CHEROKEE
BUENA VISTA
7
POCAHONTAS
15
HUMBOLDT
8
WRIGHT
FRANKLIN
16 9
BUTLER
BREMER
WEBSTER
BLACK HAWK
BUCHANAN
10-14
DELAWARE
DUBUQUE
WOODBURY
IDA
SAC
CALHOUN
HAMILTON
HARDIN
GRUNDY
TAMA
BENTON
LINN
JONES
JACKSON
MONONA
CRAWFORD
CARROLL
GREENE
BOONE
STORY
MARSHALL
CLINTON
CEDAR
HARRISON
SHELBY
AUDUBON
GUTHRIE
DALLAS
POLK
JASPER
POWESHIEK
IOWA
JOHNSON
SCOTT
MUSCATINE
POTTAWATTAMIE
CASS
ADAIR
MADISON
WARREN
MARION
MAHASKA
KEOKUK
WASHINGTON
LOUISA
MILLS
MONTGOMERY
ADAMS
UNION
CLARKE
LUCAS
MONROE
WAPELLO
JEFFERSON
HENRY
DES MOINES
FREMONT
PAGE
1-5,
15
TAYLOR
6
RINGGOLD
7
DECATUR
8 9
WAYNE
16
APPANOOSE
17
DAVIS
10-14
VAN BUREN
LEE

During the preceding season, it was noted that, when collections were made from damp fields, excessive amounts of moisture accumulated in the muslin sweep nets. This moisture made the nets heavier and resulted in the death of many of the larvae collected. Thus, during the 1971 season, a commercially available 15-in.-diam nylon-mesh insect sweep net was used.

The collected larvae were removed from each sample and placed in a 1-qt ice cream carton with host plant material or, if time permitted, larvae were placed individually in 2-in.-diam clear plastic zipper cases which also contained host plant material.

When the larvae were returned to the laboratory, they were placed individually in zipper cases and assigned an accession number. A 5 x 8-in. card, also assigned the accession number, was used for recording all notes on the specific larva. Initially, if time permitted, the stage of each larva was determined and recorded. At later times, notes were made as to parasite emergence, pupation (or pupariation) and adult parasite emergence. If the larva was not parasitized and a green cloverworm moth emerged, its sex was noted. If neither parasite nor moth emerged, the dead green cloverworm larva or pupa was dissected to determine the presence of a parasite. If none was found, the cause of death was listed as unknown. On some occasions, the larvae died of a fungus disease.

For purposes of data storage, retrieval, and analyses, quantitative data on each larva collected in the 1971 season, in both the intensive and the extensive collections, were stored on individual IBM data cards

according to the format of the data record sheet shown in Appendix A, Figure 20.

A large rack containing 21 trays was constructed to facilitate the handling of large numbers of larvae. Individual trays, capable of holding 100 zipper cases, were constructed of 1 x 2 in. lumber as a frame and 1/8-in Masonite® board for the tray.

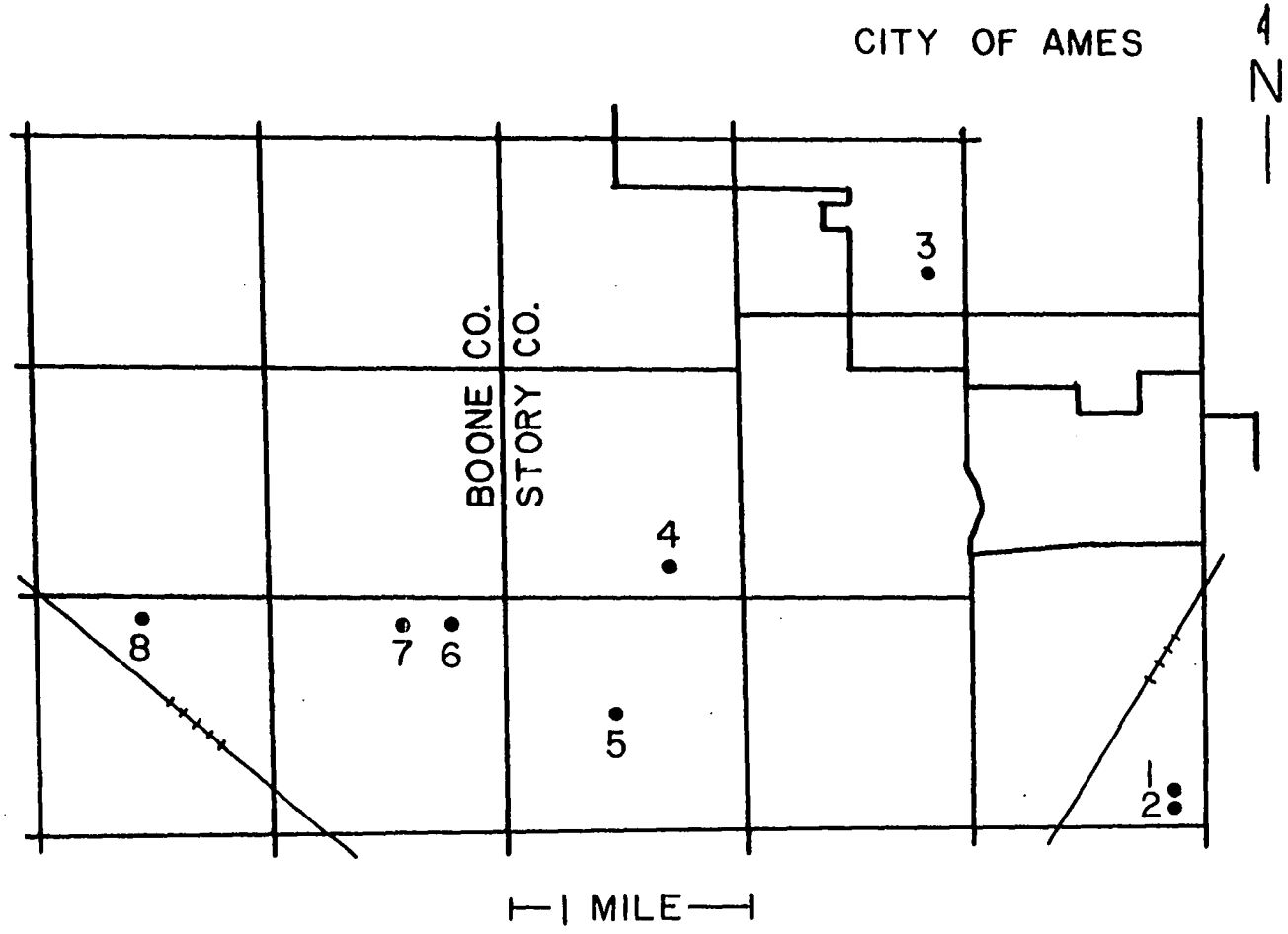
Larvae were held on the trays in the laboratory where the temperature was approximately 73° F. Attempts were made to inspect all cases daily, making the necessary notes and providing fresh food as needed. Parasites emerging were mounted and appropriately labeled.

1971 Intensive Sampling Program

An intensive sampling program was conducted near Ames, Iowa, during the 1971 season to learn more concerning parasitism within green cloverworm populations and to elucidate various host-parasite relationships. Eight fields (number 1 through 8), located near Ames (Figure 4), were selected as study sites. Four of these fields were soybean, 2 were alfalfa, and 1, a single small red clover field.

The sampling program consisted of taking weekly samples (5 of 20 sweeps each) from the clover field. The locations of the samples were arbitrarily selected. Samples taken from the remaining 7 fields consisted of 4 samples of 100 sweeps each taken along 4 transects across the field. These transects were selected systematically by 1st dividing the field (or a portion of it) into 4 parts approximately 30 yd wide and subsequently dividing each part into corridors ca. 5 yd wide. Each

Figure 4. Intensive sampling program field locations for collection of green cloverworm for parasite rearings. Ames, Iowa. Summer 1971. Odd digits are soybean field no., even digits are alfalfa and clover field no.


CITY OF AMES
N
BOONE CO.
STORY CO.
1
2
3
4
5
6
7
8
1 MILE

transect then followed longitudinally through a corridor. Samples were taken so that no corridor was sampled more than once in 3 weeks.

Larvae were swept from the plants with a 15-in.-diam nylon-mesh insect net. The pattern of sweeping along the transect was in a box like manner where the surveyor swept across ca. 6 ft of plants on all 4 sides in 25 places along the transect. Insects and plant material within the net were emptied 4 times/sample into a 1-gal wide mouth jar carried by the surveyor. At the end of the sample, the jar was brought to the edge of the field where 2 assistants sorted through plant material, retrieved the larvae and placed them individually in 2-in.-diam clear plastic zipper cases containing plant material for food. The surveyor then returned to the field to collect the next sample.

After collections were made in all fields, the samples were returned to the laboratory where they were assigned accession numbers. Records concerning each larva were again kept on the aforementioned 5 x 8 in. cards. Larvae in zipper cases were placed on the previously described holding trays, examined daily for parasite emergence and provided fresh food as required. Parasites emerging from these collections were killed, mounted, and appropriately labelled.

Biological Investigations of Rogas nolophanae

Rearing and maintenance of parasite colony

During the period from late Aug. 1971, to June 1972, a colony of Rogas nolophanae was maintained in the laboratory for the purpose of studying the biology of this important hymenopterous parasite of the

green cloverworm.

Adult wasps (reared from field collected larvae) were held in the laboratory in cages measuring 11 in. high x 1 ft^2 (Pedigo 1971). Cages were fitted with a sleeved front and a glass top and were covered on the remaining sides by Saran® screen (31 x 33 mesh/$in.^2$). Temperatures in the laboratory during this period ranged from 70° to 80° F. Relative humidity in the laboratory fluctuated between 40% and 60% during Aug.-Oct., gradually decreased during Nov., stabilized at ca. 20% during the winter months (Dec.-Mar.), and gradually increased to ca. 30% in May.

Adults were fed by streaking honey on the lower surface of the glass cage top. Distilled water was lightly sprayed into the cages twice daily. An open petri dish containing water soaked cotton was kept in the cage.

The adult colony was maintained by periodically exposing 3rd-stage green cloverworm larvae to female wasps. Approximately 15 larvae were placed in a 2-in. zipper case containing a soybean leaflet. A female wasp then was introduced into the case. After ca. 24 hr, the wasp was returned to the cage, and the exposed larvae were separated into individual zipper cases and held in the laboratory for observation. Larvae exposed to parasitization were also placed in greenhouse cages (description in next subsection). Wasps emerging from parasitized larvae were added to the caged colony. During the period the colony of Rogas nolophanae was maintained, numerous life history phenomena were observed which shall be discussed in subsequent sections.

Rearing and maintenance of P. scabra colony

The techniques for rearing green cloverworms used in these parasite studies were described by Pedigo (1971). Field collected green cloverworm moths (ca. 15 of each sex) were placed in greenhouse cages containing metal flats in which were growing ca. 50 soybean plants, 10-12 in. tall. Cages measuring 24-in.-tall x 20 x 24 in. were constructed of plywood bases and wood and Saran® screen (31 x 33 mesh/in.^{2}) sides. Each cage front was fitted with a 12-in.-tall Masonite® sleeve board on top of which was placed a 12-in.-tall glass pane. Environmental conditions in the greenhouse during the rearing program were: photophase 15 hr (supplied from 2 time-controlled overhead VHO fluorescent lamps); temperature 75° to 85° F; humidity 35% to 50% RH. Cage temperatures were less variable. The relative humidity in the plant canopy was ca. 70% RH.

Moths were allowed to oviposit on the plants for about 3 days and then were transferred to another cage. In order to prolong their lives and maximize egg production, moths were supplied water or a dilute sugar solution (1%) by spraying the cages twice daily. Larvae developing in the cages were used either in parasite studies or were transferred to other cages to maintain the green cloverworm colony. Larval populations were thinned to reduce the likelihood of disease epidemics experienced in earlier rearings. Larvae developing in the cages were allowed to pupate in the cage and as moths emerged, they were placed in cages to continue the colony.

Biological Investigations of Winthemia sinuata

Rearing and maintenance of parasite colony

During the period from late Sept. 1971, to Jan. 1972, a colony of Winthemia sinuata was maintained in the greenhouse for the purpose of studying the biology of this important dipterous parasite of the green cloverworm.

Adult flies, reared from field collected green cloverworm larvae, were held in the greenhouse in cages similar to those used for holding Rogas except Saran® screen was replaced with Fiberglas® screen (16 x 18 mesh/in.^{2}). Environmental conditions in the greenhouse were described in the preceding section.

Adults were fed by streaking a mixture of honey and Brewer's yeast on the lower surface of the glass cage top. Distilled water was lightly sprayed into the cages twice daily. An open petri dish containing water soaked cotton was kept in the cage.

The adult colony was maintained by placing 5th and 6th-stage green cloverworm larvae in the cage and allowing the flies to oviposit on the larvae. Larvae with fly eggs visible on them were removed from the cage and held individually in 2-in.-zipper cases in the laboratory where parasite development was observed. Environmental conditions in the laboratory were described in the preceding section. During the period the colony of Winthemia sinuata was maintained, numerous life history phenomena were observed which shall be discussed in subsequent sections.

Determination of Parasite Species

Identifications of the parasites reared from green cloverworms were made, so far as possible, by the author. Determinations were made to the family level using keys presented by Borror and DeLong (1964).

Species of flies emerging as adults were readily separated. Identification of the species represented was attempted by utilizing the literature and keys presented by Reinhard (1931), Curran (1934), and Cole (1969), and by comparing specimens reared from the green cloverworm with specimens loaned by other green cloverworm researchers, and specimens located in the Iowa State University entomological research collection.

In many instances, adult flies failed to emerge from puparia formed by the developing fly parasites. Determination of these specimens was made by comparing slide mounts of the posterior spiracles of the immature fly with mounts of spiracles taken from the empty puparia from which known species of flies had emerged. Slide mounts were prepared by first clearing fly larvae or puparia and then boiling these in a hot solution of KOH. The posterior end of each specimen was removed with a razor blade, and a wet mount was prepared.

Adult species of hymenopterous parasites belonging to the family Braconidae were generically placed using the key presented by Marsh (1971) and by comparing Iowa specimens with those loaned by other workers. Parasite cocoons from which adults failed to emerge were readily separated according to genus.

Adult wasps of the family Ichneumonidae were tentatively identified by keys presented by Townes (1969).

Representative specimens of the major parasites of the green cloverworm, along with rarely collected parasites and hyperparasites, were forwarded to taxonomic specialists of the USDA, Agr. Res. Serv., Systematic Entomology and Beneficial Insect Introduction Laboratory for confirmation and further identification.

RESULTS AND DISCUSSION

Extensive Sampling Programs 1970-71

Species collected

A list of the 9 species of primary parasites (representing 2 orders and 3 families) reared from green cloverworm larvae collected in 1970-71 is presented in Table 6. Five of these are reported as parasites of the green cloverworm for the 1st time.

The numbers of green cloverworm larvae collected, the total incidence of parasitism, and the incidence of parasitism by species in each of the extensive collections made in 1970-71 are presented in Tables 7, 8 and 9. No attempt was made in this study to adjust or correct parasitism in relation to the number of individuals which died of unknown causes. Thus, parasitism reported herein is a minimum which could conceivably be greater.

The most prevalent parasite found in the extensive collections was the braconid wasp, Rogas nolophanae, which was reared from 14.4% of the larvae collected in the 1970 state-wide samples, from 17.5% of the larvae collected in the 1970 Ames samples, and from 18.8% of the 1971 state-wide samples. In previous reports, R. nolophanae was reported as the most prevalent parasite of the green cloverworm in Tennessee by Hill (1925), in Delaware (6.5% parasitized) by Whiteside et al. (1967), and in Missouri (6.4% parasitized) by Barry (1970).

Other reports of this species as a parasite of the green cloverworm are obscured because of improper identifications and generic changes.

Table 6. Parasites of the green cloverworm reared from hosts collected in Iowa during 1970-71

Parasite
DIPTERA
Tachinidae
Blondelia hyphantriae (Tothill)[a]
Oswaldia assimilis (Townsend)[a]
Winthemia sinuata Reinhard
Lespesia archippivora (Riley)[a]
HYMENOPTERA
Braconidae
Apanteles flaviconchae Riley
A. marginiventris (Cresson)
Meteorus hyphantriae Riley[a]
Protomicroplitis facetosa (Weed)
Rogas nolophanae Ashmead
Ichneumonidae
Sinophorus validus (Cresson)[a]

[a]Reported for first time as parasites of the green cloverworm.

Hawley (1922) and Balduf (1923) both reported *Aleiodes intermedius* Cresson as a parasite of the green cloverworm. Muesebeck et al. (1951) placed both *Aleiodes* and *Rhogas* into synonomy under *Rogas* and further placed *A. intermedius* Cresson into synonomy under *Rogas stigmator* (Say). These latter authors did not, however, recognize the green cloverworm as a host of *R. stigmator*.

Hill (1925) reported *Rhogas canadensis* Cresson as a parasite of the green cloverworm, but Muesebeck et al. (1951) placed this species into synonomy under *Rogas scrutator* (Say) and again did not list the green

Table 7. Green cloverworm larval populations and percent parasitism by parasite species in extensive collections for green cloverworm parasite rearings. Iowa. Summer 1970

Date	County	Total no. larvae collected	Total no./ 100 sweeps	Total no. larvae parasitized	Total % parasitism	% *Rogas nolophange*	% *Apanteles marginiventris*
							Northern
6/29	Clay	12	6.0	1	8.3		
"	O'Brien	17	8.5	10	58.8	11.7(2)[a]	11.7(2)
"	"	13	6.5	6	46.2	30.8(4)	
6/30	Buchanan	7	3.5	3	42.9		
7/23	O'Brien	43	14.3	12	27.9	18.6(8)	
"	"	4	4.0	0	0		
"	Clay	16	8.0	9	56.3	18.8(3)	6.3(1)
"	Wright	11	3.7	1	9.1		
"	Franklin	21	10.5	0	0		
"	Bremer	19	19.0	6	31.6	21.1(4)	
"	Fayette	16	6.4	3	18.8	6.3(1)	
9/1	O'Brien	64	32.0	31	48.4	25.0(16)	3.1(2)
"	"	91	26.0	34	37.4	20.9(19)	
9/-	Bremer	170	--	71	41.8	20.0(34)	
	Total	504		187	37.1	18.1(91)	1.0(5)
	Mean	11.4 ± 9.0					
							Southern
6/25	Adair	24	24.0	10	41.7	33.3(8)	
"	Cass	6	3.0	1	16.7	16.7(1)	
"	Taylor	5	2.5	1	20.0		20.0(1)
"	"	7	3.5	0	0		
6/26	Wapello	20	10.0	4	20.0	5.0(1)	
7/21	Page	32	12.8	6	18.8	3.1(1)	
"	"	1	.5	1	100.0		
"	Davis	41	11.7	18	43.9		
"	"	37	37.0	7	18.9	2.7(1)	
8/31	Decatur	55	22.0	11	20.0	16.4(9)	
"	"	85	56.7	19	22.4	9.4(8)	2.4(2)
"	Page	8	1.8	3	37.5		
"	Davis	13	3.8	4	30.8	7.7(1)	7.7(1)
"	"	36	18.0	8	22.2	13.9(5)	
	Total	370	--	93	25.1	9.5(35)	1.1(4)
	Mean	14.8 ± 16.0					
Grand total		874		280	32.0	14.4(126)	1.0(9)
Grand mean		13.2 ± 13.0					

[a]No. in parentheses is the no. of larvae parasitized by given species.

[b]Two species of parasites reared from 1 host.

parasitism by						
Apanteles flavi-conchae	Proto-microplitis facetosa	Sino-phorus validus	Winthemia sinuata	Oswaldia assim-ilis	Blon-delia hyphan-triae	Lespesia archippivora
Iowa						
				8.3(1)		
			23.5(4)	17.6(3)		
				15.4(2)		
			42.9(3)			
			7.0(3)	2.3(1)		
12.5(2)			18.8(3)			
			9.1(1)			
5.3(1)			5.3(1)			
6.3(1)			6.3(1)			
			10.9(7)	9.4(6)		1.6(1)[b]
			12.1(11)	4.4(4)		
			8.2(14)	10.6(18)	1.8(3)	
0.8(4)			9.5(48)	6.9(35)	0.6(3)	0.2(1)
Iowa						
			8.3(2)			
			15.0(3)			
	3.1(1)		6.3(4)			
	100.0(1)					
	4.9(2)		39.0(16)			
	2.7(1)		13.5(5)			
	1.8(1)		1.8(1)			
	1.2(1)		9.4(8)			
	25.0(2)	12.5(1)				
			15.4(2)			
	5.6(2)		2.8(1)			
	3.0(11)	0.3(1)	11.4(42)			
.5(4)	1.3(11)	.1(1)	10.3(90)	4.0(35)	.3(3)	.1(1)

Table 8. Green cloverworm larval populations and percent parasitism by parasite species in Ames area extensive collections for green cloverworm parasite rearings. Ames, Iowa. Summer 1970

Date	No. larvae collected[a]	No. larvae parasitized	Total % parasitism	% parasitism by			
				Rogas nolophanae	Apanteles marginiventris	Apanteles flaviconchae	Winthemia sinuata
7/1	37	14	37.8	27.0(10)[b]	10.8(4)		
7/3	58	11	19.0	13.8(8)			5.2(3)
"	34	6	17.6	11.8(4)		2.9(1)	2.9(1)
7/9	38	3	7.9	5.3(2)			2.6(1)
7/13	7	0	0				
7/14	2	1	50.0				50.0(1)
8/13	36	15	41.7	36.1(13)	5.6(2)		
Total	212	50	26.6	17.5(37)	2.8(6)	0.5(1)	2.8(6)

[a]All samples were 100 sweeps except 7/14 and 8/13 when sweeps were uncounted.

[b]No. in parentheses is the no. of larvae parasitized by given species.

Table 9. Green cloverworm larval populations and percent parasitism by parasite species in extensive collections for green cloverworm parasite rearings. Iowa. Summer 1971

Date	Total no. larvae collected	$\bar{X} \pm SE$[a]	Total no. parasitized larvae	Total % parasitism	% parasitism by: *Rogas nolophanae*	*Winthemia sinuata*	*Protomicroplitis facetosa*	*Apanteles marginiventris*	*Oswaldia assimilis*	*Blondelia hypantriae*
					Northern Iowa					
7/22	129	3.80±4.82(34)	42	32.8	22.5(29)[b]	5.4(7)	0.8(1)	1.6(2)	2.3(3)	
8/20	79	2.47±2.26(32)	41	51.9	49.5(32)	2.5(2)		1.3(1)	5.1(4)	2.5(2)
Total	208		83	29.9	29.3(61)	4.3(9)	.5(1)	1.4(3)	3.4(7)	1.0(2)
					Southern Iowa					
7/15	30	.77±1.22(39)	14	46.7	20.0(6)	3.3(1)	6.7(2)	13.3(4)		
8/19	263	7.97±4.81(33)	84	31.9	10.3(27)	17.1(45)	1.9(5)	0.4(1)		1.9(5)
Total	293		98	33.4	11.3(33)	15.7(46)	2.4(7)	1.7(5)		1.7(5)
Grand total	501		181	36.1	18.8(94)	11.0(55)	1.6(8)	1.6(8)	1.4(7)	1.4(7)

[a]No. in parentheses is the no. of samples in collection.

[b]No. in parentheses is the no. of larvae parasitized by given species.

cloverworm as a host of this species.

R. stigmator and R. scrutator were not reported as parasites of the green cloverworm in recent studies conducted in Delaware and Missouri. Based on the preceding facts, it is the writer's opinion that the reports of Hawley, Balduf, and Hill refer to R. nolophanae rather than R. stigmator and R. scrutator.

Muesebeck et al. (1951) included in the distribution of R. nolophanae only the states of Maryland, Ohio, Tennessee, Wisconsin, Mississippi, Louisiana, Kansas, and Missouri. If specimens reported by Hawley (1922) and Hill (1925) are R. nolophanae, then the distribution should include both New York and Indiana. Whiteside et al. (1967) added Delaware to the distribution while Lentz and Pedigo (1972) reported it from Iowa.

Although R. nolophanae is widely distributed in the eastern portion of the U.S., its list of alternate hosts includes only a single species, Balsa malana Fitch (Muesebeck et al. 1951). Thompson (1953) included only the green cloverworm as a host of R. nolophanae.

In 1970-71 studies, Rogas was reared from larvae collected in all areas of the state. However, total seasonal parasitism by Rogas in 1970 in northern Iowa was 1.9 times greater than parasitism in southern Iowa (18.1% cf. 9.5%). Seasonal parasitism by Rogas in the Ames area (17.5%) was comparable to that of northern Iowa. In extensive collections made in 1971, total seasonal parasitism by Rogas was 1.6 times greater in northern Iowa than in southern Iowa (29.3% cf. 11.3%).

In the extensive collections of 1970-71, parasitism by Rogas at different times of the growing season was quite variable. In 1970

studies, parasitism by Rogas in late June was 14.4%, in late July, 7.3% and in late Aug. and early Sept., 17.6%. In 1971 studies, parasitism increased from 22.5% in late July in northern Iowa to 40.5% in late Aug. However, in southern Iowa, parasitism dropped from 20.0% in mid-July to 10.3% in mid-Aug.

The variation in parasitism noted at various times throughout the season was also evident at different places within the state at any one time. During both seasons, when 5 or more larvae were collected/100 sweeps, parasitism ranged from 0 to 83.3%. In 87.7% of the collections, parasitism ranged 0-40% and in 59.2% of the collections, it ranged 0-20%. It will be shown in following sections that this variation is related directly to the age structure of the population being sampled.

During the 1970 season, it was noted that Rogas was reared primarily from larvae collected as 3rd- or 4th-stage larvae. During 1971, the more exhaustive records revealed that, in extensive collections, Rogas was reared from larvae collected as 3rd-, 4th-, or 5th-stage 19.3, 50.0 and 29.5% of the time, respectively.

The 2nd most prominent parasite reared from larvae collected in 1970-71 extensive collections was the tachinid fly, Winthemia sinuata. In the 1970 state-wide samples, total seasonal parasitism was 10.3% (9.5% in northern Iowa and 11.4% in southern Iowa). Parasitism in Ames area samples, however, was only 2.8%. During 1971, parasitism in the state-wide samples was 11.0%, but was 3.7 times greater in southern Iowa than in northern Iowa (15.7% cf. 4.3%).

In comparison, in their studies in Delaware in 1965, Whiteside et al.

(1967) also found that W. sinuata was the 2nd most abundant parasite of the green cloverworm. Total seasonal parasitism was 6.2%. Barry (1970), however, found it ranked 3rd in prominence in Missouri in 1969 where seasonal parasitism was 3.3%.

Although differences in the incidence of parasitism were noted in various areas of the state in 2 growing seasons, W. sinuata was reared from larvae collected in all areas of the state. Barry (1970) also found this species in all areas of Missouri.

Previous reports of this species as a parasite of the green cloverworm have been obscured because of the morphological similarity of the species to W. quadripustulata. Reinhard (1931), in his description of W. sinuata, reported that a specimen he had determined from Iowa as W. quadripustulata was actually W. sinuata. Hill (1925) reported specimens reared from the green cloverworm in Missouri and Tennessee were W. quadripustulata. However, in his studies in Missouri in 1969, Barry (1970) found that none of the green cloverworms were parasitized by W. quadripustulata. Balduf (1923), in Ohio, also reported W. quadripustulata as a parasite of the green cloverworm. Some of the specimens upon which Reinhard's description of W. sinuata was based were collected in Ohio. In studies further east in Delaware, Whiteside et al. (1967) reared only W. sinuata from the larvae which they collected. These facts strongly suggest that parasites of the green cloverworm presented as W. quadripustulata in years past might more properly be labeled W. sinuata.

The distribution of W. sinuata, as presented by Stone et al.

(1965), includes the area from Maine to North Dakota, south to Mexico and Georgia. This distribution closely coincides with the distribution of the green cloverworm as presented by Pedigo et al. (1973). W. sinuata is reported by Thompson (1951) as being rather host specific. Although he lists 6 species as hosts of W. sinuata, only 2 (P. scabra and Erannis tiliaria) are not of questionable record.

According to previous reports, parasitism by W. sinuata is usually solitary (1 maggot/host larva). In 1970 studies, 85.7% of all larvae parasitized by W. sinuata contained only 1 maggot, 9.1% contained 2 maggots, 3.9% contained 3 maggots, and 1.3% contained 4 maggots. In 1971 extensive collections, the percentages of W. sinuata parasitized larvae containing 1, 2, 3, or 4 maggots were: 79.6, 16.7, 1.9, and 1.95, respectively.

In collections of 1970, it was noted that W. sinuata was reared from nearly mature larvae. Counts made in the 1971 extensive collections reveal that W. sinuata was reared from 6th-stage larvae 94.2% of the time and only 5.8% of the time was it reared from larvae collected in the 5th-stage.

Parasitism by W. sinuata varied not only in different areas of the state, but also at different times. In 1970, parasitism in the 3 extensive collections (late June, late July, and Late Aug.) was 10.8, 13.8, and 8.4%. In 1971, parasitism by W. sinuata in northern Iowa dropped from 5.4% in late July to 2.5% in late Aug. In southern Iowa, parasitism rose from 3.3% in mid-July to 17.1% in mid-Aug.

The 3rd most prevalent parasite was the tachinid fly, Oswaldia

assimilis, reported here for the 1st time as a parasite of the green cloverworm. In the extensive collections of 1970-71, this species parasitized 2.7% of the larvae collected. In these extensive collections, it was reared only from those taken in northern Iowa. Seasonal parasitism in northern Iowa in 1970 was 6.9% and in 1971 was 3.4%. Although O. assimilis was not reared from Ames area collections in 1970, it was reared from larvae collected in the intensive studies at Ames in 1971.

Thompson (1951) did not present any host information for this species. Stone et al. (1965) stated that members of the tribe to which it belongs (Blondeliini) parasitize larvae of Lepidoptera, Coleoptera, and Hymenoptera (Tenthredinidae). The distribution of O. assimilis, as presented by Stone et al. (1965) includes the area from North Dakota to New Brunswick south to Mississippi and Georgia.

Host larvae of O. assimilis contained single parasites in most instances. In 1970, 86.8% of O. assimilis parasitized larvae contained only 1 maggot, 10.5% contained 2 maggots, and 2.6% contained 3 maggots. In the extensive collections of 1971, 71.4% of O. assimilis parasitized larvae contained 1 maggot and 28.6% contained 2 maggots. In the 1971 collections, it was noted that 4 5th-stage and 2 6th-stage larvae were parasitized by O. assimilis. No stage designations were made on other larvae from which O. assimilis was reared.

Two other species of tachinid flies, both of which are reported here as parasites of the green cloverworm for the 1st time, were collected in the extensive collections of 1970-71. In 2 years of extensive collections, only 10 larvae were parasitized by Blondelia hyphantriae.

However, many more specimens were reared in the intensive studies at Ames in 1971. The total parasitism by B. hyphantriae for the 2 years of extensive collections was ca. 0.6%. The species was reared from larvae collected in northern and southern Iowa. In both seasons, B. hyphantriae was reared from larvae collected after mid-Aug. Records from 6 B. hyphantriae parasitized larvae collected in 1971 show that 4 were 6th-stage and 2 were 5th-stage larvae. In both years of the extensive collections, B. hyphantriae was reared only as a solitary parasite.

According to Stone et al. (1965), the distribution of the species includes the area from Minnesota to Ontario and Massachusetts, south to Washington, D.C. and also, British Columbia, Washington, and Colorado. Although Thompson (1951) did not list any hosts of the species, Tothill (1922) listed it among the parasites of the fall webworm in Canada.

The other tachinid fly reared from the green cloverworm and reported here for the 1st time as a parasite of it is Lespesia archippivora. The single specimen, reared in 1970 from a larva collected in northwest Iowa, was unique in that it emerged from a larva also parasitized by W. sinuata.

The distribution of L. archippivora presented by Stone et al. (1965) includes all of the U.S., Mexico and from British Columbia to Ontario in Canada. Although Thompson (1951) did not list any hosts of the species, it has been reared from other larvae (most of which are larger) and "is one of the most widespread parasites of lepidopterous larvae in North America" (Bryan, Jackson, and Patana 1968).

Adult flies were quite readily separated to species with one

exception. The specimen of L. archippivora was quite small and looked similar to W. sinuata. A slide mount of the posterior spiracles indicated it was a different species and subsequent identification by a specialist confirmed that it was. W. sinuata, the most common fly, is a stout bodied gray fly with a silver colored abdomen which is marked in the pleural areas by reddish spots. O. assimilis is more narrow and cylindrical and is marked by contrasting black and silver areas. B. hyphantriae, generally the largest of the 3, is uniformly gray, has a robust thorax and an abdomen which tapers to a rather sharp point.

Many of the adult flies failed to emerge from puparia, but immature parasites were readily identified to species by the posterior spiracles on the last-stage larva or the puparium. Figure 5 presents characters which permit separation of the species.

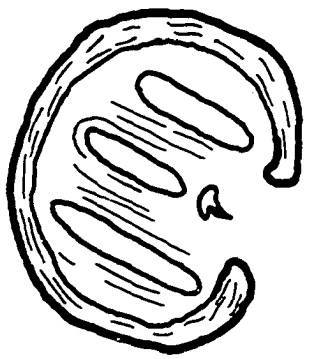
The 4th most prevalent parasite in the extensive collections was the braconid wasp, Apanteles marginiventris, whose total state-wide parasitism for 2 seasons was ca. 1.5%. In the 1970 collections, 15 specimens (5 from northern Iowa, 4 from southern Iowa and 6 from the Ames area) were reared from green cloverworms. Parasitism for each of the above areas during 1970 was 1.0, 1.1, and 2.8%, respectively. In the 1971 collections from northern and southern Iowa, parasitism was 1.4 and 1.7%, respectively.

Whiteside et al. (1967) noted that A. marginiventris was the 3rd most prevalent parasite of the green cloverworm in Delaware. Total seasonal parasitism there was 4.1%. Barry (1970), in Missouri, found that A. marginiventris was the 4th most prevalent parasite and parasitized

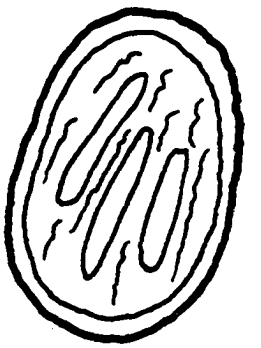
Figure 5. Pictorial key to the species of immature fly parasites of the green cloverworm in Iowa

Peritreme of posterior spiracle incomplete, horseshoe shaped

Peritreme complete and oval

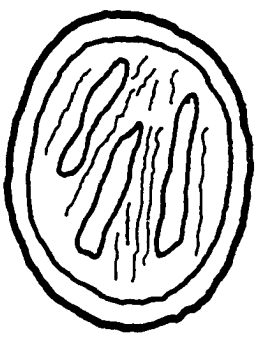


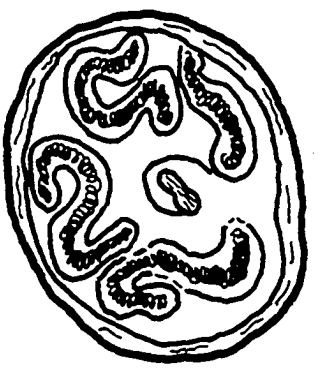
Winthemia sinuata



Respiratory slits straight

Respiratory slits sinuate





Lespesia archippivora

Heavy spines above posterior spiracles sparse

Heavy spines above posterior spiracles numerous

Oswaldia assimilis

Blondelia hyphantriae

only 2.7% of the larvae collected.

The distribution of A. marginiventris includes the area from Virginia to Florida, west to Kansas and Texas and also Ohio, Indiana, and the West Indies (Muesebeck et al. 1951). Krombein et al. (1958, 1967) added the states of Wisconsin, California, and Hawaii to this distribution. Within this broad area, many economic pests serve as alternate hosts of this parasite. Thompson (1953) presented a list of 14 species which are hosts of A. marginiventris. Among them are representatives of the genera Autographa, Heliothis, Laphygma, and Prodenia, all of which are found in Iowa. Krombein et al. (1967) added another 5 species of alternate hosts. Included in the list of natural enemies of A. marginiventris are 4 species of parasites (Thompson 1944).

Several studies have been conducted recently on this important larval parasite. Boling and Pitre (1970) reported on the life history of A. marginiventris and presented descriptions of the immature stages. Boling and Pitre (1971) discussed the efficiency of A. marginiventris as a population regulator of Trichoplusia ni. The susceptibility of A. marginiventris and Campoletis perdistinctus to insecticides was reported by Lingren et al. (1972).

A 2nd species of Apanteles, A. flaviconchae, was also reared from green cloverworms collected in 1970-71. Five specimens were reared during 1970, 4 of these from larvae collected in northern Iowa and 1 from the Ames area extensive collections. None was reared in the extensive collections in 1971, although 1 was reared from a larva collected in the Ames intensive study.

Muesebeck et al. (1951) included in the distribution of the species the area from Maine to Virginia, west to Minnesota and Texas. Krombein et al. (1967) added to its distribution the states of Utah and Washington. Thompson (1953) included 4 species of Lepidoptera as alternate hosts of this parasite.

The 5th most abundant parasite reared from larvae taken in the extensive collections of 1970-71 was the braconid wasp, Protomicroplitis facetosa. In 1970, this parasite was only reared from larvae collected in southern Iowa and total seasonal parasitism there (with 11 specimens) was 3.0%. In 1971, 7 specimens were reared from southern Iowa collections and 1 from northern Iowa. Seasonal parasitism for 1971 in the 2 areas was 2.4 and 0.5%, respectively. Total parasitism by P. facetosa in the extensive collections for 2 years was 1.2%.

Barry (1970) found parasitism in Missouri in 1969 by P. facetosa (5.0%) was almost twice as high as that reported by Whiteside et al. (1967) in Delaware (2.8) and it was more than 4 times as great as that found in Iowa.

All specimens of P. facetosa were reared from larvae collected during or after the 3rd wk of July. Whiteside et al. (1967) reported that P. facetosa was not present in appreciable numbers until after the 1st wk in Sept.

The distribution of P. facetosa includes the area from Ontario to West Virginia, west to British Columbia, Washington, and Colorado. It has also been reported from Georgia (Muesebeck et al. 1951). Although Thompson (1953) listed only P. scabra as a host of P. facetosa,

Muesebeck et al. (1951) listed 2 additional species. Krombein et al. (1958, 1967) gave 2 other hosts for this parasite.

Another primary parasite, reported as a parasite of the green cloverworm for the 1st time, was collected in Iowa in 2 years of study. A single specimen of the ichneumonid wasp, Sinophorus validus was reared from a larva collected in southwest Iowa on Aug. 31, 1970.

Muesebeck et al. (1951) stated that the distribution of S. validus is "transcontinental in the Transition and Upper Austral zones." Included in the list of hosts by these authors are 17 species of lepidopterans, most of which belong to the family Notodontidae. Thompson (1953) added 1 additional species to the list of hosts.

The last of the primary parasites of the green cloverworm reared in 2 years of study was the braconid wasp, Meteorus hyphantriae, reported here for the 1st time as a parasite of the green cloverworm. A single specimen was reared from a larva collected Aug. 24, 1971, in the intensive study at Ames.

Both Whiteside et al. (1967) and Barry (1970) reported M. autographa as a parasite of the green cloverworm. Meteorus sp. has been reported as a parasite of the green cloverworm by Hill (1925) and by Barry (1970).

The distribution of M. hyphantriae, presented by Muesebeck et al. (1951) includes all of the U.S. and Canada. Thompson (1953) presented a list of 26 hosts (all Lepidoptera) and Muesebeck listed 1 additional species. Krombein et al. (1958) added 3 additional species to the list of hosts. The list of natural enemies of the braconid includes 2 species

(Thompson 1944), 1 of which, Perilampus hyalinus, was reared in these studies as a hyperparasite associated with a dipterous parasite of the green cloverworm.

Total parasitism

Total parasitism of green cloverworms by all parasite species in extensive collections in 1970 was 30.4%. Parasitism in each of the 3 areas (northern Iowa, southern Iowa, and the Ames area) was 37.1, 25.1, and 26.6%, respectively. Total parasitism in the 1971 extensive samples was 36.1%. Parasitism in northern Iowa was 39.9% while in southern Iowa it was 33.4%.

From their studies conducted in Delaware, Whiteside et al. (1967) reported a total parasitism of 20.4%. In Missouri, the total parasitism in 1969 (Barry 1970) was ca. 18.8%.

In 1970, the total parasitism by all species in all collections for each of the months of June, July, Aug., and Sept. was 32.4, 23.5, 25.8, and 41.8%, respectively. Total parasitism in each of the 3 extensive collections of 1970 (north and south collections pooled and Ames data excluded) 32.7, 25.5, and 34.8%. In 1971, total parasitism in northern Iowa increased from 32.6% in the 1st collection (July 22) to 51.9% in the 2nd collection (Aug. 20). In southern Iowa, parasitism in the 1st collection (July 15) was 46.7% but dropped to 31.9% in the 2nd. Total parasitism in the 2 collecting trips in 1971, where results from northern and southern Iowa were pooled, did not differ appreciably (35.2% for the 1st collection and 36.6% for the 2nd).

Based on the 1970 extensive collections, percentage parasitism appears to increase late in the season. Whiteside et al. (1967) also found that parasitism increased late in the season. Barry (1970), however, found that the level of parasitism in Aug. and Sept. remained about the same.

Host population characteristics

The number of green cloverworm larvae collected in the extensive collections of 1970-71 (Tables 7, 8, and 9) was quite variable. Some of the variation related directly to the particular host plant. It was noted in the intensive studies at Ames in 1971 that alfalfa fields showed extreme differences in green cloverworm populations before and after the initial cutting of the crop. Other possible explanations for the variation in green cloverworm populations could be offered.

In the 1970 state-wide extensive collections, relative numbers of larvae generally increased as the season progressed. Little difference was noted, however, in the Ames area extensive samples.

In the 1971 extensive collections made in southern Iowa, mean numbers of larvae (not shown) increased in all 7 fields which were sampled on both collection trips. In these fields there was an average 9-fold increase over the first collection trip. However, in northern Iowa, increases (averaging ca. 3-fold) were noted only in 4 of 10 fields sampled both trips. Populations decreased in 6 fields on the average ca. 60%.

The sex ratio of the adult population in 1970, based on the number

of male and female moths which emerged from larvae collected in the extensive collections was 1.05♂:1.00♀. A test of the hypothesis that the sex ratio is 1:1 gave $\chi^2 = 0.14$, $P_{\chi^2} > 0.50$. In the 1971 extensive collections, the number of male and female moths emerging was 89 and 104. A test of the hypothesis of a 1:1 sex ratio gave $\chi^2 = 1.17$, $P_{\chi^2} > 0.10$.

In a comparison of the sex ratios in 2 different ecosystems in 1971, a χ^2 of 1.32, $P_{\chi^2} = 0.25$ was calculated for soybean and a χ^2 value of 0.73, $P_{\chi^2} > 0.25$ was calculated for alfalfa.

The incidence of fungus diseases in the host population was noted in both 1970 and 1971. However, the incidence of disease was not as great as was observed in 1968 when many green cloverworms were infected with a fungus, Beauvaria bassiana (Pedigo et al. 1973). Two species of fungi, believed to be Beauvaria and Metarrhizium, were observed in the 2 seasons. In 1970, when the seasonal incidence of disease was 2.8%, diseased larvae were noted in 4 collections, but most infected larvae were in a large collection taken in Sept. In the extensive collections taken in 1971, only 11 infected larvae were collected. Seven of the diseased larvae were collected Aug. 19 in southern Iowa.

Parasitism of green cloverworms by nematode parasites has not previously been reported. In 1968, when larval populations reached outbreak proportions, 2 larvae were collected which contained nematodes. When the host larvae were placed in alcohol, 1 nematode emerged from 1 larva and 1 from the other. However, a 2nd nematode remained coiled within the 2nd larva.

The nematodes were identified by a specialist[1] as members of the family Mermithidae, but because the specimens were juveniles, an exact generic designation could not be given, although the authority reported they were probably Hexamermis. No nematodes have been collected in green cloverworm larvae since 1968.

Collection techniques

During the 1970 season an attempt was made to collect as many parasite hosts as possible in a relatively short time. As a result of these often hurried collections, many larvae died for reasons unknown. In the state-wide extensive collections of 1970, the total mortality from unknown causes was 42.4%, ranging 0-100%, and averaging 47.7% for 28 collections. In the extensive collections at Ames in 1970, total mortality (due to unknown causes) for the summer was 51.4%, ranging 27.0-92.1%, and averaging 53.6% for the 7 collections.

It is believed that mortality was due primarily to injuries suffered in the large sample sizes, often in excess of 100 sweeps. Moisture-laden sweep nets also undoubtedly caused many injuries. Some predation also probably occurred in these samples.

In the extensive collections of 1971, sampling techniques were modified to reduce as much of this mortality as practical. A smaller, lighter, nylon-mesh sweep net was used rather than the 18-in.-diam muslin net. Samples sizes were standardized at 100 sweeps and were composed of subsamples.

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[1]G. O. Poinar, Berkeley, Calif. Identification of nematode parasites. Personal communication. 1971.

As a result of these changes, total mortality due to unknown causes was reduced to 14.8%. This mortality in northern Iowa for the 1st and 2nd collections was 20.2 and 17.7%, respectively. In southern Iowa, for these 2 collections, mortality was 36.6 and 8.7% respectively.

Hyperparasitism

During the 1970-71 seasons, only 10 hyper-, or secondary parasites, were reared from primarily parasitized green cloverworms.

A single male specimen of Perilampus hyalinus Say was reared from the puparium of a dipterous parasite of a green cloverworm collected from alfalfa in Davis Co., Iowa, on July 21, 1970. Unfortunately, the puparium was lost and a species determination of its host could not be made. Muesebeck et al. (1951) listed 34 hosts of P. hyalinus. Thompson (1958) gave an additional 3 host species. However, none of the fly species given by these authors was collected in Iowa in 2 years of collecting parasites of the green cloverworm.

Size and shape of the photographed puparium indicated that the host was probably Winthemia sinuata. Also, during 1970, of the 135 larvae parasitized by fly parasites, 93 (68.9%) were parasitized by W. sinuata. This fact, coupled with the photograph, strongly suggest the host of P. hyalinus was W. sinuata.

Muesebeck et al. (1951) reported that P. hyalinus was present in the Canadian provinces of Saskatchewan, Manitoba, Ontario and Quebec and throughout the United States. Tripp (1962) studied the biology of P. hyalinus as a primary parasite of the Swaine Jack-Pine Sawfly in

Quebec and presented descriptions of egg and larval stages.

Three species of ichneumonid wasps were reared from primarily parasitized green cloverworms. A single female of Mesochorus americanus (Cresson) was reared from a green cloverworm collected from an alfalfa field on July 23, 1970, 5 miles E of Waverly, Iowa. A specialist determined that this wasp was a hyperparasite, although the host was unknown.

A single female specimen of Mesochorus discitergus (Say) was reared from an R. nolophanae cocoon whose host larva was collected 3 miles W of Ames on Aug. 13, 1970. Barry (1970), in Missouri, reared this species from R. nolophanae and from Protomicroplitis facetosa (Weed). Muesebeck et al. (1951) listed 8 species from which the parasite was reared while Thompson (1957) included an additional 14 hosts. The distribution of M. discitergus is "transcontinental in the Transition and Upper Austral zones and in Europe" (Muesebeck et al. 1951).

During 1971, 5 additional females of M. discitergus were reared from Rogas cocoons. Of the 5 specimens, 1 was reared from a larva collected Aug. 20 in northern Iowa and 4 were reared from hosts collected in the intensive study conducted at Ames.

Two female specimens of Acrolyta nigricapitata (Cook and Davis) were reared from separate cocoons of Rogas, the hosts of which were collected 1.5 miles W of Ames during Sept. 1970. Muesebeck et al. (1951) reported 3 hosts for this parasite, none of which were found associated with green cloverworm parasites in Iowa, and included in its distribution the Transition zone from the Atlantic to the Continental Divide.

Of the 4 species of hyperparasites reared, 3 of them (P. hyalinus,

M. americanus, and A. nigricapitata) are new records in their association with parasites of the green cloverworm.

Based on the number of individual specimens reared in 1970-71, it appears that hyperparasitism was not an important factor in the regulation of green cloverworm parasite populations. An insufficient no. of hyperparasites were collected to validate this hypothesis.

Egg Parasite Study

Several hundred eggs were present on the plants which were taken to the field. Because the plants decayed after they were brought into the laboratory, only 93 eggs were recovered. Many of the eggs had also begun to hatch shortly after the plants had been retrieved.

From the 93 eggs held for parasite emergence, 1 egg parasite, the scelionid wasp, Telenomus sp., was reared. This represents a new record since no wasps of this family or genus have previously been reported in association with the green cloverworm. Thompson (1958) presented an extensive list of Telenomus species and their hosts.

Ames Intensive Sampling Program 1971

Larval populations

In the intensive sampling program conducted at Ames in 1971, larval populations were censused on a weekly basis to determine the incidence of parasitism in 2 ecosystems. Eight fields were included in the study, but only 7 (4 soybean, 3 alfalfa) were representative of standard agricultural practices. Therefore, results presented in this section deal primarily with 7 fields.

Results of the larval census, in which means and standard errors of raw data are presented for each field for each date are shown in Table 10. Population trends for 2 ecosystems are presented graphically in Figure 6. Relative variation, a measure of sample variability, where RV = $(SE/\bar{X})100$, indicated that most samples did not possess the level of accuracy (RV = 10) suggested by Southwood (1966) for intensive studies. Of 64 RV values calculated (not shown), only 3 were less than 10. Twenty-five was the level of accuracy suggested by Southwood (1966) for extensive samples. Only 21 of the 64 values were 25 or less.

The effect of cutting of alfalfa on larval populations is shown by the results presented (Table 10) for fields 4, 6, and 8. Larval populations were not censused in alfalfa following cutting until populations returned to a level of at least 1 larva in the 1st sample taken.

The analysis of variance of the mean no. larvae collected in both alfalfa and soybean fields (Table 11 and 12) indicated that significant differences existed between fields as well as for sample periods within

Table 10. Means and standard errors (SE) of green cloverworm larval populations in 2 ecosystems in the intensive sampling program. Ames, Iowa. 1971

Date	Soybean field no. 1 $\bar{X} \pm$ SE	3 $\bar{X} \pm$ SE	5 $\bar{X} \pm$ SE	7 $\bar{X} \pm$ SE	$\bar{X}_S \pm$ SE
6/17					
6/22		.25± .50			.25± .50
6/29	.25± .50	.75± 1.50	.50± .58		.50± .90
7/6	1.50± 1.29	1.75± 1.71	6.50± .58	1.50± 1.73	2.81± 2.54
7/13	.50± .58	5.25± 2.06	5.75± 1.50		3.83± 2.82
7/20	4.25± .50	17.75± 2.22	16.50± 4.12	9.25± 2.99	11.94± 6.20
7/27	7.25± 1.26	11.00± 3.56	15.25± 3.59	7.50± 4.51	10.00± 4.27
8/3	16.00± 1.41	30.25± 6.24	37.75± 7.54	22.00± 4.90	26.50± 9.83
8/10	6.75± 1.89	13.00± 2.16	17.50± 3.87	16.25± 4.72	13.38± 5.25
8/17	10.00± 1.41	18.25± 8.50	15.50± 3.51	14.75± 4.35	14.63± 5.52
8/24	6.25± 2.99	7.75± 3.77	13.75± .96	6.50± 2.38	8.56± 3.98
8/31	8.25± 4.27	3.25± 2.63	10.75± 3.86	6.00± 1.83	7.06± 4.11
9/7	2.00± 1.41		2.50± .58	3.50± .58	2.67± 1.07
9/16					
9/22					

Alfalfa field no.				
4	6	8		Pooled
$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X}_A \pm SE$	$\bar{X}_{S+A} \pm SE$
2.50± 1.00			2.50± 1.00	2.50± 1.00
1.50± 1.00	.50± .58	.50± .58	.83± .83	.69± .79
7.00± .82	3.75± 1.26	.50± .58	3.75± 2.90	2.13± 2.68
40.25± 7.80		9.50± 3.32	24.88± 17.35	10.17± 14.45
31.50± 9.88		10.00± 7.53	20.75± 14.08	10.60± 12.24
17.75± 4.43			17.75± 4.43	13.10± 6.26
				10.00± 4.27
				26.50± 9.83
				13.38± 5.25
				14.63± 5.52
15.75± 1.71	2.75± 2.36	.50± .58	6.33± 7.19	7.61± 5.58
20.25± 6.02	3.25± 1.50	7.50± 4.43	10.33± 8.53	8.46± 6.46
	1.75± 1.71	4.75± .96	3.25± 2.05	2.90± 1.52
	2.00± .82		2.00± .82	2.00± .82
	1.00± 1.15		1.00± 1.15	1.00± 1.15

Figure 6. Mean no. of larvae collected in the intensive sampling program from soybean and alfalfa. Bars represent $\pm$ SE

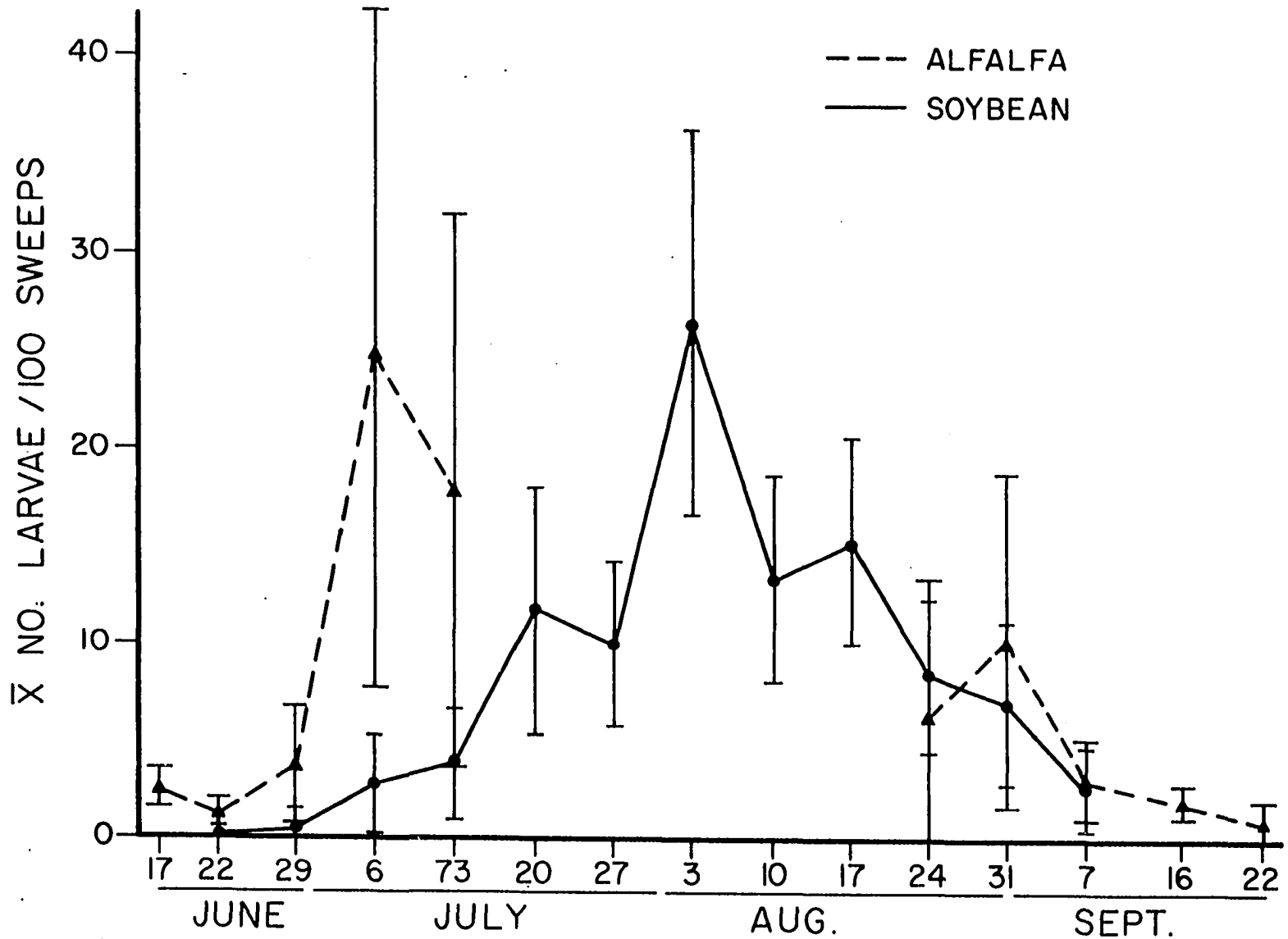

ALFALFA
SOYBEAN
$\bar{X}$ NO. LARVAE / 100 SWEEPS
40
30
20
10
0
17 22 29 6 73 20 27 3 10 17 24 31 7 16 22
JUNE
JULY
AUG.
SEPT.

Table 11. Analysis of variance of mean no. larvae per sample in soybean in intensive study. Ames, Iowa. 1971

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F
Between fields	3	1126.7	375.6	35.4**
Within fields	38	9875.8	259.9	24.5**
Residual	126	1335.3	10.6	
Corrected total	167	12337.7	73.9	

**Significant at the 1% level.

Table 12. Analysis of variance of mean no. larvae per sample in alfalfa in intensive study. Ames, Iowa. 1971

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F
Between fields	2	3870.5	1935.3	131.6**
Within fields	19	5736.8	301.9	20.6**
Residual	66	971.8	14.7	
Corrected total	87	10579.1	121.6	

**Significant at the 1% level of probability.

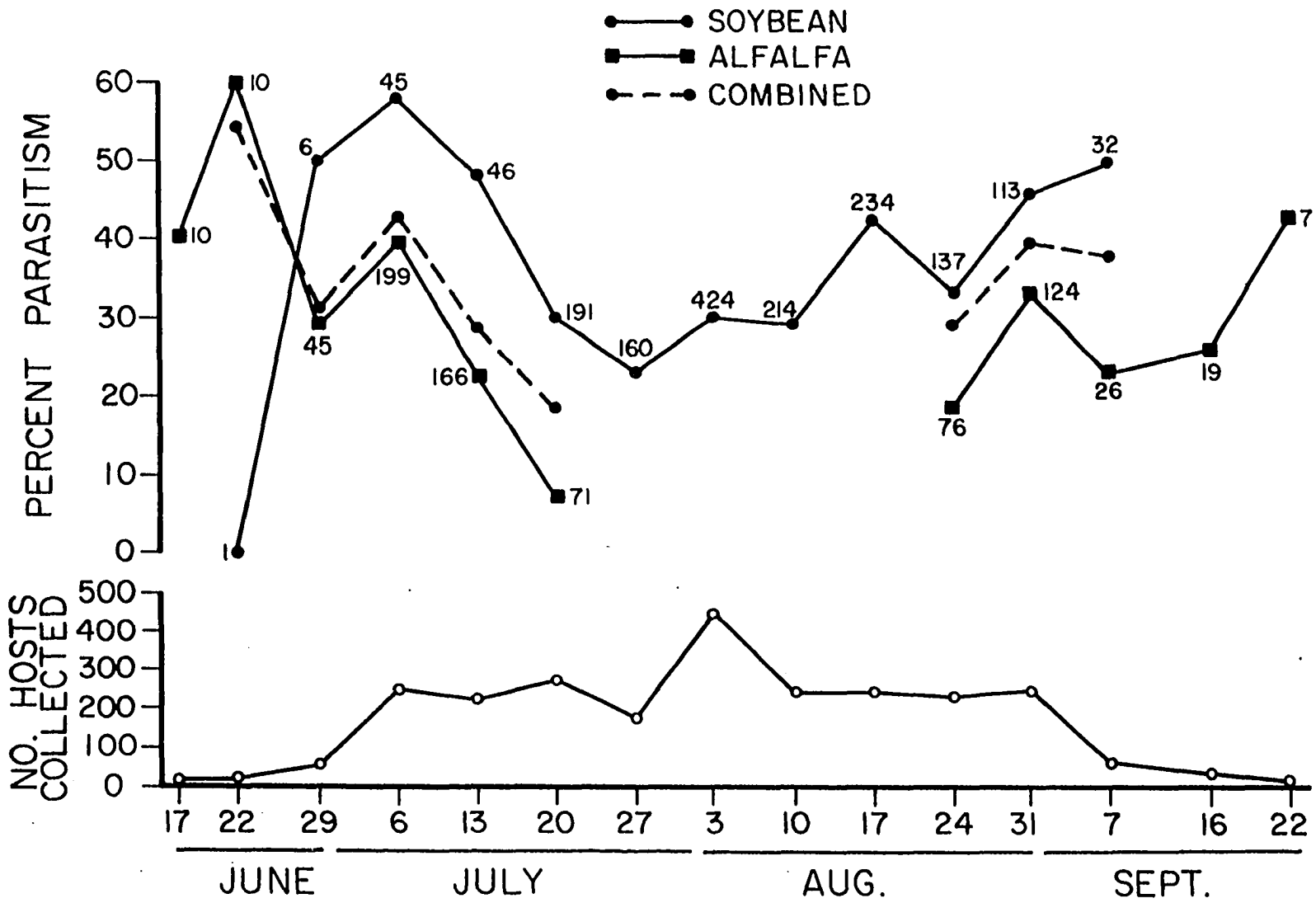
fields. Seasonal larval-population means in soybean fields 1, 3, 5, and 7 were 5.73, 9.93, 12.84, and 9.69 larvae/100 sweeps, respectively, with an overall seasonal mean of 9.54 larvae/100 sweeps in soybean. In alfalfa fields 4, 6, and 8, means were 17.06, 2.14, and 4.75 larvae/100 sweeps, respectively, with an overall mean of 8.40 larvae/sample.

Total parasitism

Total weekly parasitism of green cloverworm larvae in 2 agroecosystems by all parasite species combined is presented graphically in Figure 7. In the alfalfa ecosystem, the level of parasitism in the early season began quite high (40-60%) and gradually dropped to 7.0% by July 20. The high early-season parasitism may be due to an abundance of parasites and few hosts. From late Aug. to late Sept., total parasitism in alfalfa generally increased. Total parasitism in the soybean ecosystem early in the season is more difficult to describe owing to the small no. of larvae collected. Beginning the first wk in July, the level of parasitism declined from 57.8% to 23.1% on July 27 and then generally increased the remainder of the season. Total parasitism curves were generally concordant in all 4 soybean fields. Three of the 4 dropped to mid-season lows on July 20, the other the following wk. In all 4, decreases in the level of parasitism were noted from Aug. 17 to Aug. 24. The mid-season increase noted in soybean may be due, in part, to a shift of adult parasites from the cut alfalfa to habitats where hosts were more abundant.

In the intensive program, total seasonal parasitism of all larvae

Figure 7. Total weekly percent parasitism in intensive sampling program compared to the total no. of hosts collected on a given date. No. at each point represent the total no. of larvae collected in each ecosystem on a given date


SOYBEAN
ALFALFA
COMBINED
PERCENT PARASITISM
60
50
40
30
20
10
0
10
1
6
45
45
46
199
166
71
191
160
424
214
234
137
113
32
124
26
76
19
7
NO. HOSTS COLLECTED
500
400
300
200
100
0
17 22 29 6 13 20 27 3 10 17 24 31 7 16 22
JUNE
JULY
AUG.
SEPT.

collected was 31.6%, considerably higher than that reported by Whiteside et al. (1967) in Delaware (20.4% parasitized) or Barry (1970) in Missouri (18.8% parasitized). Total seasonal parasitism in the soybean ecosystem was 33.3% while in alfalfa, it was 28.4%. For soybean fields 1, 3, 5, and 7, the total seasonal parasitism was 47.2, 35.5, 27.6, and 29.8%, respectively. A null hypothesis was formed that the probability of parasitism was the same in all soybean fields. A calculated χ^2 value of 33.4 with 3 degrees of freedom gave a $P_{\chi 2} > .005$ indicating it was highly unlikely that percentage parasitism was the same in the 4 soybean fields.

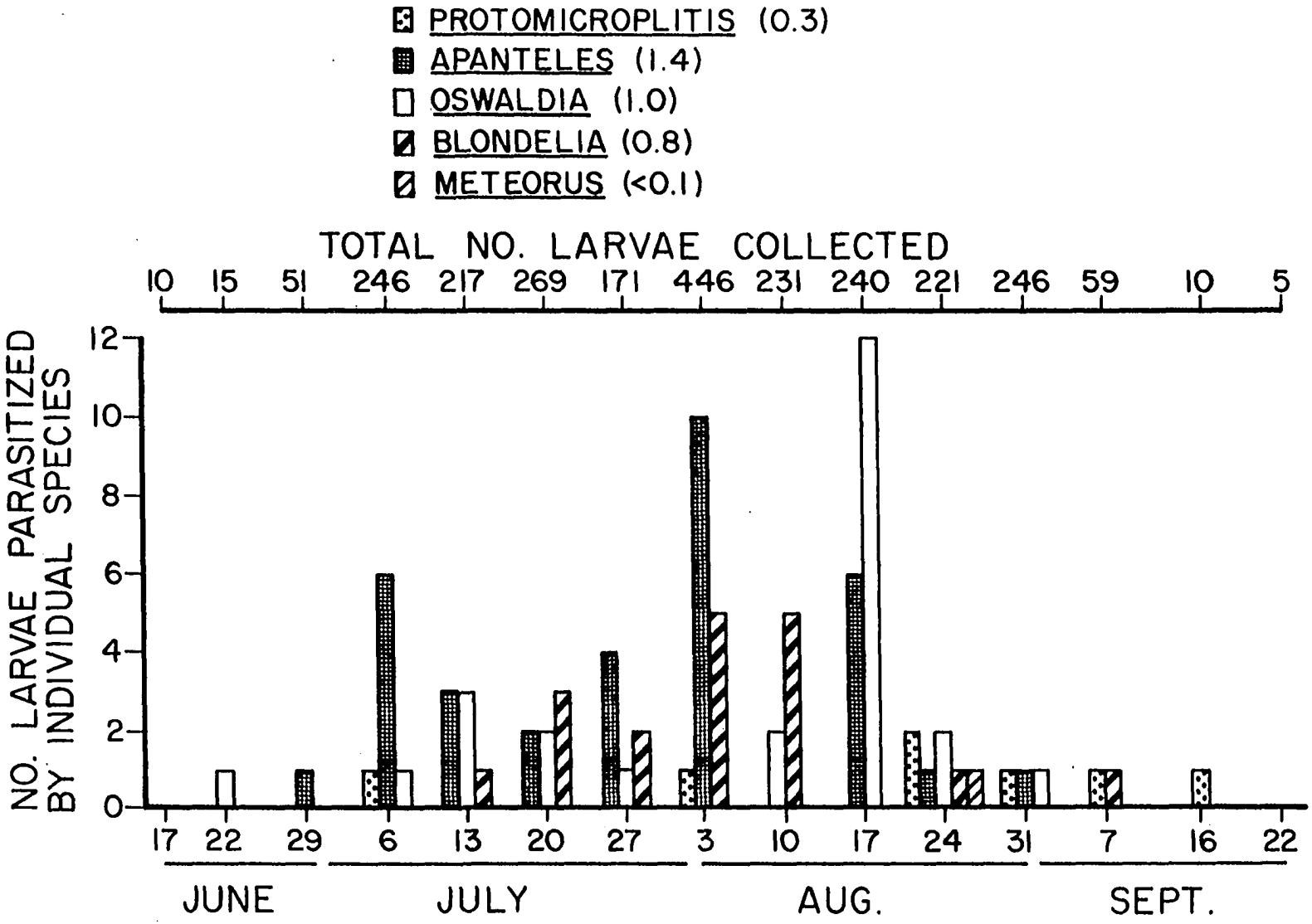
Total seasonal parasitism in alfalfa fields 4, 6, and 8 was 27.8, 25.0, and 30.8%, respectively. A test of the null hypothesis that the probability of parasitism was the same in the 3 alfalfa fields gave a calculated χ^2 value of 2.15 with 2 degrees of freedom and $P_{\chi 2} > .25$ indicating acceptance of the null hypothesis.

Species present

Eight species of primary parasites were collected in the intensive studies. All the species listed previously in Table 6, except S. validus and L. archippivora, were collected in these studies. The total seasonal parasitism for 6 of the 8 species was less than 1.5%. The no., total seasonal parasitism, and the seasonal occurrence of these 6 species in relation to the total host population are shown in Figure 8.

Of these less prominent parasites, the tachinid fly, O. assimilis,

Figure 8. No. of larvae collected on given date which were parasitized by given species. No. in parentheses are total seasonal percent parasitism


PROTOMICROPLITIS (0.3)
APANTELES (1.4)
OSWALDIA (1.0)
BLONDELIA (0.8)
METEORUS (<0.1)
TOTAL NO. LARVAE COLLECTED
10 15 51 246 217 269 171 446 231 240 221 246 59 10 5
NO. LARVAE PARASITIZED BY INDIVIDUAL SPECIES
0 2 4 6 8 10 12
17 22 29 6 13 20 27 3 10 17 24 31 7 16 22
JUNE
JULY
AUG.
SEPT.

was reared from larvae collected in almost all of the weekly samples from June 22 to Aug. 31 (except June 29 and Aug. 3). The peak no. of larvae parasitized by O. assimilis (12) was collected on Aug. 17. A second tachinid fly, B. hyphantriae, was reared from larvae collected July 13 through Sept. 7. Peak no. of larvae parasitized by B. hyphantriae (5) were collected on both Aug. 3 and Aug. 10.

Of the less prominent braconid wasps, parasites of the genus Apanteles were most abundant. Because of their infrequent occurrence and morphological similarity, both A. marginiventris and A. flaviconchae were combined in this discussion of Apanteles wasps. A total of 34 larvae were parasitized by Apanteles spp. from June 29 to Aug. 31, except for 1 collection date (Aug. 10). Ten Apanteles parasitized larvae were collected Aug. 3 and 6 on both July 6 and Aug. 17.

Single larvae, parasitized by the braconid wasp, P. facetosa, were collected in each of 5 collections from July 6 through Sept. 16. Two P. facetosa-parasitized larvae were collected on Aug. 24. A single M. hyphantriae-parasitized larva was collected on Aug. 24.

Total parasitism from lost or unidentified flies (1 specimen) and wasps (13 specimens) in the intensive study was 0.53%, most of which occurred in Aug.

The coexistence of 2 species of parasites within 1 host was observed on 2 occasions in 1970-71. Two specimens of W. sinuata and 1 of O. assimilis from 1 larva collected July 27, 1971 emerged. In the previous year, 1 larva was parasitized by both W. sinuata and L. archippivora. To my knowledge, reports of such coexistence are rare.

Biological data on all the primary parasites reared from these studies are presented in Table 13. The mean no. days from host collection to adult emergence for each species (presented in the 1st column) can be quite variable depending on the stage of development of the parasite when the host was collected. It is presented here as a minimum developmental period for these parasites under the specified rearing conditions.

The figures presented in column 2 for the mean no. of days within the cocoon or puparium are considered an accurate estimate of the time spent in the cocoon or puparium since observations were made on a daily basis.

It should be noted from the table that all the wasp parasites were solitary in development. The incidence of gregarious parasitism (more than one maggot/host) among the tachinid flies does not differ appreciably from that observed in 1970. However, it should be noted that, in 1970, B. hyphantriae was found only as a solitary parasite, but in these 1971 studies, 5.3% of the B. hyphantriae parasitized larvae contained 2 maggots. The previous report by Barry (1970), indicated that W. sinuata was solitary in development. In 2 years of study in Iowa, W. sinuata was observed to be solitary in development only ca. 80% of the time.

The proportion of parasitized larvae in each stage at time of collection is shown in the right-hand column of the table. For the prominent primary parasites, Rogas and W. sinuata, these figures do not differ appreciably from the results of the extensive collections.

Table 13. Summary of biological data on parasite species reared from green cloverworm larvae collected in the intensive sampling program. Ames, Iowa. Summer 1971

Species	No. days from collection to adult emergence	No. days from cocoon formation to adult emergence	% of larvae collected with:				% of parasitized larvae collected in larval stage:				
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	1 Parasite	2 Parasites	3 Parasites	4 Parasites	6	5	4	3	2
Winthemia sinuata	23.21±5.08(16)[a]	11.98±2.63(55)	77.4	17.9	3.6	1.0	93.2	5.2	1.6		
Blondelia hyphantriae	27.41±4.52(17)	12.00±4.30(5)	94.7	5.3			63.2	26.3	10.5		
Oswaldia assimilis	27.06±10.72(16)	20.80±3.19(5)	81.8	18.2			70.8	25.0	4.2		
Apanteles spp.	11.76±4.28(26)	7.17±3.14(23)	100.0					6.0	47.0	47.0	
Protomicroplitis facetosa	19.33±4.17(3)	11.67±3.51(3)	100.0					57.1	28.6	14.3	
Rogas nolophanae	14.25±3.83(398)	9.05±2.43(383)	100.0				0.6	22.0	59.8	16.1	1.5
Meteorus hyphantriae	18	8	100.0					100.0			

[a]No. in parentheses indicates no. of observations on which statistic is based.

Results presented for the less-prominent species are based on more individuals than were obtained in the extensive studies and are thus considered more reliable.

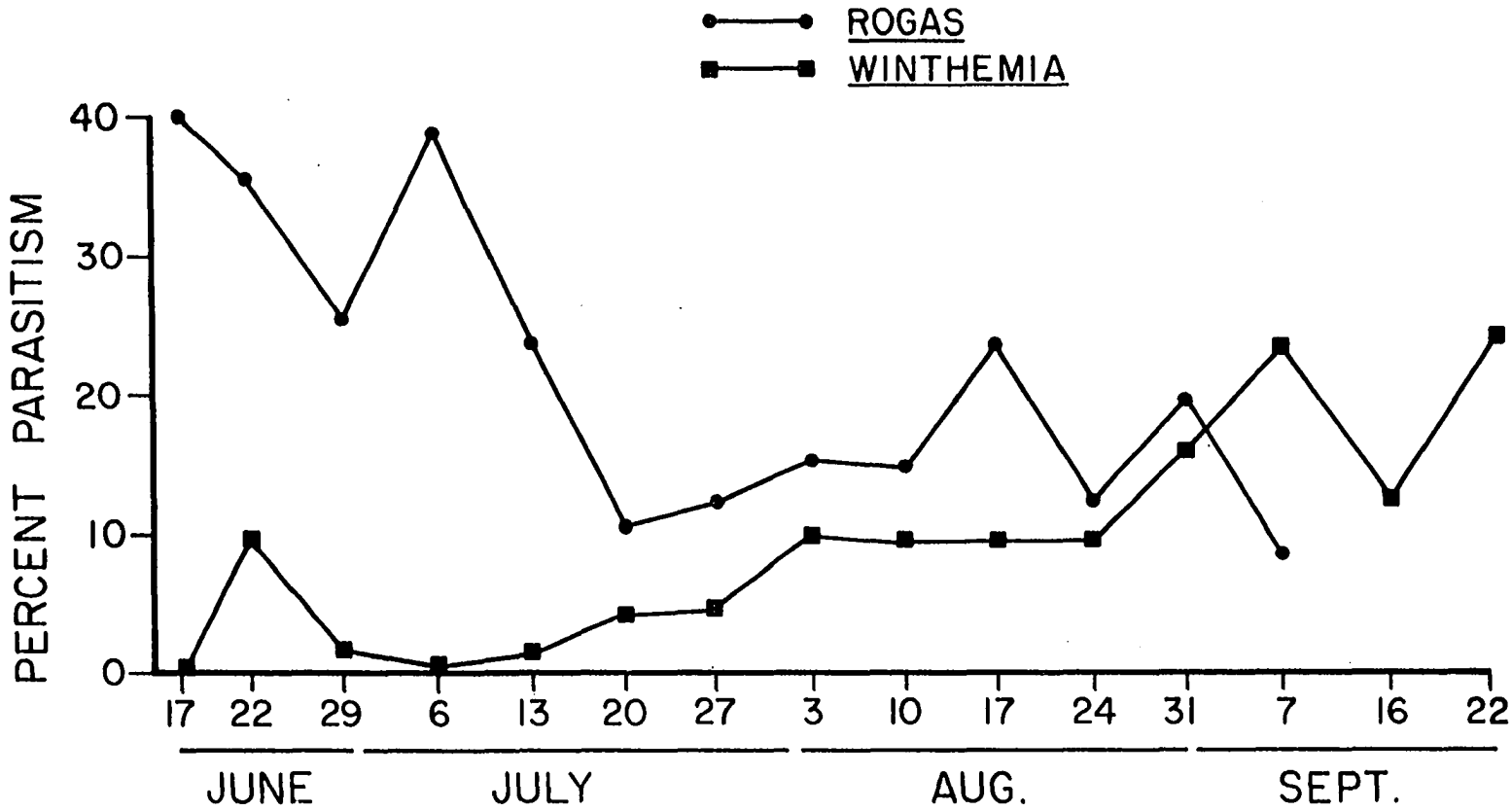
The most prominent parasite reared in the intensive studies was R. nolophanae. Total seasonal parasitism by this species alone was 19.0%, considerably higher than the 6.5% parasitism reported by Whiteside et al. (1967) and the 6.4% parasitism reported by Barry (1970) and only slightly higher (5.0% higher) than in extensive collections from 1970-71. Total seasonal parasitism in the soybean ecosystem was 18.1%, and in the alfalfa ecosystem, it was 22.8%.

Total weekly parasitism of green cloverworm larvae by R. nolophanae is shown in Figure 9. Early season parasitism is somewhat difficult to ascertain because of the relatively small no. of larvae collected. Beginning July 6, when 246 larvae were collected in all samples, total parasitism by R. nolophanae was 38.6%. Parasitism by R. nolophanae declined sharply and reached a mid-season low of 10.8% after which time it gradually increased and fluctuated between 9 and 24% of the remainder of the season.

Parasitism in each of the 4 soybean fields (not shown) was similar in the early and mid-season, but beginning Aug. 10, parasitism in 2 fields (1 and 3) increased while parasitism in the other 2 remained ca. 12 $\pm$ 5%. Parasitism trends in alfalfa fields are not easily described because different cutting schedules so markedly affected sampling procedures, host populations, and consequently, parasitism trends.

In order to better understand the role of the parasite in the host's

Figure 9. Total weekly percent parasitism of green cloverworm larvae by Rogas and Winthemia in both host crops combined


ROGAS
WINTHEMIA
PERCENT PARASITISM
40
30
20
10
0
17
22
29
6
13
20
27
3
10
17
24
31
7
16
22
JUNE
JULY
AUG.
SEPT.

life system, it is desirable to understand the response of the parasite to different host population densities. Regression analyses were therefore used to examine this response of R. noloplanae (in terms of no. of parasitized larvae collected) at various host population densities. Attempts to determine any density-related relationships between the incidence of parasitism by R. nolophanae and the total host population, were totally unsuccessful. However, since the analysis of variance of larval populations indicated significant differences existed between soybean fields, each field was examined separately to determine the relationship of the no. of R. nolophanae-parasitized larvae to the no. of susceptible individuals present. The no. of susceptible individuals present in each field was calculated by adding together the no. of 3rd- and 4th-stage larvae collected. Both a linear and a quadratic fit of the data were made. The observed values, the best predictive regressions and the r^2 values for each field are presented in Figures 10 through 13. In only 1 field (no. 7) did the quadratic account for more variation than did the linear regression. Based on the results of these analyses, parasitism by R. noloplanae did not appear to be density-dependent, because the proportion of insects parasitized did not usually increase with increasing host density. Further investigations should be made to determine this point.

The 2nd most abundant parasite in the intensive study was the tachinid fly, W. sinuata. In this aspect of the study, the total seasonal parasitism was 8.1%, somewhat higher than that reported from Delaware (6.2% parasitized) and considerably higher than that reported

Figure 10. Regression of the no. of Rogas parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 1

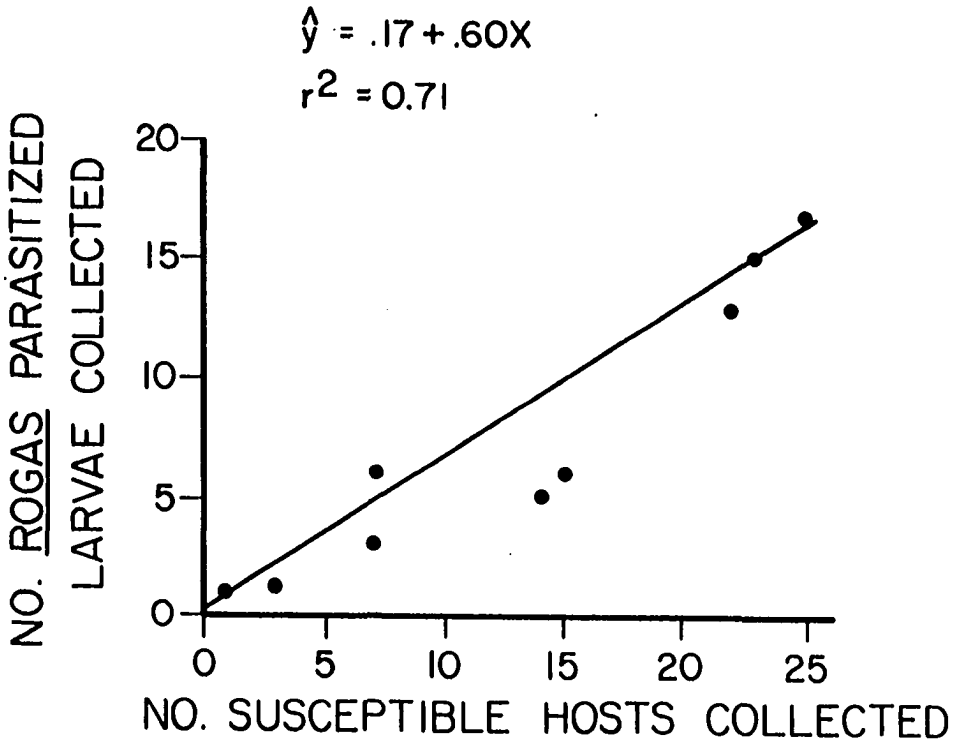

$\hat{y}$ = .17 + .60X
r^2 = 0.71
NO. ROGAS PARASITIZED LARVAE COLLECTED
0
5
10
15
20
25
NO. SUSCEPTIBLE HOSTS COLLECTED

Figure 11. Regression of the no. of Rogas parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 3

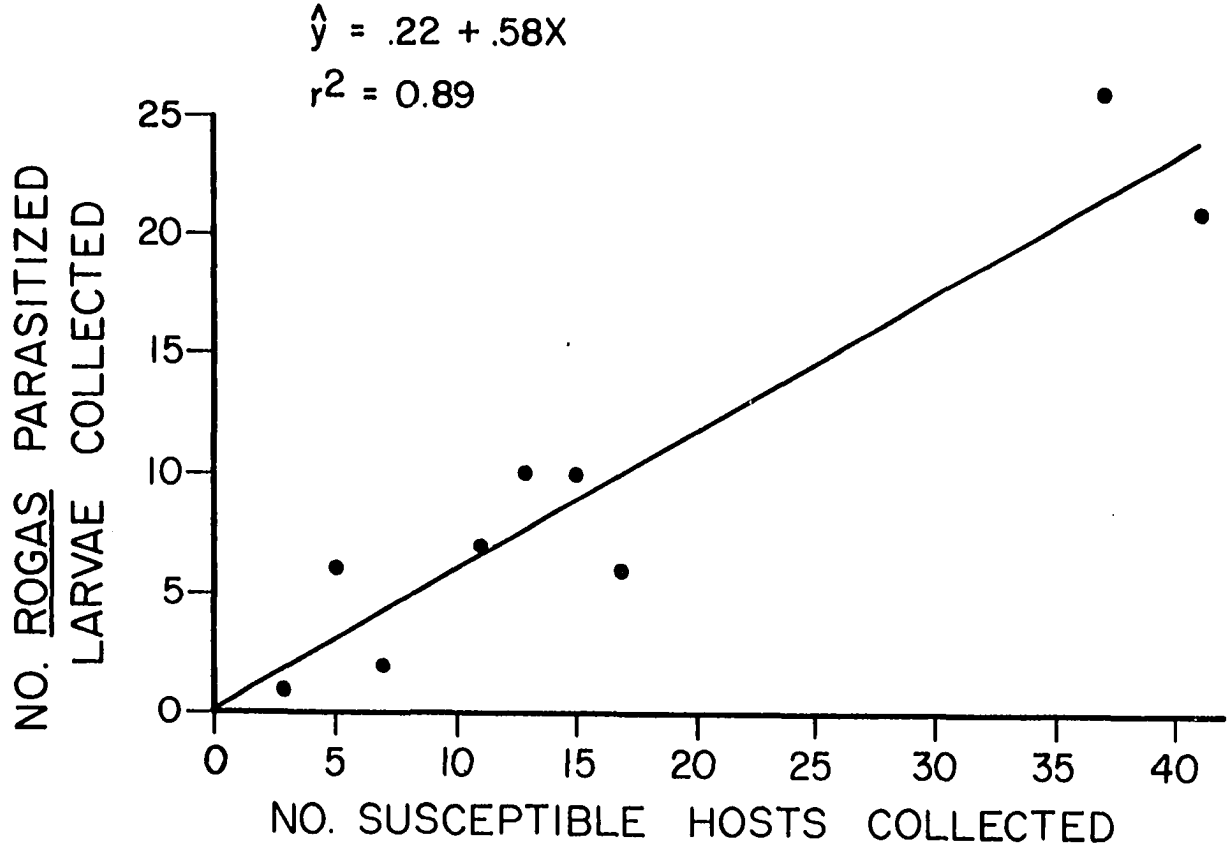

$\hat{y}$ = .22 + .58X
r^2 = 0.89
NO. ROGAS PARASITIZED LARVAE COLLECTED
0
5
10
15
20
25
0
5
10
15
20
25
30
35
40
NO. SUSCEPTIBLE HOSTS COLLECTED

Figure 12. Regression of the no. of Rogas parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 5

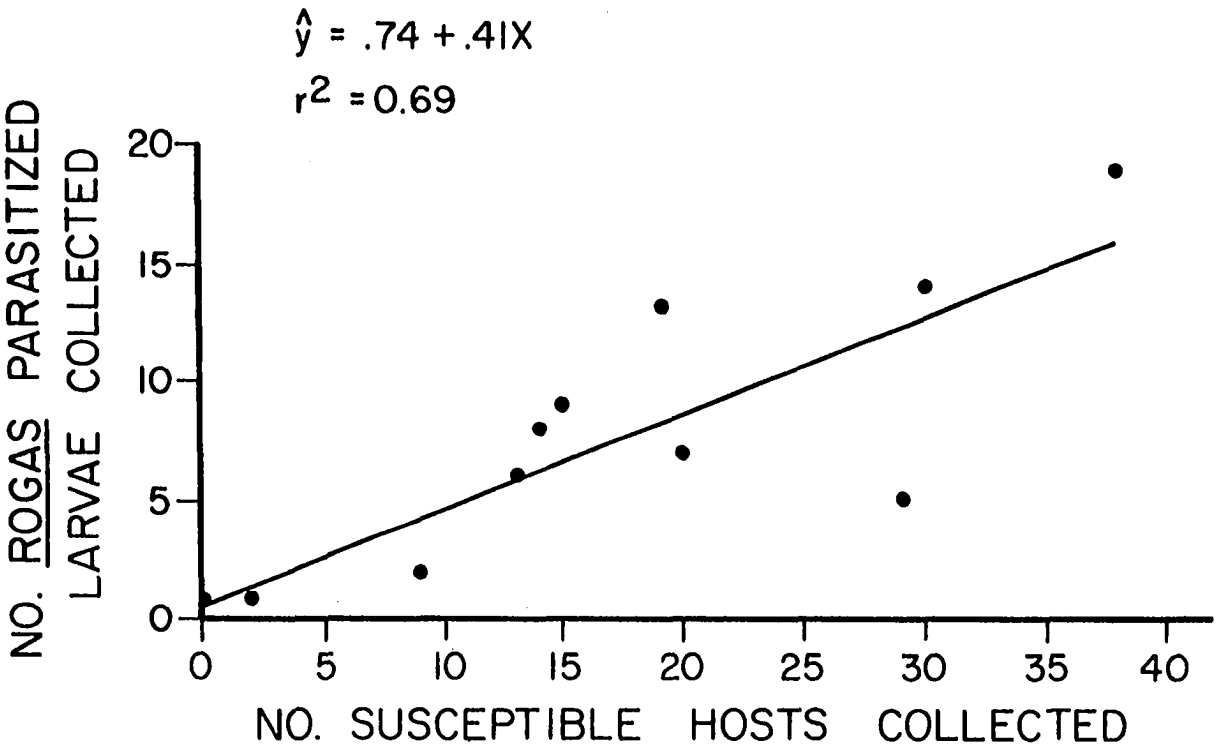
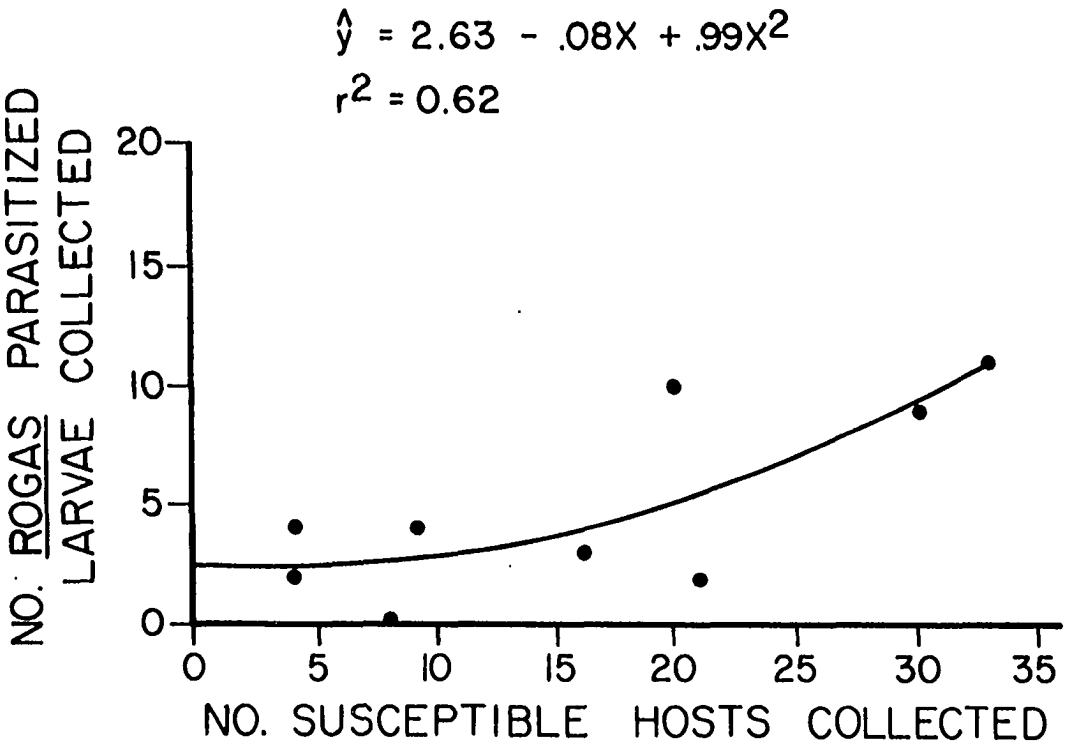

$\hat{y}$ = .74 + .41X
r^2 = 0.69
NO. ROGAS PARASITIZED LARVAE COLLECTED
0
5
10
15
20
0
5
10
15
20
25
30
35
40
NO. SUSCEPTIBLE HOSTS COLLECTED

Figure 13. Regression of the no. of Rogas parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 7


$\hat{y} = 2.63 - .08X + .99X^2$
$r^2 = 0.62$
NO. ROGAS PARASITIZED LARVAE COLLECTED
0
5
10
15
20
0
5
10
15
20
25
30
35
NO. SUSCEPTIBLE HOSTS COLLECTED

from Missouri (3.3% parasitized). This was, however, lower than that observed in the extensive collections of 1970 (10.3% parasitized) and of 1971 (11.0% parasitized).

Total weekly parasitism of green cloverworm larvae by W. sinuata was shown, along with that by R. nolophanae, in Figure 9. Early season parasitism was low except on June 22 when 1 of 11 larvae collected (9.1% was parasitized. Parasitism gradually increased until the 1st wk in Aug. From Aug. 3 to Aug. 24, parasitism generally remained the same. During the period Aug. 24 through Sept. 7 (date of the final collections from soybean), parasitism more than doubled, reaching a seasonal high of 24.1%. Total parasitism exceeded this on Sept. 22 when only 4 larvae were collected from alfalfa and parasitism by W. sinuata was 25.0%.

Parasitism of green cloverworm larvae by W. sinuata in the 2 ecosystems was quite different. In the alfalfa ecosystem, total seasonal parasitism was 3.9% compared to 10.0% in soybean. Only 28 W. sinuata-parasitized larvae were collected from alfalfa while 160 were collected from soybean. Parasitism trends in both ecosystems were comparable in that the incidence of parasitism was low early in the season and increased rapidly late in the season. The increase in parasitism in alfalfa occurred ca. 2 wk later than that noted in soybean.

Parasitism by W. sinuata in the 4 soybean fields was quite variable, but remained less than 20% at each collection (with 1 exception) until after Aug. 24, at which time, the level of parasitism increased for the remainder of the season in 3 of the 4 fields.

The relationship of the susceptible host population in each

individual soybean field to the no. of W. sinuata-parasitized larvae collected was examined in all 4 fields. In only 2 of the 4 did the r^2 value exceed 0.50. These curvilinear regressions for fields 3 and 5 are shown in Figures 14 and 15. In field no. 3, it appears that the no. of parasitized larvae increases as the no. of susceptible hosts increases, but in field no. 5, there is a point at which the no. of parasitized larvae levels off while the no. of hosts increases.

The linear regressions of the no. of W. sinuata-parasitized larvae collected on a given date on the no. of susceptible larvae collected in all fields (soybean and alfalfa combined) on that date is shown in Figure 16. Although the r^2 value for the curvilinear fit was greater (0.78 cf. 0.76), the probability of a greater F (P = 0.64) for the fit of the quadratic after the linear, indicated the linear fit would adequately express this relationship. It appears from these analyses that W. sinuata like R. noloplanae did not respond in a density-dependent manner, because the proportions of parasitized insects did not increase with increasing host density.

One aspect of the field biology of W. sinuata which has not been discussed is the no. of fly eggs recorded on field-collected larvae. From counts made on 100 larvae from which W. sinuata maggots eventually emerged, a mean of 2.07 $\pm$ 1.69 eggs/larva was noted. The no. of eggs ranged from 1 to 10. Though it is recognized that probably not all eggs were laid by W. sinuata and that many were possibly nonviable, most eggs were probably laid by W. sinuata and these counts showed that W. sinuata was not deterred from laying eggs on previously parasitized

Figure 14. Regression of the no. of Winthemia parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 3

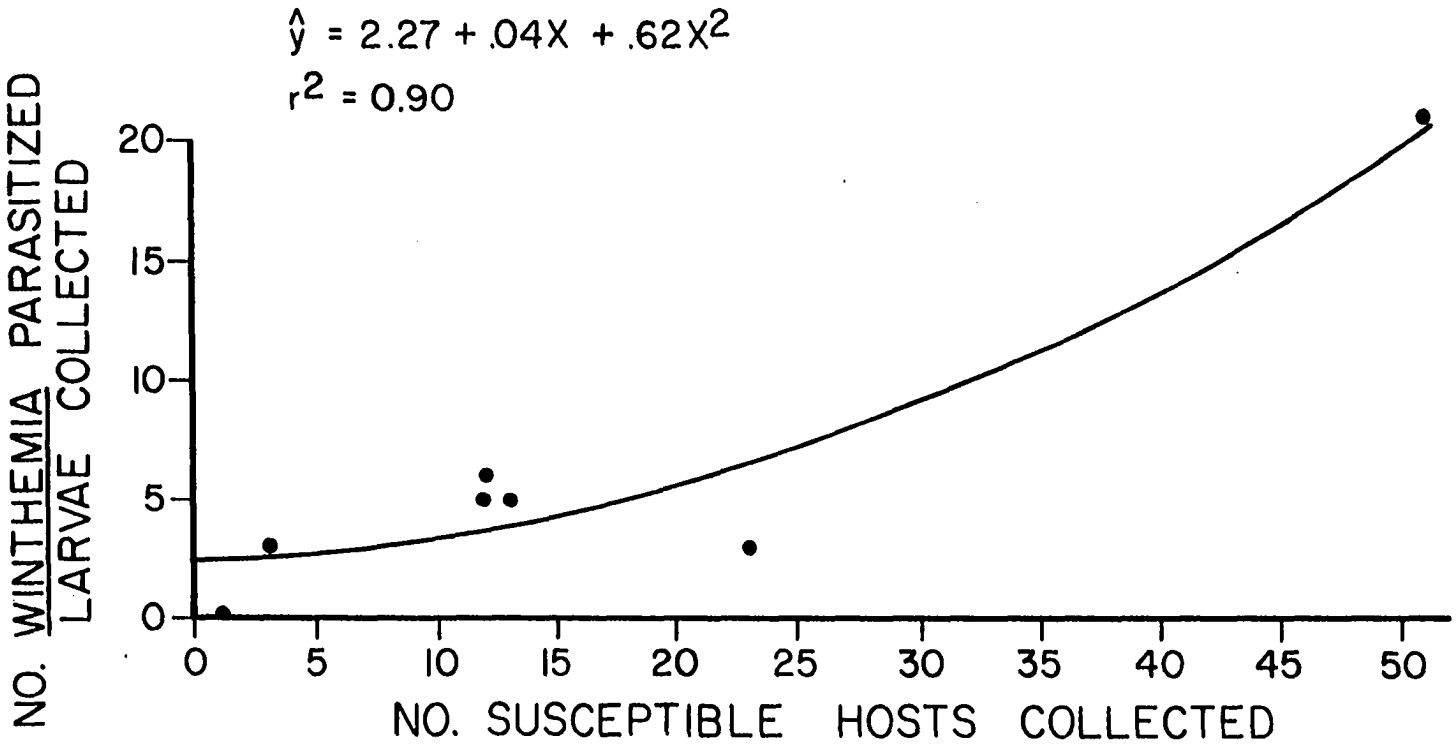

$\hat{y} = 2.27 + .04X + .62X^2$
$r^2 = 0.90$
NO. WINTHEMIA PARASITIZED LARVAE COLLECTED
0
5
10
15
20
0
5
10
15
20
25
30
35
40
45
50
NO. SUSCEPTIBLE HOSTS COLLECTED

Figure 15. Regression of the no. of Winthemia parasitized larvae collected on the no. of susceptible hosts collected in soybean field no. 5

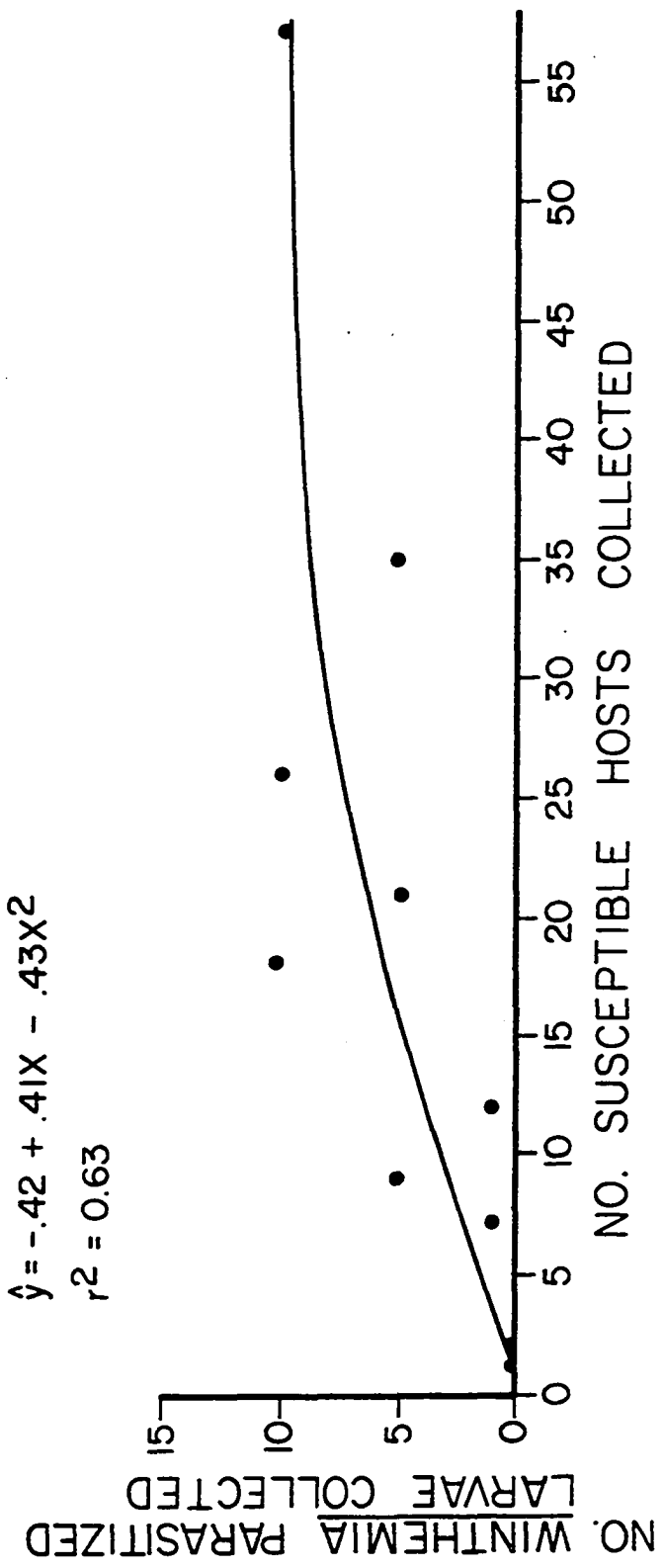
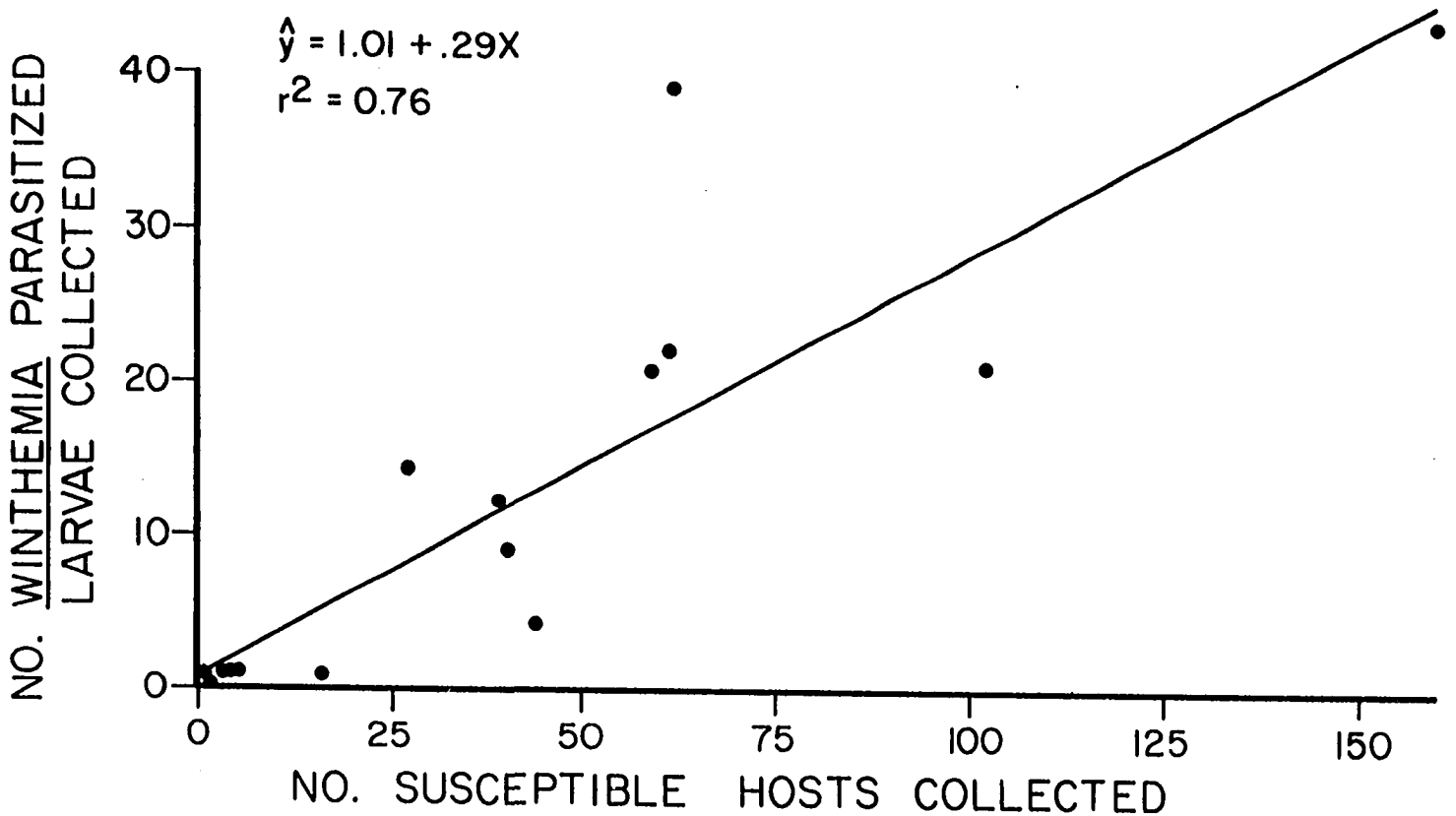

$\hat{y} = -.42 + .41X - .43X^2$
$r^2 = 0.63$
NO. WINTHEMIA PARASITIZED LARVAE COLLECTED
NO. SUSCEPTIBLE HOSTS COLLECTED
0
5
10
15
20
25
30
35
40
45
50
55

Figure 16. Regression of the no. of Winthemia parasitized larvae collected on the no. of susceptible hosts collected in soybean and alfalfa fields combined


$\hat{y}$ = 1.01 + .29X
r^2 = 0.76
NO. WINTHEMIA PARASITIZED / LARVAE COLLECTED
0
10
20
30
40
0
25
50
75
100
125
150
NO. SUSCEPTIBLE HOSTS COLLECTED

hosts.

Host population characteristics

The no. of host larvae collected in the intensive study and the population trends in 2 ecosystems were presented previously in Table 10 and Figure 6.

The age structure of the host population in the soybean ecosystem was not accurately measured in this study as indicated by the relatively few no. of 1st- and 2nd-stage larvae collected. Most of this bias toward larger stage larvae can be attributed to the sampling technique in which large no. of larvae were being collected in a short time and in these large samples which contained some plant debris, small larvae were easily overlooked. However, a general shift in the proportions of various stages of larvae present from 3rd-, 4th-, and 5th-stage larvae to 4th-, 5th-, and 6th-stage larvae was noted as the season progressed. Evidence of this shift to more mature larvae is shown by the age-structure polygons in Figure 17.

The percentage composition of green cloverworm larval populations in each stage in each of 7 individual fields for the entire season is presented in Table 14. No appreciable differences were noted except that in 2 alfalfa fields the percentage of 3rd-stage larvae was greater than in most other fields and the percentage of 6th-stage larvae was less than in other fields. These differences were due to the alfalfa being cut when most of the larvae present were in the 3rd- and 4th-stage.

Fungal disease incidence (caused by Beauvaria and Metarrhizium)

Figure 17. Green cloverworm age-structure polygons from intensive sampling in soybean

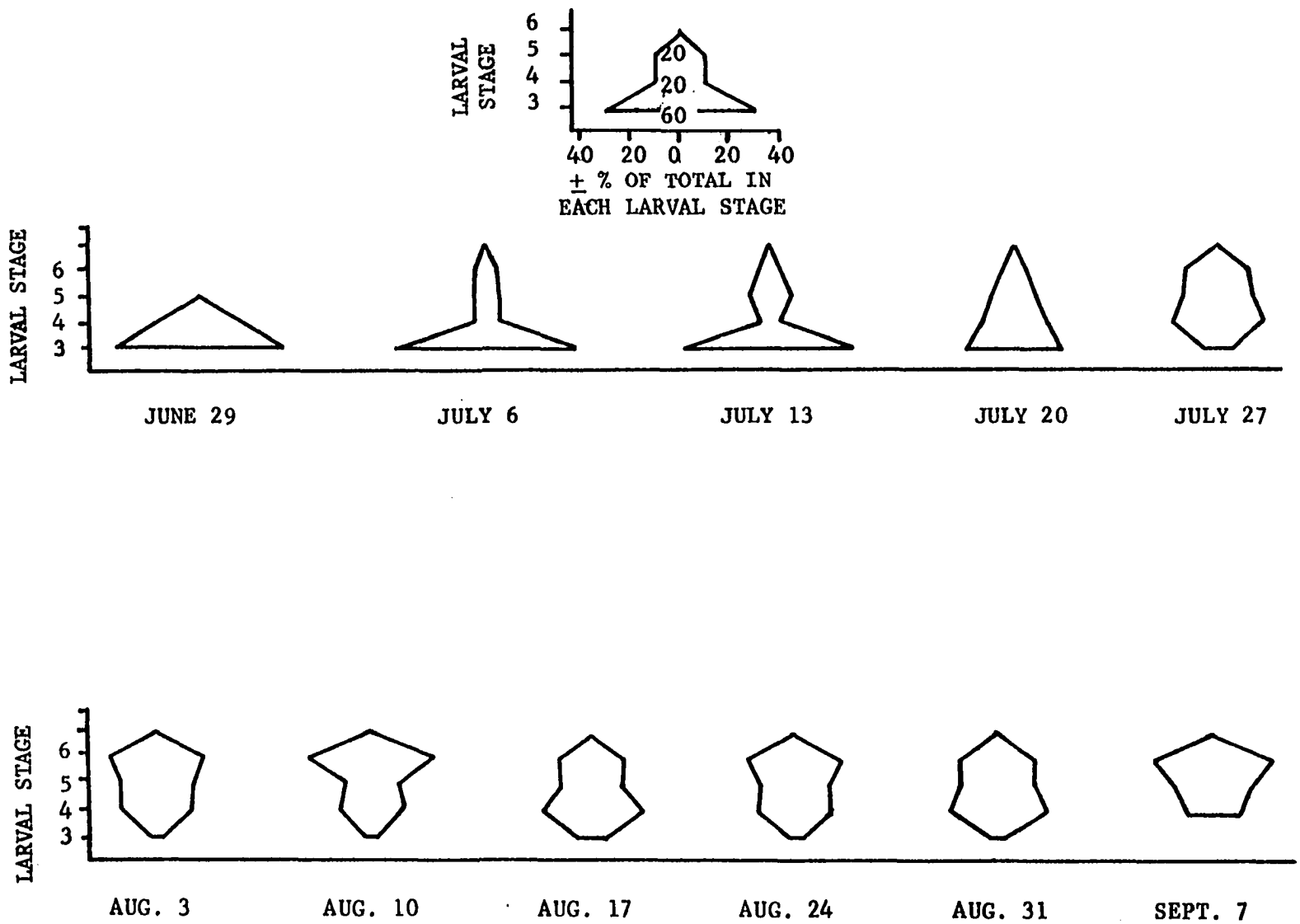

LARVAL STAGE
6
5
4
3
20
20
60
40 20 0 20 40
± % OF TOTAL IN
EACH LARVAL STAGE
LARVAL STAGE
6
5
4
3
JUNE 29
JULY 6
JULY 13
JULY 20
JULY 27
LARVAL STAGE
6
5
4
3
AUG. 3
AUG. 10
AUG. 17
AUG. 24
AUG. 31
SEPT. 7

Table 14. Percentage composition of green cloverworm populations in individual fields. Intensive samples. Ames, Iowa. 1971

Crop field no.	Total no. larvae collected	% of total number collected in larval stages						
		1	2	3	4	5	6	Unknown
Soybean 1	252		0.4	11.9	36.1	21.8	28.6	1.2
" 3	437	0.2	1.8	18.3	27.5	24.0	27.2	.9
" 5	565		1.4	11.9	21.6	28.7	33.3	3.2
" 7	349		2.3	8.3	33.2	24.4	30.4	1.4
Alfalfa 4	546		2.9	29.3	21.6	22.2	16.9	7.1
" 6	60		1.7	11.7	16.7	28.3	35.0	6.7
" 8	133		3.0	18.8	27.1	30.1	17.3	3.8

in the host population was 2.6% in the intensive studies and differed little from that observed in 1970 (2.8% infected). The incidence of disease in fields 1 through 8 was 1.2, 1.1, 2.1, 1.1, 6.2, 0.0, 4.3, and 0.8%, respectively. Fields 5 and 7, in which the incidence of disease was greatest, were soybean fields located in the same vicinity. Both were characteristically alike in that plant growth was rank and fields were relatively moist. Both characteristics may have favored the fungal diseases.

Viral diseases in field populations of green cloverworms have not previously been reported. During 1971, a single larva was collected from field no. 5 which died of an apparent virus infection. Subsequent

examination by a specialist[2] confirmed the cause of death was, in fact, due to a granulosis virus.

Sex ratios of adults reared from larvae collected in these studies were very close to those presented in previous aspects of this study. The chi-square test of a 1:1 sex ratio in soybean gave a χ^2 value of 0.82, $P_{\chi 2} > 0.25$. In alfalfa, the χ^2 value was 0.004, $P_{\chi 2} > 0.95$, and for moths produced in both crops combined, the χ^2 value was 0.21, $P_{\chi 2} > 0.50$.

Collection techniques

The collection of larvae in the intensive study undoubtedly produced some mortality. Although mortality due to unknown causes in the extensive studies of 1971 was only 14.8%, mortality in the intensive study was 21.4%. Mortality in the soybean ecosystem was much less than that in the alfalfa ecosystem (16.5% cf. 29.2%), possibly because more plant debris and insect predators were collected from alfalfa. Most of the mortality occurred in the larval stage (14.6% mortality), but many of the larvae survived only to die as pupae. Death in this category was 6.8% (9.3% mortality from alfalfa and 5.2% mortality from soybean).

In contrast to this mortality, the percentage of larvae collected in the intensive study which survived to emerge as moths was 37.1%. Moth emergence for each of the 8 study fields ranged from 30.6 to 52.6%. Moth emergence from larvae collected in the soybean ecosystem was 38.7% and from alfalfa, the emergence was 33.7% of the larvae collected.

---

[2]C. C. Beegle, Ames, Iowa. Identification of insect virus. Private communication. 1971.

These figures are presented not only as an indication of the amount of survival, but also as the maximum amount of parasitism that could have occurred at the time of collection.

Biological Investigations of Rogas nolophanae

During the 9 month period the R. nolophanae colony was maintained, over 960 larvae were exposed to parasitization by female wasps. During this time, however, only 131 parasite cocoons were formed. From the 131 cocoons, 123 wasps emerged (61♂, 62♀). Thus, the minimum parasitism was 13.6%. It should be noted though that during this period only 12 green cloverworm moths emerged. Based on this fact, I believe that a great deal of predation, in the form of host feeding and mutilation, was being carried out by the parasites.

Mating

During the rearing of this parasite, many observations were made on the behavior and biology of R. nolophanae. Newly emerged virgin females were removed from the zipper cases in which their hosts had been held and were placed in the parasite holding cage. The following mating sequence was observed through the glass cage top. Most of the wasps were actively feeding or moving about the lower surface of the glass. When the virgin female alighted on the glass, she was usually recognized immediately by any male within a 1-in. radius. The male quickly ran to the female. If the female showed no aggressive behavior, he quickly mounted, and they both fell, in copula, to the bottom of the cage and

then immediately separated. This entire mating sequence lasted less than 2 seconds. On rare occasions, the female would escape before the male could mount. Occurrences of mating between males and mated females were not observed.

Oviposition

No preoviposition period was required by this parasite. Newly mated females, as well as others which had mated some time earlier, were removed from the holding cage and placed in zipper cases each containing 10-15 green cloverworm larvae and a single soybean leaflet. These females were often observed searching, attacking, stinging, mutilating, and ovipositing in host larvae.

Some introduced females readily sensed that host larvae were present. Others moved about the case and flew quickly if they came in contact with a larva. For those which sensed that host larvae were present, the act of searching for a suitable host was generally as follows. The parasite curled the antennae down, toward the leaf surface, in front of the head. The female moved cautiously, but not quickly, about the case or leaflet surface until it came in contact with a suitable larva. First- and 2nd-stage larvae were usually ignored by these searching females.

After a prospective host was located, the wasp moved quickly to the larva which was less than 1 cm distant. An attempt was made by the parasite to grasp the larva, usually in the thoracic region, and hang on to the leaflet or zipper case surface and thrust the abdomen forward

in order to sting and paralyze the host. Parasites often fell to the bottom of the zipper case while holding the larva.

In most instances, the wasp held the larva until the injected venom had taken effect, usually less than 60 sec. Subsequently, the wasp began probing with the ovipositor. Oftentimes, this probing took place in the thoracic region of the larva. After several wounds had been made, the parasite turned around and fed on the exuding fluids. Host feeding by adults is not uncommon among the Hymenoptera, and in some species, it is a necessary source of protein needed for ovigenesis. It is not known whether adult host feeding prevents the development of a parasite within a host. Probing and oviposition in the abdominal region were often observed while the parasite was feeding on the body fluids. At other times, the probing and oviposition took place only in the abdominal region and no adult host feeding was observed.

The act of oviposition, or what was believed to be oviposition, differed considerably from probing. Oviposition was not confirmed by dissection of eggs in these studies because of the lack of individuals which could be sacrificed. When probing took place, the ovipositor was inserted through the insect body wall and then soon removed. When the parasite was ovipositing, the abdomen and ovipositor were manipulated in a manner which led me to believe an egg was being deposited. Oviposition occurred only in the posterior region of the host abdomen and lasted ca. 1 min.

One parasite was observed ovipositing in several larvae in sequence. The 1st larva was stung and oviposition was observed. Within

15 min of the 1st attack, the wasp attacked another larva. The interval of time between succeeding attacks was 10, 7, 9, and 43 min. Second-, 3rd-, and 4th-stage larvae were attacked in these observations.

If probing and oviposition were not too severe, the host larva soon recovered and moved away. I did not observe parasitized larvae being stung a 2nd time.

Parasite development

After the larvae had been exposed to ovipositing females, they were separated into individual zipper cases and fed soybean leaflets until the developing parasite caused the larva to cease feeding. There was no external evidence of a developing parasite until ca. 8 days after oviposition. At this time, the presence of the developing parasite was detected because the host larva exhibited some swelling in the abdominal region and was a lighter green color than an unparasitized larva.

While the host larva was green, the parasite chewed an opening in the sternum of the larva in the area of the meso- and metathorax. The developing parasite larva then secreted an adhesive material which prevented the green cloverworm larval skin (parasite cocoon) from being dislodged from the surface of attachment. Within 2 days, the parasite had transformed the green larval skin into a shriveled brown skin in which the parasite completed its development. This use of the host's larval skin for a cocoon is characteristic of members of the subfamily Rogadinae.

The mean developmental time from oviposition to brown-cocoon development was 10.00 ± 2.34 days for 23 developing male parasites

and 10.36 ± 1.03 days for 11♀♀. The mean time spent in the cocoon was 7.97 ± 1.06 days for 32 ♂♂ and 8.17 ± 1.38 days for 18♀♀.

The mean developmental time from oviposition to adult emergence was 17.97 days for males and 18.53 days for females. In the Hymenoptera, males often develop more rapidly than females and mate with them as the females emerge. This phenomenon was not observed with R. nolophanae because parasites were reared individually.

Emergence of the adult parasite from the cocoon was accomplished by the adult chewing an exit hole in the dorsum near the tip of the abdomen. Parasites were placed in the colony holding cage where they fed on honey streaks, mated and were used periodically to parasitize more larvae and continue the colony.

No attempts were made to isolate or mark individuals in order to determine the longevity of adults. At one point, however, the colony consisted of a single female which lived for at least 6 wk. Several individuals were observed to die in ca. 1 wk.

One experiment was conducted to determine the preferred host stage of ovipositing R. nolophanae females. Ten parasites were introduced into individual zipper cases, each of which contained 25 larvae (5 of stages 1 through 5). After a 24-hr exposure, the wasps were removed from the zipper cases. The experiment was terminated when it was noted that many of these larvae were dead or dying. Some time after the experiment was terminated, I realized that this form of predation (adult-wasp predation) may be quite important and should have been quantified.

A new experiment then was conducted with individual females.

Females were placed individually in zipper cases, with each zipper case containing ca. 20 larvae. After a 24-hr exposure, the wasps were removed and the dead larvae counted. Of the 99 larvae exposed, 51 died. The mortalities in the zipper cases ranged from 30 to 70%.

Although the preferred host stage was not determined precisely, it should be noted that 3rd-stage larvae were preferred above 2nd- and 4th-stage larvae. Females were not observed attacking 1st- or 5th-stage larvae.

Life stages

Some, but not all, of the life stages of R. nolophanae were observed while the rearing study was being conducted. A live gravid female was sacrificed and dissected for eggs. The eggs, measuring ca. 0.28 X 0.11 mm, were of the hymenopteriform type and not of the acuminate type (long and stalked) which is common among braconids and other internal parasites.

The egg shape was slightly curved and somewhat oval along the longitudinal axis. Under the dissecting microscope (60X) the egg surface appeared finely etched. When the egg was mounted on a slide and viewed under the compound microscope (100^{+}X), the etching was seen as coarse, short, irregularly curved ridges, densely scattered over the egg surface. At one end, believed to be the micropyle, the ridges were quite close together and formed a darker broken-ring pattern.

The no. of larval instars is not known. Endoparasitic forms generally have fewer than 5. Some larvae were dissected from cocoons, but these may have been last stage larvae or pronymphs. One larva was

7.0-mm long and 1.5-mm in diam. Some of the noted life stages are shown in Figure 18.

Biological Investigations of Winthemia sinuata

During the 4 month period the W. sinuata colony was maintained, over 450 parasitized larvae were taken from the parasite holding cage and held for parasite development. Each of the more than 450 larvae had deposited on it at least 1 visible macrotype egg. Of this no. exposed, only 24 flies (15♀, 9♂) were able to complete development. An additional 28 puparia were formed from which flies failed to emerge. Maggots emerged from 3 additional larvae, but these failed to form puparia. The minimum percent parasitism by W. sinuata was, therefore, 12.2%. However, only 7 moths emerged from these larvae which had fly eggs deposited on them. For this reason, I believe that the mortality due to parasitism was greater than 12.2%, but for reasons given shortly, few adults emerged.

Mating and oviposition

While this parasite was being reared in the greenhouse, males and females were seen in copula (male above female) on several occasions, but no courtship or premating behavior was observed. No preoviposition period was noted either, but it should not be construed that both of the preceding do not exist, but rather that they were never observed.

Oviposition by W. sinuata was a function of several factors. Two factors observed to stimulate oviposition by the flies are larval size and activity. In 1 experiment in which larvae were exposed to the female

flies, 8 6th- and 3 5th-stage larvae had deposited on them a mean of 8.25 ± 6.39 and 3.33 ± 0.59 eggs, respectively. Two of the 6th-stage larvae had 16 eggs deposited on each of them. In another experiment in which 40 larvae (20 6th-stage and 20 5th-stage) were exposed, 11 6th-stage and 3 5th-stage larvae were parasitized. Egg counts were not made in this study. In a 3rd experiment, 30 larvae of stages 4, 5, and 6 (10/stage) were exposed to the flies. Eight 6th-stage larvae and 1 5th-stage were parasitized. Exposure periods for the preceding experiments were ca. 24 hr.

The act of oviposition was observed on numerous occasions. When larvae were 1st introduced into the cage, a few of the females would run quickly to them. Fifth- or 6th-stage larvae which dispersed rapidly were followed by 1 or more females. The prospective host moved rapidly away while trying to avoid the fly which was attempting to oviposit. The fly moved laterally along the same line the larva was moving and nearly always faced the host. From time to time, the ovipositor was quickly extended from beneath the fly (between the legs) to ca. 1/8 in. beyond the face of the fly. If the larva moved away before the egg was laid, the fly retracted the ovipositor only slightly and continued its pursuit of the larva. The egg was placed on the host larva with a quick gentle downward stroke of the ovipositor and was apparently attached with a mucilaginous material.

As the active larvae that had eggs laid on them were removed from the cage, a unique response by the flies resulted. A fly would approach a larva and if the larva did not begin moving, the fly would move close

and place 1 of the fore tarsi on the larva. If the fly, by such action, could not cause the larva to move, it would not oviposit on it. Larvae which are about to molt are characteristically sluggish and move very little. Since 3 days are required before the parasite eggs hatch, any eggs laid on a premolting larva would be shed with the cast larval skin before the hatching fly larva could enter the host. The evolution of response by the fly, allows W. sinuata to avoid considerable egg mortality.

The creamy white, macrotype eggs, measuring ca. 0.38 mm X 0.75 mm, were laid, 1 at a time, on the host, generally in the thoracic region. The eggs were apparently monoembryonic (1 developing parasite/egg), and were of the dehiscent type with a fracture line around the anterior end. As noted previously, more than 1 egg may be laid on a host and the female flies are not readily deterred from ovipositing on parasitized larvae.

Parasite development

The eggs hatched in ca. 3 days. The 1st-stage maggots emerged from the egg at the fracture line and soon cut through the larval integument and entered the host. Two stages of larvae were observed (1st and last), although 3 generally occur in the Tachinidae. After entering the host, the maggot completed its development and emerged either from the mature green cloverworm larva or the pupa. Since this endoparasite completes its development in either form of the host, it should be considered both a larval and a larval-pupal parasite.

When the maggot was completing its development in the host pupa, respiration was carried on by means of a funnel-like structure which

was observed attached to the host's body wall. Mature green cloverworm larvae were not dissected to determine the presence of these structures.

The mean developmental time from exposure to puparium formation for 9♂ was 9.56 ± 1.02 days, and for 15♀, 10.00 ± 1.85 days. The no. of days which 9♂ spent in the puparium was 12.00 ± 1.50. Fourteen females spent 13.21 ± 2.52 days in the puparium.

A little over 2 months after the colony was initiated, many of the exposed green cloverworm larvae began to die before the maggots could complete development. A bacterium was isolated from these larvae which, when cultured, would not grow in the presence of chloromycetin or chloramphenicol. An attempt was made to reduce this mortality by feeding the green cloverworm larvae leaves which had been treated with an antibiotic. Parasitized larvae continued to die and the colony was eventually lost. When the bacterium was fed to the larvae, none of them died. The bacterium was apparently not a true pathogen, but an opportunist which was in some way involved with the maggots which entered host larvae.

Life stages

Some of the life stages and particular morphological aspects associated with them are shown in Figure 19. The 1st-stage maggot was observed emerging from the host and was preserved in that manner. The macrotype egg's surface apparently bears the impressions of the cells of the ovarioles.

SUMMARY AND CONCLUSIONS

Extensive collections of green cloverworm larvae were made in 1970 and 1971 to determine the relative abundance of larval populations in various areas of the state. These collections were also made to collect and identify the parasites of the green cloverworm and to determine their distribution, abundance, seasonal occurrence and host-parasite relationships in Iowa.

An intensive study was conducted near Ames in 1971 to determine the seasonal abundance and characteristics of green cloverworm larval populations in selected fields and also to determine the response of parasites to these natural populations. The seasonal occurrence and abundance of parasites of the green cloverworm, host-parasite relationships, and environmental factors affecting host and parasite populations were all examined in an attempt to evaluate the role of parasites in regulating green cloverworm larval populations.

Nine species of primary parasites (Table 6) were reared from green cloverworm larvae collected in 2 years of study. Five of these are reported as parasites of the green cloverworm for the 1st time. Of the 9 species of parasites, only 4 (A. flaviconchae, S. validus, L. archippivora, and M. hyphantriae) were not collected from all areas of the state. Of these 4, single specimens were collected of the latter 3.

The most abundant parasite collected was the braconid wasp, R. nolophanae. Including the intensive collections of 1971, R. nolophanae was reared from 17.8% of all larvae collected in 2 years. Early season

parasitism by R. nolophanae was high, but declined sharply at mid-season and became variable the remainder of the season (Figure 9). The weekly percent parasitism by R. nolophanae was similar early in the season in 4 soybean fields, but became variable late in the season. Little difference was noted between total parasitism in the alfalfa and soybean ecosystems. Regressions of the no. of R. nolophanae-parasitized larvae collected on the no. of susceptible larvae present in individual fields indicated that the no. of parasitized larvae increased as the susceptible population increased (Figures 10-13).

The 2nd most abundant parasite collected was the tachinid fly, W. sinuata. Total parasitism by this species in 2 years of study was 8.6%. Total weekly percent parasitism by W. sinuata was low early in the season (Figure 9), but increased late in the season. The total percent parasitism by W. sinuata differed in the 2 ecosystems (3.9 and 10.0% parasitized in alfalfa and soybean, respectively). Although the incidence of parasitism by W. sinuata was variable in the 4 soybean fields, it generally remained low early in the season and increased late in the season. Density-related relationships between the no. of parasitized larvae and the no. of susceptible hosts did not appear very strong.

Based on the results of the intensive study, it became obvious that possible reasons for the changes in the incidence of parasitism by individual species should be recognized. Previous reports concerning parasitism among natural populations rarely, if ever, offered possible reasons for any change in the level of parasitism. Rather, parasitism

by individual species was reported as increasing, decreasing, or remaining the same. In these studies, I believe that parasitism by the 2 prominent species is directly related to the general age structure of the host population. As the age structure of the population shifted from less mature to more mature, the percentage of the population which was susceptible to attack by R. nolophanae decreased and the percentage of the population susceptible to attack by W. sinuata increased. Comparable decreases and increases in the level of parasitism by these 2 species were noted.

The total percent parasitism by each of 6 of the primary parasites was less than 1.5% in the intensive study. The no., total seasonal parasitism, and the seasonal occurrence of these 6 species in relation to the total host population are shown in Figure 8.

The total percent parasitism of all larvae collected in the 2 years of study was 31.8%, higher than any previous reports from studies with the green cloverworm.

Biological data on all of the primary parasites were summarized in Table 13. All of the hymenopterous parasites reared were solitary in development. In most instances, the dipterous parasites were solitary in development, but occasionally they were gregarious. Most of the dipterous parasites were reared from larvae collected in the 5th- or 6th-stage. Depending on the individual species, the wasps were generally reared from larvae collected as 3rd-, 4th-, or 5th-stage.

The coexistence of 2 parasite species within 1 host (more appropriately termed multiple parasitism) was observed on 2 occasions. In 1970,

1 larva was parasitized by both W. sinuata and L. archippivora. In 1971, 2 specimens of W. sinuata and 1 of O. assimilis emerged from a single larva. To my knowledge, occurrences of this phenomenon are rare.

The incidence of hyperparasitism in these studies was very low. Only 10 hyperparasites (4 species) were reared in the 2-year study. Three of these (P. hyalinus, M. americanus, and A. nigricapitata) are new records in their association with parasites of the green cloverworm. M. discitergus, the other species, had been reported previously in association with the green cloverworm.

In the egg parasite study, only 1 parasite (Telenomus sp.) was collected from 93 exposed eggs. This represents a new record since no scelionid wasp has previously been reported as a parasite of green cloverworm eggs.

Mermithid nematodes, probably Hexamermis, were reared from 2 green cloverworm larvae collected in 1968. This is the 1st report of nematode parasites from field populations of green cloverworm larvae. Other mortality factors observed in green cloverworm larval populations were the fungus diseases Beauvaria and Metarrhizium, and a granulosis virus.

Other characteristics of the host population which were noted were the existence of a 1:1 sex ratio among the moths and generally a similar age structure from 1 field to another.

The 2 most prominent parasite species were colonized for a period of time. Great difficulty was experienced in attempting to rear them, however, many observations were made and recorded concerning the biology and behavior of these 2 species. Some of the life stages are described

and are illustrated in Figures 18 and 19.

The results of these studies indicated that parasitism is a very important mortality factor in the regulation of field populations of green cloverworm larvae. R. nolophanae was the most prevalent parasite reared from larvae collected in these investigations and appeared to be the most important parasite.

However, the criteria one uses to evaluate the importance of a parasite in the regulation of natural populations must be considered carefully. It may be that the parasite which successfully parasitizes the most larvae during the season is the most important as a population regulator. On the other hand, a parasite which suppresses the 1st generation or the overwintering population of the host may be the single factor responsible for changes in the population density from generation to generation or from season to season.

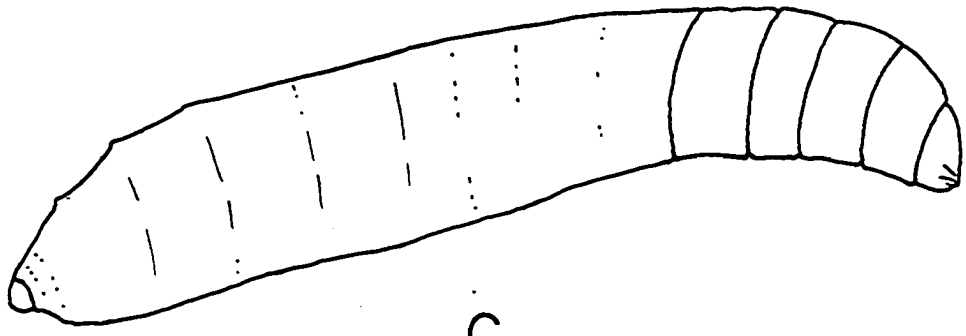
Morris (1959) referred to a mortality factor which causes a degree of mortality that is related to the changes in population density from generation to generation (and which has some predictive value) as a key factor. Some parasite species were considered here as possible key factors. It quickly became apparent that more intensive studies must be made before a parasite could be considered as a key factor of the green cloverworm.

Some of the following improvements should be incorporated into a program where parasitism is being evaluated as a population regulator. The improvement of the collection technique by taking smaller samples will reduce sampling mortality and increase the precision in sampling

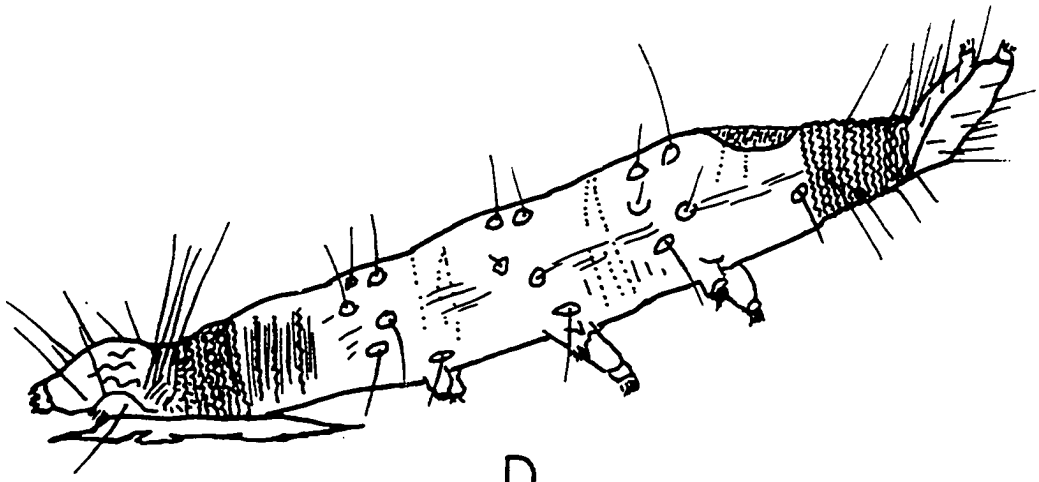
Figure 18. Selected life stages of Rogas nolophanae: A, sculptured egg chorion; B, hymenopteriform egg; C, last stage larva dissected from cocoon; D, empty cocoon formed from host larval skin

A

B

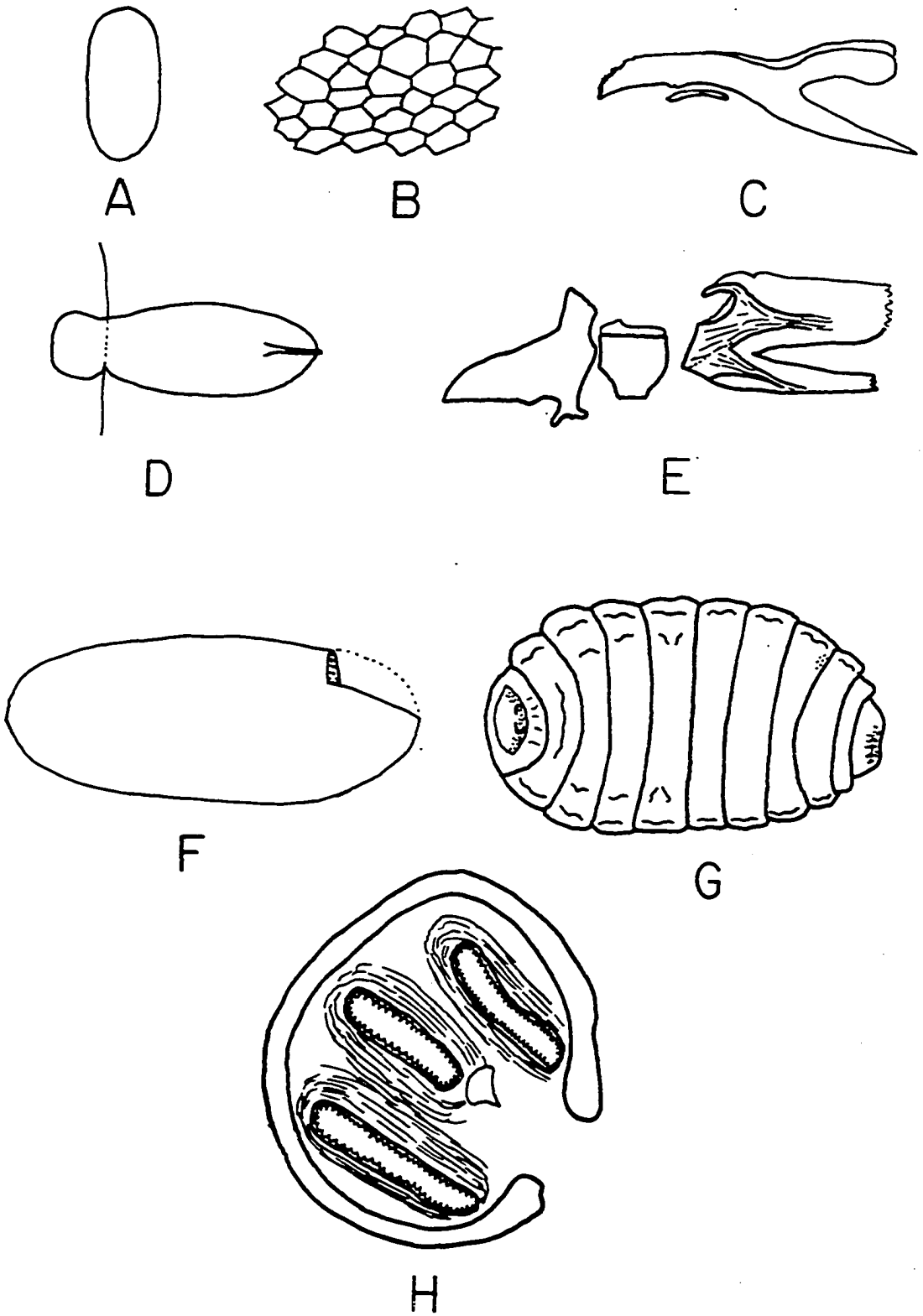


C



D

Figure 19. Selected life stages of Winthemia sinuata: A, macrotype egg; B, sculptured egg chorion; C, 1st-stage maggot cephalopharyngeal skeleton; D, 1st-stage maggot; E, last-stage maggot cephalopharyngeal skeleton; F, puparium; G, last-stage maggot nearing pupariation; H, left posterior spiracle


A
B
C
D
E
F
G
H

all stages of the population. Sampling of eggs and pupae for parasites should also contribute to the knowledge of the role of parasitism in regulating larval green cloverworm populations.

Studies such as these need to be encouraged and continued so that entomologists may arrive at a better understanding of the natural forces that operate in the life systems of pest and beneficial insects. An improved knowledge of these forces will allow entomologists to encourage and conserve those which would be useful in the pest-management process. The lack of a proper understanding may lead to actions which destroy the natural enemies and allow pest species to increase to more damaging levels which has historically placed farmers and growers on the insecticide treadmill.

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No words can truly express the deepest feeling of gratitude due to my devoted and deserving wife, Aneita, for the sacrifices made in our years of graduate studies together.

APPENDIX

Figure 20. Green cloverworm collection record data sheet

GREEN CLOVERWORM COLLECTION RECORD

Host Plant or Habitat — 1

(1) Soybean
(2) Alfalfa
(3) Clover
(4) Alf-Clo Mix
(5) Unknown

Insect Stage — 2 3

(8) Unknown
(9) Prepupa
(10) Pupa
(11) Moth
(12) Egg

Date of Collection — 4 5 6 7 8 9 (1-7)

4 5: Day
6 7: Mo.
8 9: Yr.

Day of Year — 10 11 12

144

Method of Collection — 13

(1) Sweep 15" net
(2) Sweep 18" net
(3) Vacuum
(4) Shake
(5) Insitu
(6) Other

Sample Size — 14 15

(01) 100 Sweeps
(02) 50 Sweeps
(03) 48 Sweeps

Accession Number

16 17 18 — Field Number

19 20 — Sample Period Number

21 22 — Sample Number

23 24 25 — Larva Number Within Sample

County or Location — 26 27 28

(1) Ames
(2) North
(3) South

Laboratory Diagnosis or Finding

Final Diagnosis or Stage at Death — 29 30 (1-7)

(8) Unknown
(9) Prepupa
(10) Pupa Formed
(11) Moth Emerged
(12) Egg
(13) Moth Within Pupa
(14) Lost

Cause of Death — 31 32

(1) Injured at Colln.
(2) Accident in Lab
(3) Parasitized
(4) Unknown
(20) Bacterium
(30) Fungus
(40) Virus
(50) Protozoan

Method of Death Determination — 33

(1) Reared Parasite
(2) Observed
(3) Microscopy
(4) Biochemical
(5) Electron Microscopy

Date of Death or Moth Emergence — 34 35 (Day) 36 37 (Mo.)

Day of Year — 38 39 40

Number of Fly Eggs Present — 41 42

00=00
01=1
⋮
10=10
99=unknown

Fly Eggs on Body Segments — 43 44

01 Prothorax
02 Mesothorax
03 Metathorax
04 Abdomen
05 1,2
06 1,3
07 1,4
08 2,3
09 2,4
10 3,4
11 1,2,3
12 1,2,4
13 1,3,4
14 2,3,4
15 1,2,3,4
16 Unknown

Egg Position — 45 46

01 Right side
02 Top side
03 Left side
04 Bottom
05 1,2
06 1,3
07 1,4
08 2,3
09 2,4
10 3,4
11 1,2,3,
12 1,2,4
13 1,3,4
14 2,3,4
15 1,2,3,4
16 Unknown

Day of Year Parasite Emerged From Host

1st — 47 48 49
2nd — 50 51 52
3rd — 53 54 55

Day of Year Cocoon Formed

1st — 56 57 58
2nd — 59 60 61
3rd — 62 63 64

Day of Year Adult Emerged

1st — 65 66 67
2nd — 68 69 70
3rd — 71 72 73

Number of Parasites Emerging — 74

Parasite Species — 75 76

01 Rogas
02 Winthemia
03 Protomicroplitis
04 Apanteles
05 Oswaldia
06 Blondelia
07 Unknown flies (lost, died or escaped)
08 Unknown wasps (lost, died or escaped)
09 02 + 05
10 Meteorus

Number of ♀ — 77

Number of ♂ — 78

Hyperparasite Species — 79

(1) Present

Moth Sex — 80

(1) Female
(2) Male
(3) Unknown