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THE INTERACTIONS OF ROOT MAGGOTS AND TWO PARASITOIDS *ALEOCHARA BILINEATA* (GYLL.) AND *APHAERETA PALLIPES* (SAY)

By

Eleanor Groden

A THESIS

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ABSTRACT

THE INTERACTIONS OF ROOT MAGGOTS AND TWO PARASITOIDS ALEOCHARA BILINEATA (GYLL.) AND APHAERETA PALLIPES (SAY)

by

Eleanor Groden

This thesis examines the temporal and spatial distributions of Aleochara bilineata (Gyll.) and Aphaereta pallipes (Say), two parasitoids of the onion maggot (OM) Hylemya antiqua (Mg.). The effect of temperature on A. bilineata development was quantified. Since the parasite develops slower than its host, a corrector was developed for the bias this imposes on field data.

A. bilineata adults emerged in mid-June and were parasitizing larvae and were synchronized with first generation OM pupae. Cabbage maggot, Hylemya brassica (Bouche), and OM pupae provided a continuous supply of hosts for A. bilineata when radishes and onions were grown together.

A. pallipes was not present in onion fields during the growing season, but it was observed on cow dung. A. pallipes activity increased dramatically after harvest on maggot-infested culls in the field. Both parasitoids showed increased activity near weedy field borders.

DEDICATION

To Nate and Brie, in hopes that they may
live in a cleaner world.

And to my mother, Helen P. Groden,
who always presented me with a model
of women as strong, intelligent and
compassionate people.
And to my sisters following in her footsteps.

ACKNOWLEDGMENTS

I would like to thank the entire faculty, staff, and students in the Entomology Department at Michigan State University, particularly Dr. Jim Bath, for creating an atmosphere conducive to professional growth and individual expression. I sincerely doubt that this educational opportunity could be exceeded elsewhere.

It has been an honor to be a student of Dr. Dean Haynes. Dean's challenges and inspirations always kept the gears going, allowing one to realize more than I had thought possible.

I would like to thank the other members of my guidance committee, Drs. Stuart Gage and Fred Stehr, for their advice and encouragement and for reviewing this manuscript. Also, I appreciate the advice and time spent reviewing this manuscript by Dr. Dick Casagrande.

For their humor, encouragement, and discussions, I would like to thank my fellow graduate students: Dr. Mike Mispagel, Mr. Nick Bolgiano, Ms. Julia Pet, Drs. Ray Carruthers and Gary Whitfield. I would also like to thank Mr. Tom Ellis for his frequent assistance on this project, and Dr. Emmett Lampert and Mr. Ken Dimoff for their assistance and advice in the data analysis, and Ken for the assistance with the graphics and the hundreds of little computer-related problems I inevitably encountered.

I am indebted to Ms. Susan Battenfield, not only for the assistance in editing and pulling together this manuscript, but for her friendship which made it a more enjoyable process. Also, a considerable amount of work on this project was done by Ms. Robin Rosenbaum, my extra eyes and hands in the field. Robin's dedication and friendship proved essential.

Most of all, I would like to thank my colleague and dearest friend, Frank Drummond. Often our fellow graduate students become our teachers, and this was frequently the case with Frank. His encouragement, companionship, and love were the true catalyst in the completion of this goal.

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INTRODUCTION

In the U.S. and many developed countries, the structure of agriculture has changed in the last 50 years. Cheap and abundant fossil fuels (energy) increased chemical fertilizer and pesticide use and promoted farm mechanization (Edens and Haynes 1982). Cheap energy also lengthened food distribution networks, such that food grown in one part of the country could be shipped, cheaply, almost anywhere in the world. More importantly, however, old crop varieties were replaced with less stable varieties that required heavy fertilizer, water, and chemical pesticide use, and the heterogeneous farms were transformed into mono-cropping production systems. These structural changes have profoundly affected farm ecosystems.

First, the less diverse habitat concentrates the food resources and attracts greater numbers of herbivorous insects. The habitat's design also makes it less likely that the insects will emigrate out of the system (Risch 1981). Second, pesticides eliminate the natural enemy complex. As a result, severe insect outbreaks occur in mono-cropping systems.

Realizing the importance of natural enemies in controlling pest insects, researchers have been improving application methods (e.g., eliminating some pesticides and using ULV application). However, merely changing or eliminating pesticides will not guarantee biological control, because agricultural systems are not designed to support natural enemies.

Adult parasitoids do not solely depend on host distributions. Ecological factors influence adult distribution patterns. Abiotic characteristics of the habitat, particularly relative humidity, affect habitat preferences of some hymenopteran parasitoids (Weseloh 1972, 1975, 1979, Merritt and Anderson 1977, Townes 1957). The abundance and success of many parasitoids depends on the availability of a nectar and/or pollen source for adult parasitoid nutrition (Symes 1975). The effectiveness of some parasitoids in controlling pest populations depends on the proximity of habitats that support alternate hosts (Hsiao and Holdaway 1966, Doutt and Nakata 1973). Many of the essential links between the components of the ecosystem are lost in the simplified large scale monocultures.

The onion production system typifies this scenario (Haynes et al. 1980). The existing production system has resulted from decades of heavy reliance on organic insecticides to control the major insect pest, Hylemya antiqua (Meigen), the onion maggot (OM). Figure 1 (Haynes et al. 1980) details the onion ecosystem with the onion plant as the reference point. However, to understand the dynamics of the parasitoids of the OM and the potential for parasitoid management, parasitoids must be the reference point (Ravlin 1981). Also, the system boundaries must include the alternate hosts of the parasitoids and their habitat (Figures 2 and 3). From this perspective a considerable number of common components emerge between the habitat types (Table 1).

In a system including onions, radishes, and beef or dairy production (pasture), the only overlapping species within the "pest" complexes is H. platura, the seed corn maggot (SCM). A minor pest in onions and radishes, the SCM is an alternate host for most of the parasitoids, predators, and diseases of the major pests in both crops. It is also a host for the OM and H. brassicae (Bouche), the cabbage maggot (CM). The SCM may therefore be an important component in parasitoid dynamics. There is, however, considerable overlap between many of

Figure 1. Conceptualization of the onion agroecosystem showing levels of interaction within the object of control and the monitored environment (Haynes et al. 1980).

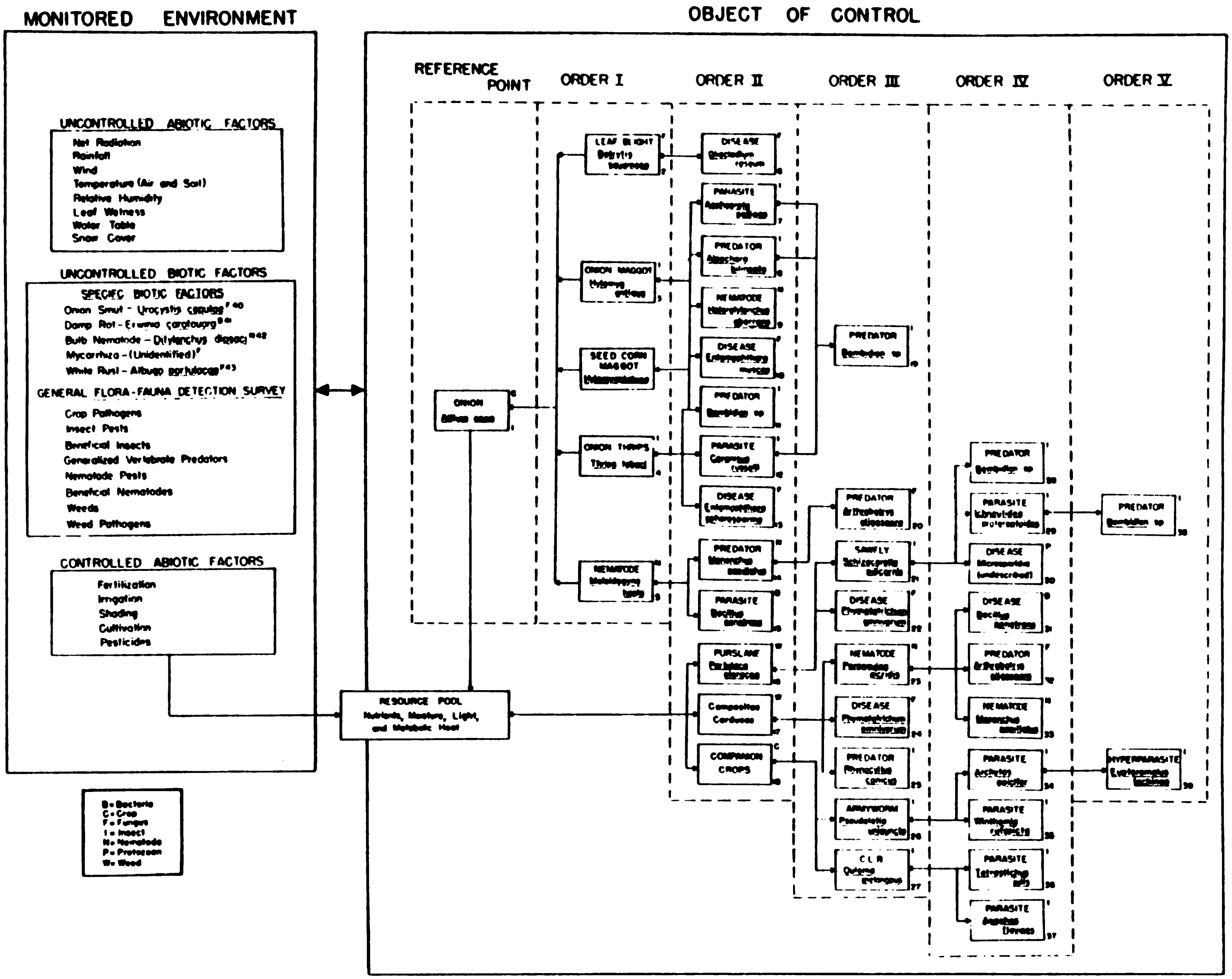
MONITORED ENVIRONMENT
UNCONTROLLED ABIOTIC FACTORS
Net Radiation
Rainfall
Wind
Temperature (Air and Soil)
Relative Humidity
Leaf Wetness
Water Table
Snow Cover
UNCONTROLLED BIOTIC FACTORS
SPECIFIC BIOTIC FACTORS
Onion Smut - Urocystis cepulae F 40
Damp Rot - Erwinia carotovora B 41
Bulb Nematode - Ditylenchus dipsaci N 42
Mycorrhiza - (Unidentified) F
White Rust - Albugo portulacae F 43
GENERAL FLORA-FAUNA DETECTION SURVEY
Crop Pathogens
Insect Pests
Beneficial Insects
Generalized Vertebrate Predators
Nematode Pests
Beneficial Nematodes
Weeds
Weed Pathogens
CONTROLLED ABIOTIC FACTORS
Fertilization
Irrigation
Shading
Cultivation
Pesticides
B = Bacteria
C = Crop
F = Fungus
I = Insect
N = Nematode
P = Protozoan
W = Weed
OBJECT OF CONTROL
REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
ONION
RESOURCE POOL
Nutrients, Moisture, Light, and Metabolic Heat
LEAF BLIGHT
Botrytis
ONION MAGGOT
SEED CORN MAGGOT
ONION THRIPS
Thrips tabaci
NEMATODE
DISEASE
PARASITE
PREDATOR
NEMATODE
DISEASE
PREDATOR
PARASITE
DISEASE
PREDATOR
PARASITE
PURSLANE
Portulaca oleracea
Compositae
Carduus
COMPANION CROPS
PREDATOR
PREDATOR
SAWFLY
Schizocerella pilicornis
DISEASE
NEMATODE
DISEASE
PREDATOR
ARMYWORM
C L R
PREDATOR
PARASITE
DISEASE
Microsporidia (undescribed)
DISEASE
Bacillus
PREDATOR
NEMATODE
PARASITE
PARASITE
PARASITE
PARASITE
PREDATOR
HYPERPARASITE
C
1
2
3
4
5
6
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Figure 2. Conceptualization of an onion-radish agroecosystem using *Aleochara bilineata* as a reference point. (* refers to components common to both *Aleochara bilineata* and *Aphaereta pallipes* life systems.)

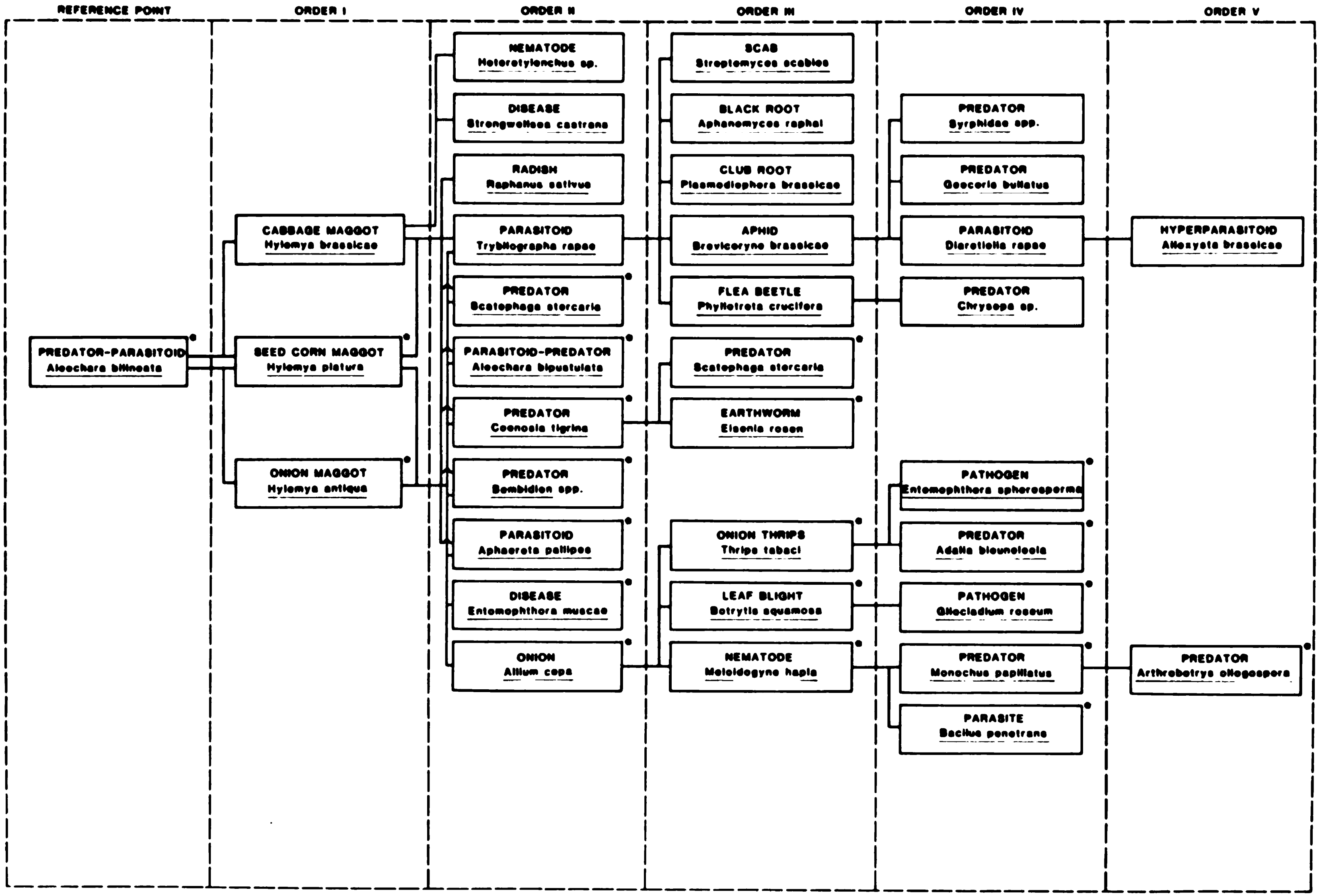

REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
PREDATOR-PARASITOID
Aleochara bilineata
CABBAGE MAGGOT
Hylemya brassicae
SEED CORN MAGGOT
Hylemya platura
ONION MAGGOT
Hylemya antiqua
NEMATODE
Heterotylenchus sp.
DISEASE
Strongwellsea castrans
RADISH
Raphanus sativus
PARASITOID
Trybliographa rapae
PREDATOR
Scatophaga stercoria
PARASITOID-PREDATOR
Aleochara bipustulata
PREDATOR
Coenosia tigrina
PREDATOR
Bembidion spp.
PARASITOID
Aphaereta pallipes
DISEASE
Entomophthora muscae
ONION
Allium cepa
SCAB
Streptomyces scabies
BLACK ROOT
Aphanomyces raphai
CLUB ROOT
Plasmodiophora brassicae
APHID
Brevicoryne brassicae
FLEA BEETLE
Phyllotreta crucifera
PREDATOR
Scatophaga stercoria
EARTHWORM
Eisenia rosea
ONION THRIPS
Thrips tabaci
LEAF BLIGHT
Botrytis squamosa
NEMATODE
Meloidogyne hapla
PREDATOR
Syrphidae spp.
PREDATOR
Geocoris bullatus
PARASITOID
Diaretiella rapae
PREDATOR
Chrysopa sp.
PATHOGEN
Entomophthora sphaerosperma
PREDATOR
Adalia bleunelcola
PATHOGEN
Gliocladium roseum
PREDATOR
Mononchus papillatus
PARASITE
Bacillus penetrans
HYPERPARASITOID
Alloxysta brassicae
PREDATOR
Arthrobotrys oligospora

Figure 3. Conceptualization of an onion-pasture agroecosystem using Aphaereta pallipes as a reference point. (* refers to components common to both Aleochara bilineata and Aphaereta pallipes life systems.)

[1] See Merrit (1974) for further description of interactions in the fresh cow dung habitat.

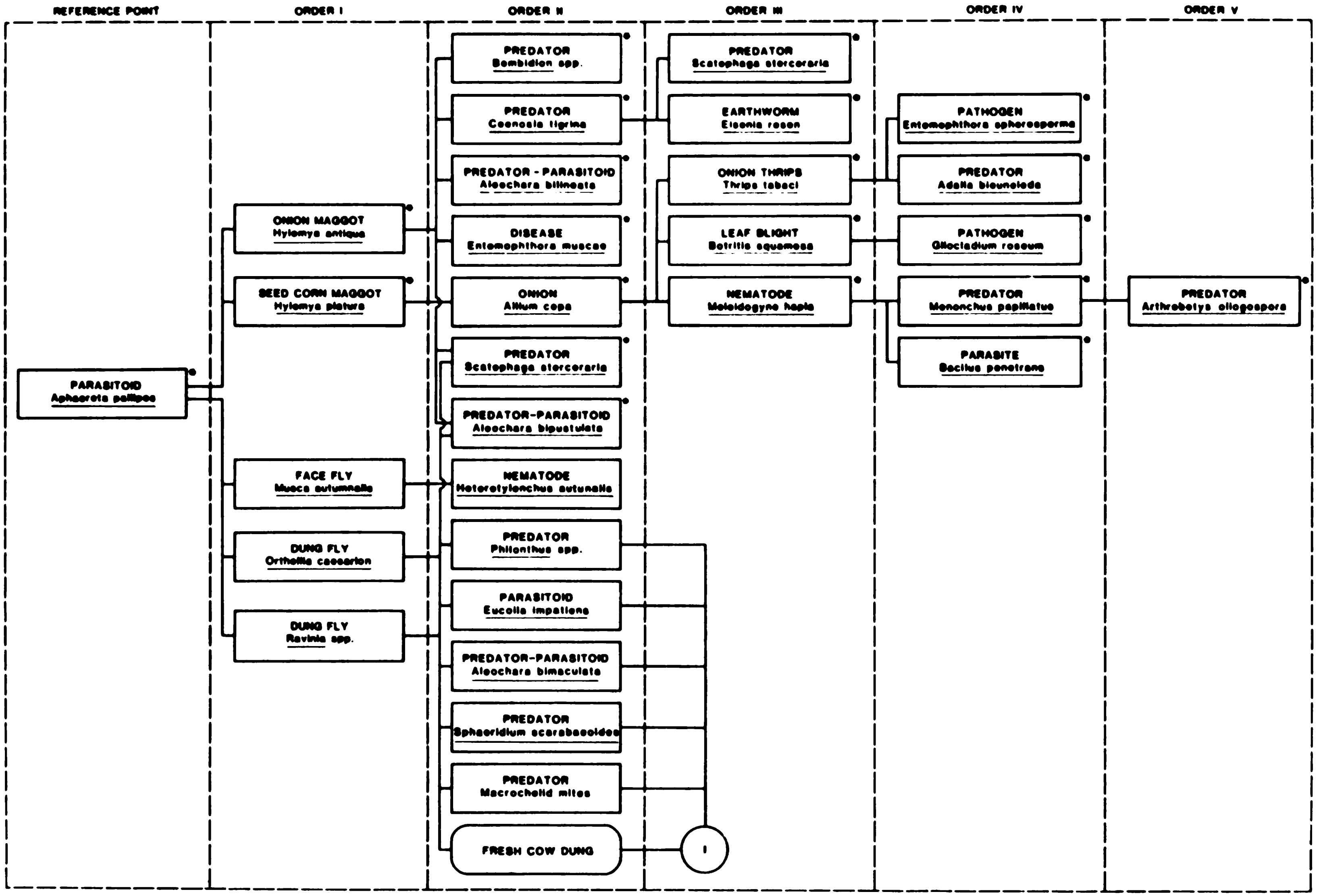

REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
PARASITOID
Aphaereta pallipes
ONION MAGGOT
Hylemya antiqua
SEED CORN MAGGOT
Hylemya platura
FACE FLY
Musca autumnalis
DUNG FLY
Orthellia caesarion
DUNG FLY
Ravinia spp.
PREDATOR
Bembidion spp.
PREDATOR
Coenosia tigrina
PREDATOR - PARASITOID
Aleochara bilineata
DISEASE
Entomophthora muscae
ONION
Allium cepa
PREDATOR
Scatophaga stercoraria
PREDATOR-PARASITOID
Aleochara bipustulata
NEMATODE
Heterotylenchus autumnalis
PREDATOR
Philonthus spp.
PARASITOID
Eucoila impatiens
PREDATOR-PARASITOID
Aleochara bimaculata
PREDATOR
Sphaeridium scarabaeoides
PREDATOR
Macrochelid mites
FRESH COW DUNG
I
PREDATOR
Scatophaga stercoraria
EARTHWORM
Eisenia rosea
ONION THRIPS
Thrips tabaci
LEAF BLIGHT
Botritis squamosa
NEMATODE
Meloidogyne hapla
PATHOGEN
Entomophthora sphaerosperma
PREDATOR
Adalia bipunctata
PATHOGEN
Gliocladium roseum
PREDATOR
Mononchus papillatus
PARASITE
Bacillus penetrans
PREDATOR
Arthrobotrys oligospora

Table 1. The common components in the onion, radish and pasture (fresh dung) habitats.

	Onion	Radish	Pasture (fresh dung)
Major Colonizers			
Onion maggot, *Hylemya antiqua*	━━━		
Seedcorn maggot, *H. platura*	━━━	━━━	
Cabbage maggot, *H. brassicae*		━━━	
Face fly, *Musca autumnalis*			━━━
Ravinia species			━━━
Orthella caesarion			━━━
Onion thrips, *Thrips tabaci*	━━━		
Flea beetle, *Phyllotreta crucifera*		━━━	
Aphid, *Brevicoryne brassicae*		━━━	
Nematode, *Meloidogyne hapla*	━━━		
Natural Enemies			
Aphaereta pallipes	━━━	╍╍╍	━━━
Aleochara bilineata	━━━	━━━	
A. bipustulata	━━━	━━━	━━━
A. bimaculata			━━━
Coenosia tigrina	━━━	━━━	━━━
Scatophaga stercoraria	━━━	━━━	━━━
Bembidion species	━━━	━━━	━━━
Entomophthora muscae	━━━	╍╍╍	╍╍╍
Trybliographa rapae	╍╍╍	━━━	

Table 1. (continued)

	Onion	Radish	Pasture (fresh dung)
Strongwellsca castrans		▬	
Heterotylenchus sp.		▬	
Heterotylenchus autumnalis			▬
Eucoila impaticas			▬
Sphaeridium scarabacoides			▬
Philonthus species			▬
Macrochelid mites			▬
Syrphidae spp.		▬	
Geocoris bullatus		▬	
Diaretiella rapae		▬	
Chrysopa sp.		▬	
Entomophthora sperospera	▬		
Adalia bieuneleda	▬		
Monochus papillatus	▬		
Bacilus penetrans	▬		
Arthrobotrys oliogospora	▬		

the major natural enemies in the three habitats. Given the complexity of the system, probably more interactions occur than are presently understood.

The OM and onion thrips, *Thrips tabaci*, are the major herbivores in the onion habitat, with nine natural enemies. The radish habitat is slightly more complex with 3 major herbivores and 12 natural enemies. An extremely complex ecosystem lives in fresh dung. An estimated 68 species of dung feeders, 31 species of predators, and 18 species of parasitoids have been reported in fresh cow dung in California (Merritt 1977). Some species are predaceous as larvae yet dung feeders as adults (*Sphaeridium* spp.), and others are dung feeders as larvae yet predaceous as adults (*Scatophaga* spp.)

The objectives of this study were (1) to investigate the biologies and dynamics of the two major parasitoids of the OM, *Aphaereta pallipes* (Say), and *Aleochara bilineata* (Gyll.) and (2) to elucidate ecological factors influencing their distributions within the onion agroecosystem. The dynamics of the parasitoids were examined with the OM and the major alternate hosts of each parasitoid in a multicropping system. The potential of parasitoid management as a major component of an integrated management program was also studied.

This thesis represents one sub-project in an interdisciplinary study of the onion agroecosystem initiated at Michigan State University in 1976. A systems approach (Carruthers 1981, Haynes et al. 1980) has been used to examine the economics of onion production as well as the biotic and abiotic components of the onion ecosystem. Research cooperators include economists Mr. Alex Russell, Ms. Sharon Hart, and Dr. Thomas Edens; plant pathologists, Mr. Nick Bolgiano and Dr. Gene Safir; nematologists, Ms. An MacGuidwin and Dr. G. W. Bird; entomologists, Mr. Frank Drummond, Dr. Raymond Carruthers, Dr. Gary H.

Whitfield and this author; and system scientists, Dr. Lal Tummala and Ms. Julia Pet. The entire project was managed by Mr. Thomas Ellis and directed and inspired by Dr. Dean L. Haynes.

BACKGROUND

ONION MAGGOT

The OM has been the major insect pest in many onion growing regions in the United States and Canada since it was first introduced to North America from Europe in the mid 19th century (Fitch 1867). Scott (1969) compiled an extensive bibliography of the material published on this pest since 1826. Recent reviews of the literature pertaining to the biology and control of the OM have been done by Whitfield (1981), Carruthers (1981, 1979), Loosjes (1976), Perron (1972), and Ellington (1963).

OM attack only the Allium species, of which the bulbing onion, Allium cepa L., is the prefered host (Ellis et al. 1979). Ellis and Eckenrode (1979) and Drummond (1982) suggest that the microbial activity on or near the plant, perhaps governed by the plant age and quality, determines its attractiveness to ovipositing flies.

The distribution of OM damage in a uniform onion field is initially random, but due to the migratory behavior of the larvae, damage becomes contagious (Carruthers 1979). However, sprouting volunteer onions in a field act as attraction points for adult OM flies, which then oviposit in adjacent seedling onions (Whitfield 1981). Damage spreadS from these focal points, because flies oviposit on previously damaged onions (Workman 1958, Armstrong 1924, Loosjes 1976, Carruthers 1979).

The OM overwinters as diapausing pupae in the soil, and emerges as an adult in mid to late spring. Spring emergence (50%) occurs around 390 degree-days (base temperature 4.4°C) (Whitfield 1981, Carruthers 1979, Eckenrode 1975). Adult fly activity within the onion field follows a diurnal pattern, particularly early in the growing season (Carruthers 1981, Whitfield 1981). Fly activity in the fields peaks between 5:30 - 9:30 AM and 5:30 - 8:30 PM; the remainder of the time is spent the cover along the field borders.

After a preoviposition period of ca. 10 days (Theunissen 1976), gravid females lay their eggs in the soil around the base of the onion plant or on the leaves of the plant itself. OM eggs require 50 degree days with base temperature 3.88°C (Carruthers 1979) to develop to eclosion.

The OM larvae feed directly on the tissue of the onion bulb. In the early season when the food resource per plant is small, larvae migrate along the onion row consuming several seedling onions. A density-dependent migratory behavior is also exhibited later in the season as previously infested plants become loaded with new eggs (Drummond 1982). Carruthers (1979) reports that the three larval instars of OM complete development in 37, 89, and 161 degree days (base 4.4°C).

Third instar larvae migrate from the onion plant and pupate in the soil. Pupal depths range from 5 to 15 cm in muck soils in Michigan (Carruthers 1979). Drummond (1982) discovered a shift in this profile with the third generation, such that more individuals pupated in the deeper zones.

OM complete one to five generations per year in different regions around the world (Drummond 1982). In Michigan, OM regularly produce three generations per year (Drummond 1982, Whitfield 1981, Carruthers 1981, 1979); however, most investigations have focused on the first and the second generation as they coincide with the onion growing season. The reports on the percentage of diapausing individuals from each OM generation vary (Ellington 1963, Loosjes 1976). Whitfield (1981) reported only 3% of the second generation OM pupae entering diapause in Michigan. Drummond (1982), investigating the post-harvest dynamics of the OM, reported that the larger proportion of the overwintering OM population develops in cull onions left in the field after harvest.

Of the natural enemies attacking the OM, the fungal disease Entomophthora muscae (Cohn), and the parasitoids Aphaereta pallipes (Say) and Aleochara bilineata (Gyll.) appear to have the most impact on OM populations in Michigan. Several species of Carabidae have also been reported as important predators of OM eggs. Drummond (1982) reviewed the literature concerning carabids associated with OM and CM, and reported on trap catches of carabid species in and about onion field in Michigan.

Carruthers (1981), investigating the biology and ecology of E. muscae in the onion agroecosystem in Michigan, reported that the border habitats about onion fields were of primary importance for the interaction between the host and pathogen. He suggests that field infection levels can be enhanced by maximizing the grassy border habitats.

APHAERETA PALLIPES (SAY)

A. pallipes parasitize OM (Hammond 1924, Sleesman 1931, Workman 1958, Salkeld 1959, Perron 1972, Whitfield 1981). Parasitized pupae have been detected in the overwintering generation of OM in which A. pallipes parasitism has ranged from 12 percent (Perron 1972) to 29 percent (Salkeld 1959).

Aphaereta pallipes (Say) is a member of the family Braconidae, subfamily Alysiinae. Wharton (1977) recently revised the genus Aphaereta to include 16 New World species. McComb (1958) details the species pallipes. Shenefelt (1974) gives the most recent list of synonyms and host lists for the species. The more commonly appearing synonyms include A. auripes (Provancher), A. muscae

(Ashmead), *A. californica* (Ashmead), and *A. sarcophagae* (Gahan).

Besides the OM, the most commonly reported hosts of *A. pallipes* include species of muscoid Diptera associated with fresh cow dung, particularly the face fly (*Musca autumnalis*, DeGeer), *Orthellia caesarion* (Meigen), several *Ravinia* species, and *Sarcophaga kellyi* (Aldr.) (Mohr 1943, Blickle 1961, Benson and Wingo 1963, Houser and Wingo 1967, Turner et al. 1968, Thomas and Wingo 1968, Poorbaugh et al. 1968, Garry and Wingo 1971, Merritt and Anderson 1977). *A. pallipes* has also been reported as a parasitoid of dipterous larvae on poultry manure (Abeles and Shepard 1974) and the agricultural pest, *H. brassicae*, cabbage maggot (Wishart 1957).

Although several studies of *A. pallipes* biology have investigated its potential for biological control of the face fly, the parasitoid adults cannot emerge from face fly puparia (Blickle 1961, Benson and Wingo 1963). However, *A. pallipes* completing development on preferred hosts (*Ravinia* species and *O. caesarion*) still exert considerable mortality on the overwintering population of the face fly Thomas (1967). Thomas (1967) also reported 24% mortality of *M. autumnalis* larvae exposed to *A. pallipes* from adult parasitoid oviposition.

A. pallipes is attracted to fresh manure very quickly after deposition, as is its preferred host, *Ravinia querula*. *R. querula* larvae oviposit on the fresh dung. The larvae must remain near the surface of the very moist manure, which exposes them to parasitoid attack (Houser and Wingo 1967). As the dung ages and begins to desiccate, dipterous larvae move deeper in the pat and are less susceptible to attack. Gary and Wingo (1971) reported that the presence of *Sphaeridium scarabaeoides* (L.) tunneling in dung increased contact between fly larvae and the parasitoid, resulting in increased parasitism.

Salkeld (1959) investigated the life history and behavior of A. pallipes attacking OM in the laboratory. The adult A. pallipes emerge from the fly puparium by chewing a hole in it (Salkeld 1959, Wharton 1977). An average of 10 adults emerge from one pupa, with a sex ratio of 2 males to 5 females (Salkeld 1959). A. pallipes oviposits on all instars of its hosts, but prefers 1st and 2nd instars of the face fly (Salkeld 1959, Garry and Wingo 1971). A. pallipes may locate its host habitat with olfactory cues. It then detects the specific location of its host tactically as its host moves (Salkeld 1959).

Once laid in the host larvae, the parasitized eggs increase in size, but do not hatch until the host pupates. The time required for egg development, therefore, varies with the age of the host. At 23^{o}C, 5 to 8.5 days are required for egg development, 2 to 3 for larvae, and 7 to 9 for pupae in OM (Salkeld 1959).

Houser and Wingo (1967) found that at 32^{o}C and 55% RH, adult A. pallipes lived an average of 4 days when supplied with fresh apple slices, fresh cow manure, and distilled water. Individuals supplied with distilled water but no food lived almost a week (Salkeld 1959).

ALEOCHARA BILINEATA (GYLL.)

A. bilineata has been regarded as the most important parasitoid of the OM (Perron 1972). Most investigations on the biology of A. bilineata and its potential for biological control deal with predation and parasitism of the cabbage maggot (CM) (Wadsworth 1915, Colhoun 1953, Wishart et al. 1956, Read 1962, Coaker 1965, Finlayson et al. 1976, Nair and McEwen 1977, Esbjerg and Bromand 1977, Bromand 1980). However, A. bilineata parasitism of OM has been reported (Hammond 1924, Smith 1922, Perron 1972, Loosjes 1976, Beglyarov and Smetnik

1977, Bromand 1980, Whitfield 1981).

Aleochara bilineata (Gyllenhal) is a member of the family Staphylinidae, subfamily Aleocharinae. Of the 87 species of Aleochara reported in North America, all of the eight for which life histories have been investigated are ectoparasitoids on the pupae of Diptera within the puparium (Moore and Legner 1971). Though this parasitoid has been referred to in the literature as Baryodma ontarionis (Casey) and A. anthomyia (Sprague), it is now called A. bilineata.

A. bilineata parasitism has been reported on several Hylemya species, most commonly H. antiqua (OM), H. brassicae (CM), and H. platura (SCM). However, SCM is more commonly parasitized by the closely related species A. bipustulata (L.) (Finlayson and Campbell 1976). A. bilineata and A. bipustulata are frequently found in the same habitat, and although A. bipustulata parasitizes CM and OM, it is much less frequent than bilineata (Jorgenson 1979, pers. comm.; Wishart 1957).

Adult A. bilineata are thought to be general predators, but are commonly associated with CM, OM, and SCM, the hosts of its parasitic larvae. A. bilineata is one of the most common predators trapped in CM-infested cropping systems (Coaker 1965, Wishart et al. 1956, Finlayson and Campbell 1976). Read (1962) determined that each A. bilineata adult can destroy an average of 23.8 CM eggs or first instar larvae per day, or 2.6 third instars per day. Rear-and-release programs for A. bilineata predation reduced CM populations. Beglyarov and Smetnik (1977) achieved full protection from CM by releasing 20,000 to 40,000 beetles per hectare at 2 to 3 times a season, beginning at egg laying. In addition, 33,000 beetles per hectare reduced OM egg densities by 76% after three days. Bromand (1980) found that 20,000 beetles per hectare reduced CM damage on cauliflower by 30%.

Female A. bilineata lay their eggs in the soil about the base of the host plant (Wadsworth 1915). Each female lays an average of 10 to 15 eggs per day or 500 to 700 eggs over its lifetime (Colhoun 1953, Bromand 1980). Eggs hatch in about five days at 23°C (Colhoun 1953, Bromand 1980).

Newly-hatched larvae burrow into the soil immediately, presumably a negative phototrophic response (Wadsworth 1915). On locating a fly puparium, the larva attaches itself to the puparium by the tip of the abdomen and gnaws an entrance hole. This process takes 12 to 36 hours; the average lifespan of the larvae is 8.7 days (Colhoun 1953).

The larva punctures the cuticle of its host pupa as it enters the puparium; haemolymph wells out, coagulates, and effectively seals the hole. The larva crawls to the dorsal thoracic region of the host pupa where it feeds. After about eight days at 23°C, it molts into a more parasitic form (Colhoun 1953).

A. bilineata overwinters as a first instar larva within the puparium. Second instars are intolerant of cold temperatures (Colhoun 1953). The second and third instars require ca. five and seven days, respectively, to complete development, and the pupa requires ca. 14 days (Colhoun 1953). The adult staphylinid emerges by gnawing an exit hole in the puparium.

The hosts of A. bilineata are found in agroecosystems dominated by the heavy use of pesticides (Haynes et al. 1980, Harris et al. 1967). Kirknel (1978) investigated the impact of several insecticides on CM parasitism by A. bilineata in the laboratory. Each insecticide lost toxicity proportional to the exposure time in the field. Eventually, parasitism in treated soil exceeded that of the control. The time span for this reversal was shortest for chlorfenvinphos, which was also the least toxic to the parasitoids. Finlayson et al. (1980) reported that after seven days, chlorfenvinphos caused no mortality to A. bilineata adults, but the seasonal parasitism of CM on cauliflower was reduced 60% in chlorfenvinphos-treated field plots. Whitfield (1981) found A. bilineata parasitism of OM to be significantly less in commercial fields receiving between three and five foliar spray applications of parathion or Sevin®, than in a research field receiving no foliar insecticide treatments.

ALTERNATE HOSTS

The CM and SCM emerge in the spring two to three weeks earlier than the OM (Eckenrode 1972, Whitfield 1981). CM emerge around 243 degree days, base temperature 6.1°C (Eckenrode and Chapman 1971). The SCM is a primary pest of seedling beans and corn, and is a secondary pest of onions and cruciferous crops (Miller and McClanahan 1960). The CM is the primary insect pest of most cruciferous crops. Of the root crops, CM prefers for rutabaga, Brassica napobrassica (Mill.), and turnip, B. rapa (L.) (Doane and Chapman 1962). CM is also highly attracted to radish, Rapharus sativus (L.), but the plant's age affects how attractive it is to the CM (Ellis et al. 1979).

LABORATORY INVESTIGATIONS

Most of the following laboratory investigations were to quantify relationships between temperature and A. bilineata development and survival. As the activity and development of insects is often correlated with temperature, models quantifying these relationships may allow for a more accurate interpretation of the population dynamics observed in the field. The other laboratory experiments, oviposition preferences of A. bilineata and the influence of diet on A. pallipes longevity, were designed to gain insight on factors influencing the spatial distribution of the parasitoids in a multicropping system.

A. BILINEATA EGG DEVELOPMENT AND MORTALITY

Materials and Methods

Eggs were collected daily from isolated pairs of mating A. bilineata adults held in controlled temperature chambers at 13°, 17°, 23° and 29°C. Groups of up to 30 eggs per day were then held at the same temperatures and monitored daily to determine the number of days required to complete development and egg mortality at constant temperatures. Standard error determination (Casagrande 1971) was used to estimate the lower developmental threshold. A least squares regression analysis was performed to quantify the relationship between temperature and percent development per day.

Results and Discussion

Table 2 shows the number of days required to complete A. bilineata egg development. These data agree with data by other investigators. Colhoun (1953) found 76% of 2,880 eggs held at 23°C hatched on the fifth day, and Bromand

Table 2 . *A. bilineata* egg development at constant temperatures.

Temperature (°C)	$\bar{x}$ Days to Develop	s	n
29	3.25	.543	40
23	4.98	.699	193
17	7.70	.642	92
13	19.48	3.820	25

(1980) found that 80% of 716 eggs held at 22°C also required five days to complete development. Percent development per day can be accurately predicted with temperature over the range of temperatures tested; temperature explains 99% of the variation in mean development (Figure 4). The estimated lower developmental threshold was calculated to be 10°C (Figure 5) with an average of 59.74 ± 4.59 degree days required to complete development. The time required to complete development varied more at the lower temperatures, ranging from 14 to 27 days at 13°C. Egg mortality was lowest at 23°C with a mean of 32% of the sample population never hatching (Figure 6). Slightly greater mortality was experienced at 17°C and 29°C with 36 and 37%, respectively, not completing development. Accurate data are not available for mortality at 13°C.

TEMPERATURE AND PARASITOID AGE EFFECTS ON SUCCESSFUL PARASITISM BY A. BILINEATA LARVAE

Materials and Methods

Test A: Newly-hatched A. bilineata larvae were collected from eggs developing in controlled temperature chambers at 17° and 23°C. Larvae from each chamber were transferred with a fine point paint brush to petri dishes containing 12 OM pupae covered with moist sand. Eighty-one parasitoid larvae were distributed, 12 per dish (one dish contained only 9) and returned to the respective temperature chamber in which the larvae had originally hatched. Pupae were examined 48 hours later to determine the number of attacks on the pupae, the number of parasitoid larvae successfully entering the pupae, and the incidence of superparasitism.

Test B: Newly-hatched A. bilineata larvae were collected from the

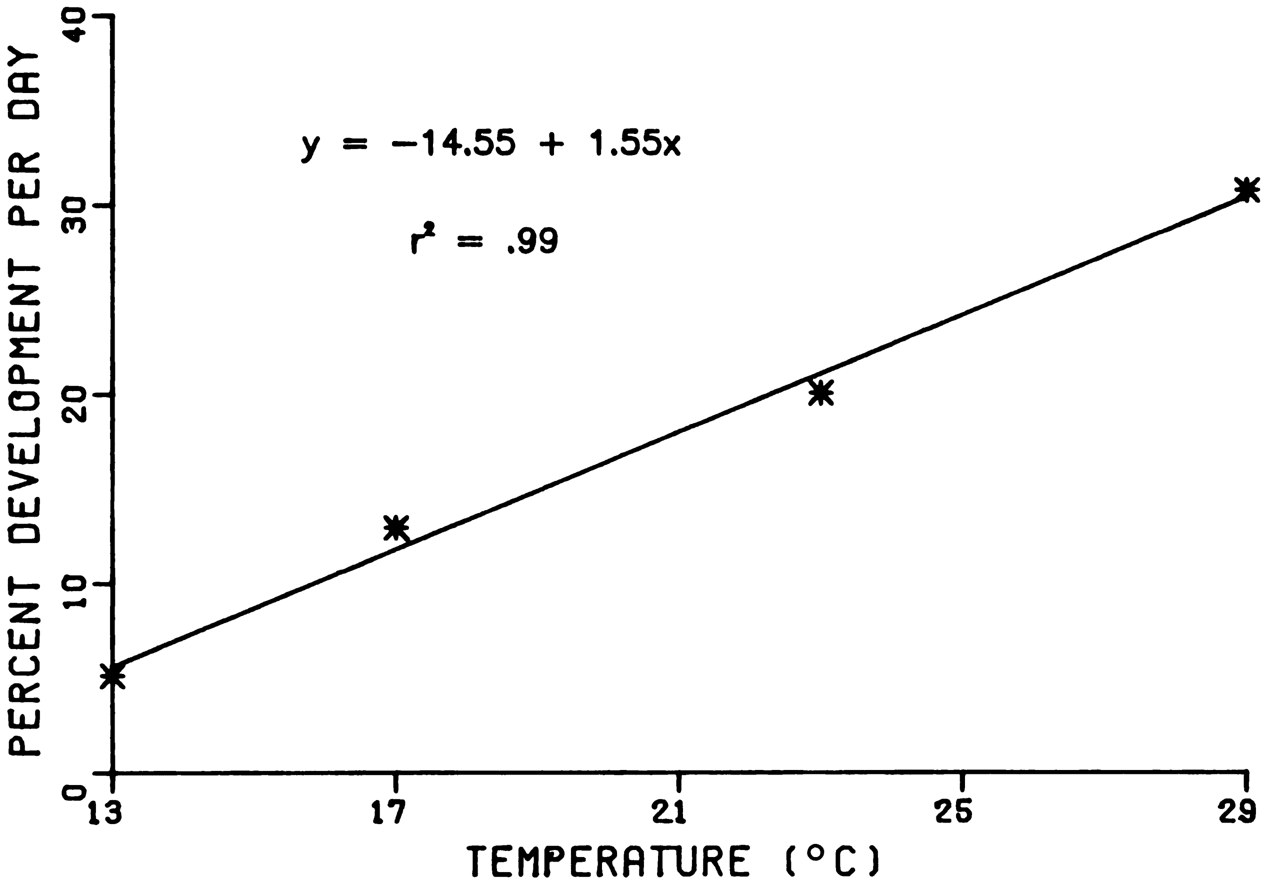


Figure 4. _A. bilineata_ egg development as a function of temperature.

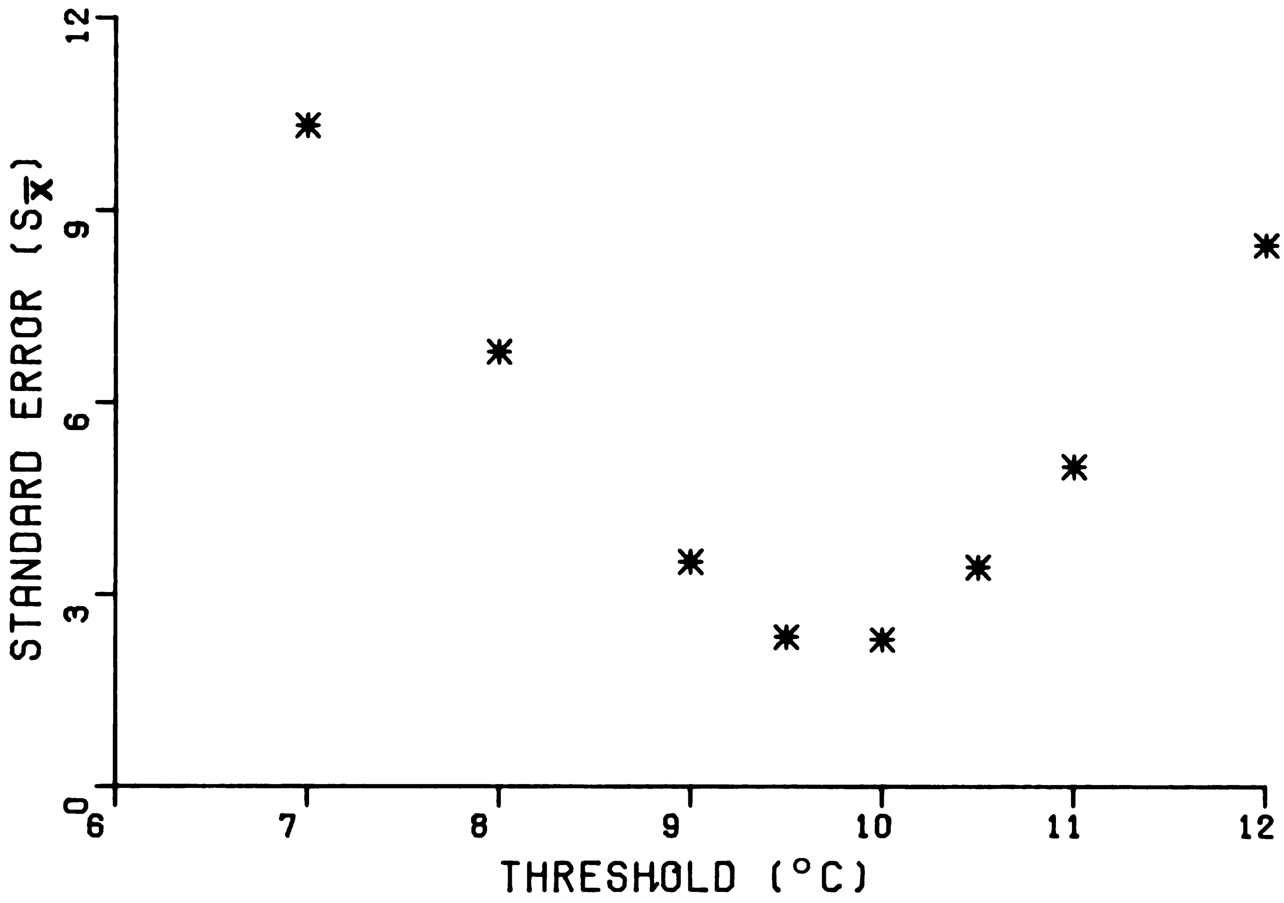


Figure 5. Standard error determination of developmental base temperature for A. bilineata eggs.

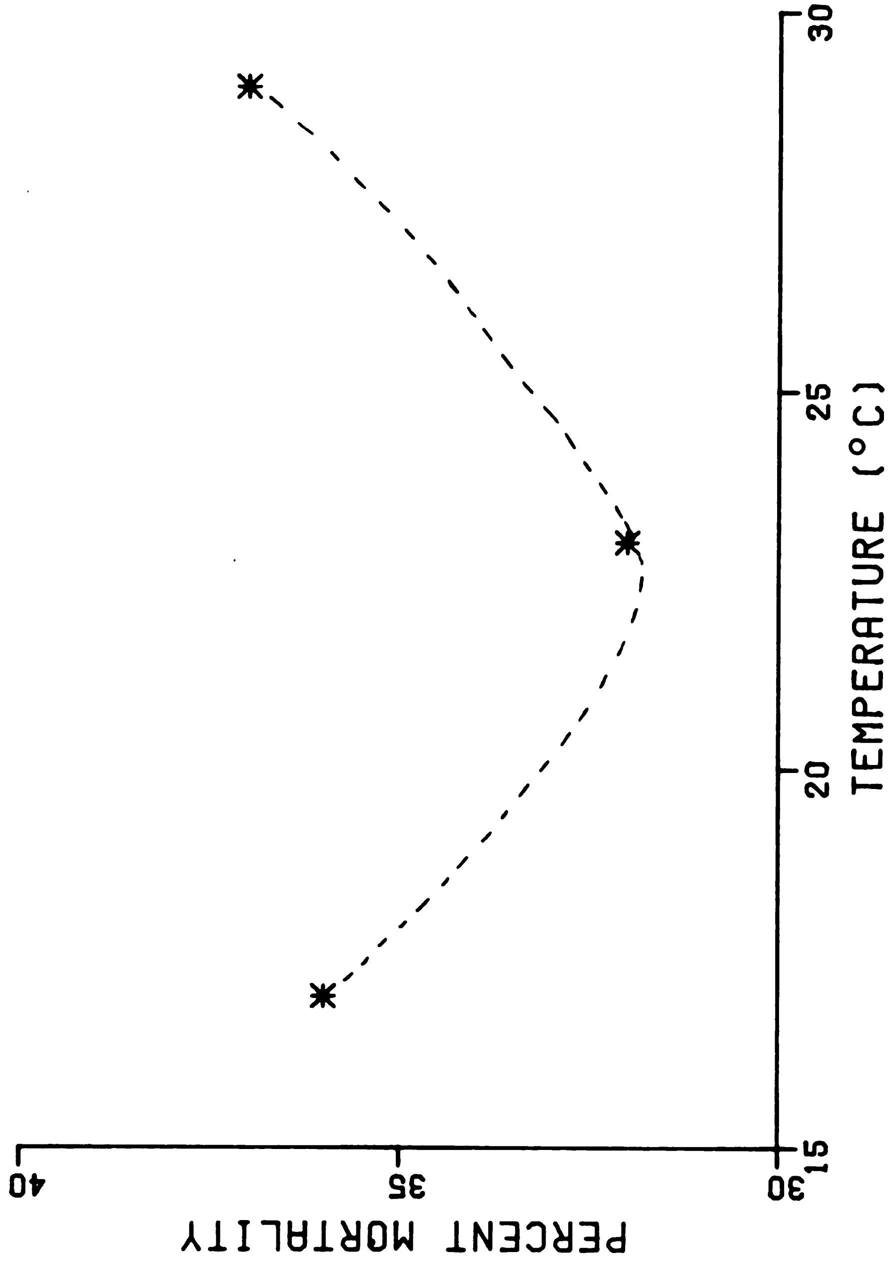


Figure 6. _A._ _bilineata_ egg mortality at constant temperatures.

controlled temperature chambers at 23° and $29^{\circ}C$. Larvae from each chamber were distributed 10 per dish (one dish contained only 5 larvae) in petri dishes with a small amount of moist sand. Larvae were kept in their respective controlled temperature chambers. On each of the following four days, ten pupae were added to one dish with parasitoid larvae at each temperature and covered with moist sand. (The experiment was conducted for only four days at $17^{\circ}C$ due to a limited number of parasitoid larvae.) Four days following the addition of pupae, pupae were checked for successful attack by the parasitoids. The number of attack holes as well as parasitoid larvae within the fly puparium were seen by submerging puparia in water and viewing them under a dissecting microscope.

Results and Discussion

The results are presented in Table 3. The percentage of pupae attacked and parasitoids successfully parasitizing OM pupae did not differ significantly at 17° and $23^{\circ}C$. Thirty-three to 75% of the available pupae were attacked at $23^{\circ}C$, while 25% to 58% were attacked at $17^{\circ}C$ after 48 hours. Successful parasitism (parasitoids in the fly puparium and feeding) after 48 hours ranged from 8 to 80% at $23^{\circ}C$ and 25 to 50% at $17^{\circ}C$. These values do not include subsequent parasitoid mortality due to superparasitism. One fly puparium was entered by five parasitoid larvae.

None of the 50 parasitoid larvae (of varying ages) successfully attacked fly pupae at $29^{\circ}C$. This dramatic decrease in parasitoid performance at the higher temperature suggests a thermal threshold between 23° and $29^{\circ}C$ beyond which larval parasitoid activity is terminated. Although this could contribute to the varying impact A. bilineata has on its host populations from one year to the next (Nair and McEwen 1975), the abrupt drop in larval activity at $29^{\circ}C$ could be due

Table 3. The effect of temperature and parasitoid age on successful parasitism by *A. bilineata*.

A.

Temperature (^{o}C)	Number of Exposed Pupae	Number of Parasitoid Larvae	% Attached Pupae		% Successful Parasitoid Entries	
			$\bar{x}^1$	$s_{\bar{x}}$	$\bar{x}^2$	$s_{\bar{x}}$
17	36	33	.417	.167	.389	.127
23	48	48	.583	.205	.375	.259

[1] F ratio = 1.29 with 1 degree of freedom, = .05

[2] F ratio = .01 with 1 degree of freedom, = .05

B.

Temperature (^{o}C)	Number of Exposed Pupae	Number of Parasitoid Larvae	Age of Parasitoid Larvae (Days)	% Attached Pupae	% Successful Parasitoid Entries
23	10	10	1	10	10
	10	10	2	50	80
	10	10	3	30	30
	5	5	4	60	60
29	10	10	1	0	0
	10	10	2	0	0
	10	10	3	0	0
	10	10	4	0	0
	10	10	5	0	0

to a combination of moisture and heat stress. In this experiment all replicates received the same amount of moisture, yet the evaporation rate would have been greater in those at 29^{o} than at the lower temperatures, which could have contributed to the decreased parasitoid activity.

Within the time span of the experiment, successful parasitism did not appear to be related to the age of the parasitoid larvae. Sixty percent of the four-day-old larvae successfully parasitized OM pupae, while 30% of the three-day-old and 50% of the two-day-old larvae were successful. Colhoun (1953) examined the mortality of 300 starved first-instar parasitoid larvae at $23^{o}C$ with age. After four days, mortality was only 23%. The average life span was estimated at 8.7 days. As other factors besides parasitoid age are most probably acting on parasitism success, an experiment designed to reflect any differences in parasitism with age would have to be carried on over a longer period of time.

The results of Colhoun's study are depicted in Figure 7 with percent survival as a function of age. A least squares regression analysis was performed to examine the relationship between age and mortality. The resulting regression equation follows:

$$Y=99.73 - 5.914x, \quad r^2 = .98.$$

However, as the data represent cumulative survival over 20 days, each observation depends on the other. Thus, the computed regression equation may not result in accurate predictions of survival at one point in time, as any error in the estimated survival in the first few days could dramatically shift the resulting curve.

Another method of quantifying mortality, which does not require independent observations, is to assign a probability for mortality at each age. Using

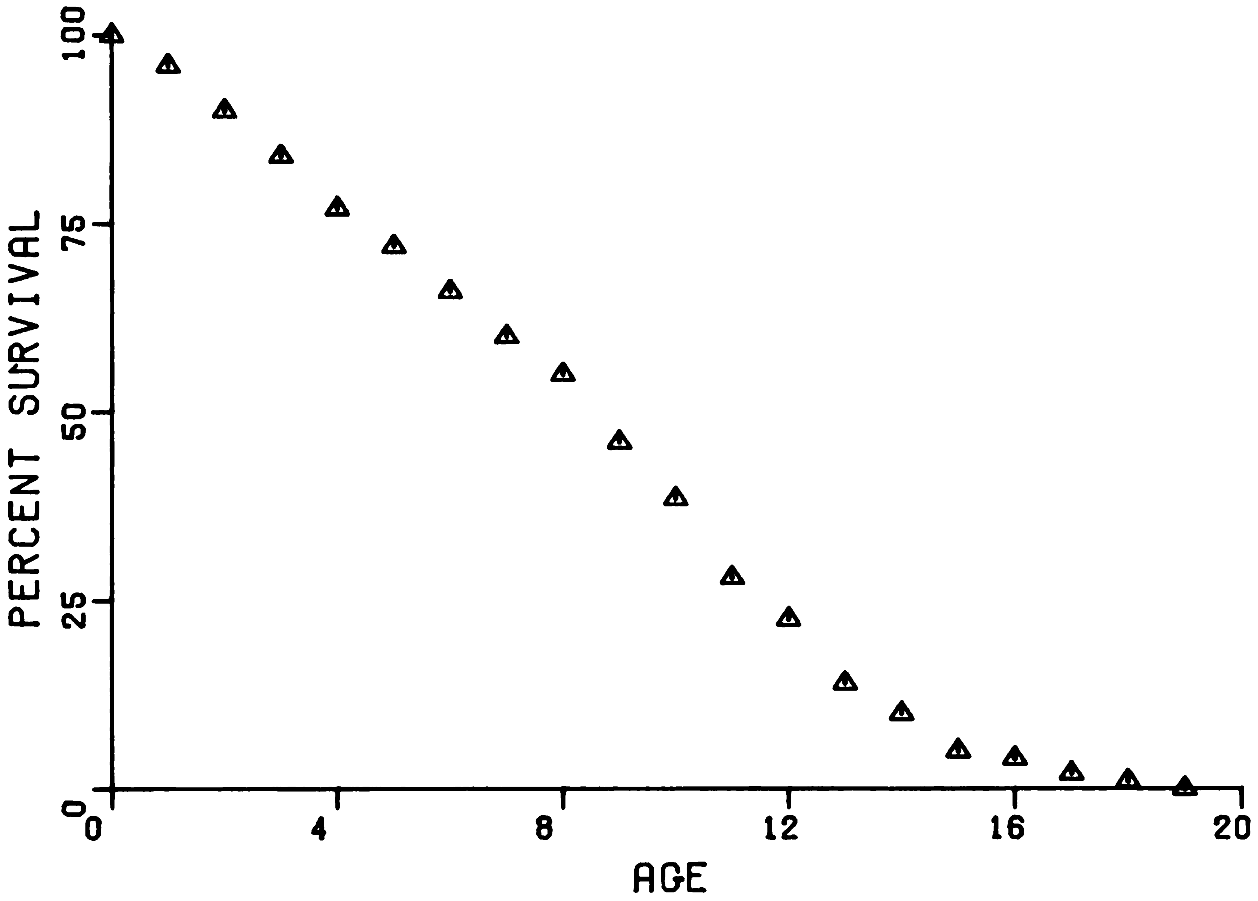


Figure 7. Survival of first instar _A_. _bilineata_ larvae under laboratory conditions. (Data from Colhoun 1953).

data extrapolated from Colhoun (1953) (Figure 7), the probability density function for mortality and hazard rate was calculated for each day. The probability density function, $f(t_{mi})$, is the estimated probability of an individual dying during a particular interval (day) and is computed as follows (Gross and Clark 1975):

$$f(t_{mi}) = S(t_i)q_i/h_i$$

where: $S(t_i)$ = cumulative probability of surviving,

q_i = the proportion dying in a given interval, and

h_i = the width of the interval (day).

The hazard rate (t_{mi}) or the instantaneous death rate is an estimate of the probability that an individual who has survived to the beginning of a given interval (day) will die within that interval (day). The hazard rate is computed as follows:

$$g(t_{mi}) = 2\ q_i/h_i\ (1 + p_i)$$

where: $p_i = 1 - q_i$

The results are presented in Table 4. The hazard rate for first instar A. bilineata larvae generally increases slightly with each day of age for the first seven days. There is then a marked increase in the hazard rate on the eighth and subsequent days. This corresponds with the estimated mean (8.7 days) and median (8.6 days) longevity for this life stage. The population of individuals surviving beyond the average experience a greater instantaneous death rate.

A. BILINEATA PARASITOID DEVELOPMENT AND MORTALITY

Materials and Methods

The rate of development for A. bilineata life stages parasitizing OM was

Table 4. Probability of mortality with age for _A_. _bilineata_ first instar larvae.

Interval (Day)	Number alive at beginning of interval	Number dying during interval	Hazard Rate	SE[2]	Probability density function	SE[2]
1	306	12	.040	.012	.039	.0001
2	294	19	.067	.015	.062	.0002
3	275	17	.064	.015	.056	.0002
4	258	22	.089	.019	.072	.0002
5	236	16	.070	.017	.052	.0002
6	220	18	.085	.020	.059	.0002
7	202	18	.093	.022	.059	.0002
8	184	16	.091	.023	.052	.0002
9	168	27	.175	.033	.088	.0003
10	141	25	.195	.039	.082	.0002
11	116	30	.297	.054	.098	.0003
12	86	17	.219	.053	.056	.0002
13	69	26	.464	.089	.085	.0003
14	43	12	.324	.092	.039	.0001
15	31	16	.696	.163	.052	.0002
16	15	3	.222	.127	.010	.0000
17	12	6	.667	.257	.020	.0001
18	6	3	.667	.363	.010	.0000
19	3	3	0.000	0.000	0.000	0.0000

[1] Data extrapolated from Colhoun (1953).

[2] Standard Error (SE) computed as to formular in Gross and Clark (1975).

estimated from temperature dependent developmental data for A. bilineata parasitizing CM (Read 1962). It was assumed that as A. bilineata lives as an external parasitoid within the puparium of several Hylemya species, its developmental zero and rate of development are not necessarily synchronized with its hosts. Read (1962) collected overwintering parasitized CM pupae from the field in early November. A. bilineata overwinters as a first instar larva within the puparium of its host. The pupae were stored at 2.2°C (36°F) for ca. two months before being transferred to soil cylinders in Wisconsin tanks where they were reared at constant temperatures ranging from 10° to 23.3°C (50° to 74°F). The pupae were monitored every 3 to 5 days for 90 days for emergence of adult A. bilineata and cabbage maggot flies.

These data were summarized as to the mean number of days required to complete development at each temperature. The standard error determination (Casagrande 1971) was used to estimate a lower developmental threshold and the mean degree day accumulation required to complete development of the parasitizing life stages. The percent development per day was regressed with temperature to quantify this relationship. Percent mortality as a function of temperature was extrapolated from Read's emergence data, given that he began with 160 parasitized pupae at each temperature. This relationship was examined.

Results and Discussion

The mean days required to complete development at each temperature are given in Table 5. The lower developmental threshold was calculated to be

Table 5. Development of _A_. _bilineata_ parasitizing CM at constant temperatures.

Temperature (^oF)	Temperature (^oC)	Days Required to Complete Development[1] $\bar{x}$	Days Required to Complete Development[1] s^2
50	10	0.00	0.00
54	12.22	85.77	13.12
56	13.33	82.05	22.07
60	15.55	67.73	11.87
62	16.67	48.17	19.75
64	17.78	43.48	24.17
66	18.89	38.09	19.50
68	20.00	34.29	8.01
70	21.11	27.77	8.93
72	22.22	26.19	5.37
74	23.33	24.76	8.07

[1] Data summarized from Read, 1962.

8.6°C (Figure 8) with a mean of 384 degree days required to complete development. This threshold and required degree day accumulation differs from that of two of its hosts, the OM and the CM. The OM requires an average of 306 degree days (base 4.4°C) (Carruthers 1979) and the CM requires 243 degree days (base 6.1°C) (Eckenrode 1972). As this parasitoid attacks the pupal stage of its host, it is not suprising that it would develop slower and hence emerge later in the spring than its host which must go through an adult, egg, and larval stage before it reaches a stage suitable for parasitism.

The percent development per day for the parasitizing life stages of A. bilineata can be predicted with temperature (r^2 = .97, see Figure 9). Over the range of 13° to 21°C there appears to be no appreciable difference in the mortality of A. bilineata parasitizing CM (Figure 10). The average mortality experienced over this range of temperatures was 38%. Mortality increased sharply to 100% at 10°C and decreased with higher temperatures of 22°C and 23°C. It is likely that at some higher temperature mortality increases again.

Bromand (1980) reported 43 to 52% mortality to parasitoids in singly-attacked field-collected CM pupae. He noted that superparasitism was responsible for some of the mortality in the laboratory culture where parasitoid mortality in CM pupae was 64% and 52% in OM.

A. BILINEATA FECUNDITY AND PREDATION AS A FUNCTION OF TEMPERATURE

Materials and Methods

Mating pairs of A. bilineata adults of various ages were collected from the laboratory colony and isolated by pairs into petri dishes lined with a three-layer disc of moist newspaper. The moist newspaper was thought to provide an easily

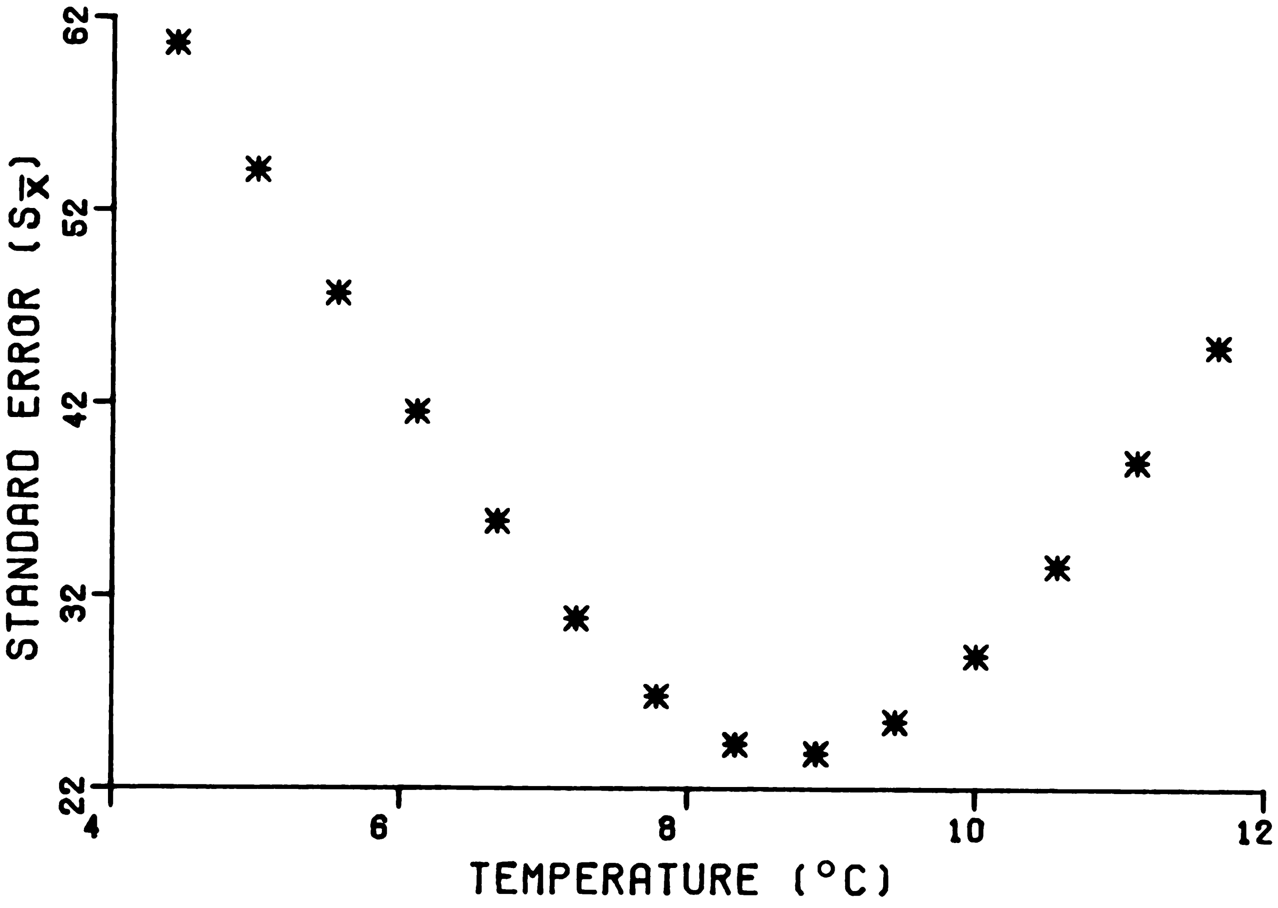


Figure 8. Standard error method for determination of developmental base temperature for A. bilineata parasitizing life stages.

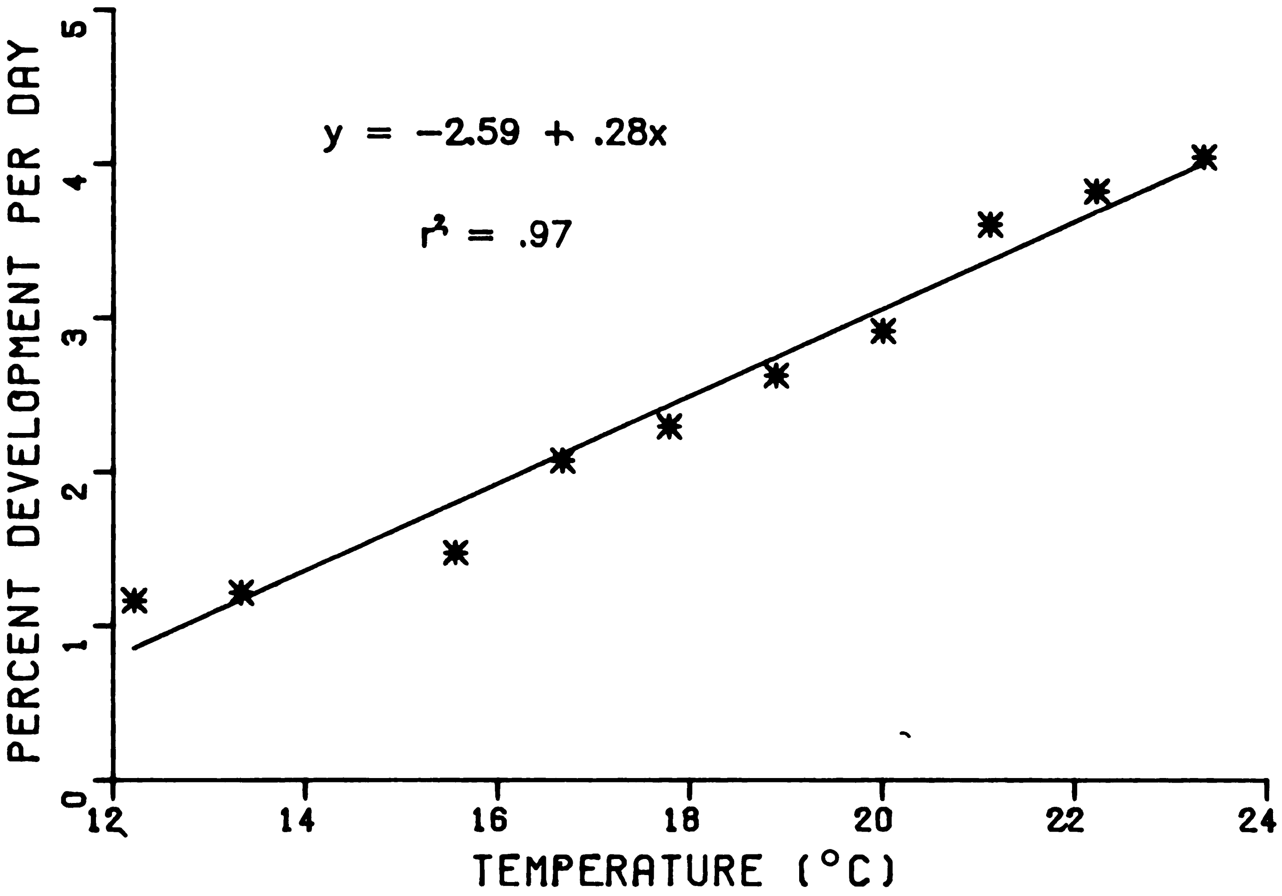


Figure 9. A. bilineata parasitoid development as a function of temperature.

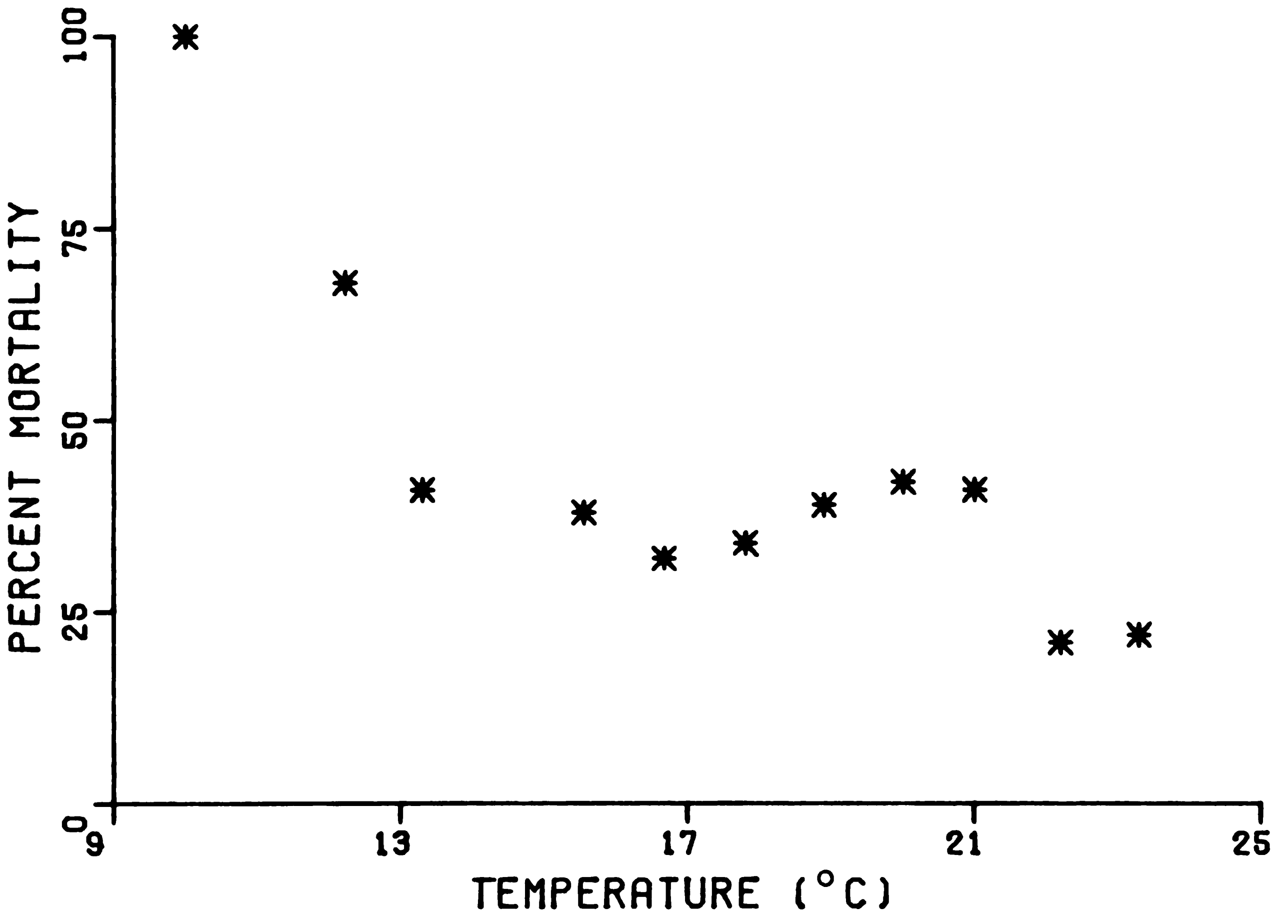


Figure 10. A. bilineata parasitoid mortality at constant temperatures.

examinable substrate for egg laying, as well as a moist environment where the food supply, OM larvae, could survive. Each pair of adults was supplied with three third instar OM larvae. The dishes were distributed in four controlled environmental chambers set at constant temperatures of 13°, 17°, 23°, and 29°C. Every 24 hours the dishes were removed, and the staphylinid pair and its food supply were transferred to another dish. The maggot consumption per pair was recorded and a maggot was replaced for every maggot consumed, such that at the beginning of each 24 hour period each _A. bilineata_ pair always had three OM larvae for a food supply. The new dish was then returned to the respective temperature chamber. The dish from which the pair had come and both sides of each newspaper disc were examined under magnification for eggs. Egg laying activity and maggot consumption were monitored for five to ten days.

For the data summary, the egg production per female per day was pooled over all pairs at each temperature. Egg production was evaluated from the time an individual began laying at least one egg. Therefore, egg production of zero for the first day for an individual was not included in the data set. Once an individual initiated egg laying, any subsequent days for which egg production equalled zero were included. A least squares regression analysis was performed on the mean number of eggs per female per day and temperature. The regression line was extended to its intersection with the x-axis to predict a lower thermal threshold for fecundity. An analysis of variance for repeated measures (Winer 1971) was performed on the egg production per female on each of the five to ten days. The intent of this procedure was to (1) evaluate the variability between individuals and within an individual through time, and (2) to determine if the data reflect an interaction between temperature and time.

The consumption of larvae per pair per day was also pooled over all pairs at each temperature for the data analysis. A least squares regression analysis was performed on the mean number of larvae consumed per pair per day and temperature. The regression line was extended to its intersection with the x-axis to determine a predictive lower thermal threshold for predation.

Results and Discussion

The mean number of eggs laid per female per 24 hours for each temperature is listed in Table 6. The greatest number of eggs laid by a single female in one day was 46 at 29°C. At least one female laid no eggs on at least one day at every temperature except 29°C. At 29°C all females laid at least one egg every day. Bromand (1980) found an average of 9-10 eggs per female per day at 22°C and 500-600 eggs per female over a lifetime (ca. 55 days). Both Colhoun (1953) and Read (1962) found that females produced an average of 15 eggs per day and an average of more than 700 eggs during their lifetime. This agrees with the mean of 12.03 eggs per female per day at 23°C found by the author.

Egg production per female per day varied at all temperatures tested. The variability within a single individual through time (mean square estimated, s^2 = 358) is greater than that between individuals (mean square = 153). The analysis of variance for repeated measures indicates a significant interaction between temperature and time; however, at all temperatures except 13°C, egg production did not necessarily increase or decrease with time (age). Perhaps individual variability is more a function of food consumption or some unmeasured factor unknown to this author. Egg production per female per day did decrease with time at 13°C. This is thought to be due to the prolonged exposure to cold temperatures rather than age.

The mean egg production per female per day shows a positive trend with increasing temperature (Figure 11) and can be predicted (r^2 = .98). Assuming a linear model at the lower temperatures, the extension of the regression line estimates a lower thermal threshold for egg production of 10°C.

The mean number of third instar onion maggot larvae consumed per day is also linearly related to temperature (Table 7, Figure 12). However, a lower threshold for feeding could not be estimated by extending the regression line, as this method yields an estimate less than 0°C. Consumption does not appear to be linearly related to temperature below 13°C; therefore, the regression model cannot be used as an accurate predictor below this temperature. Read (1962), testing one individual per dish over time, presumably each at 23°C, found that A. bilineata adults destroyed an average of 2.6 third instar larvae or pupae per day. In this author's experiment, with three maggots available, a pair of staphylinid adults at 23°C rarely consumed their entire food supply ($\bar{x}$ consumption per pair per day = 1.13 maggots).

From observations of predation behavior, when a staphylinid attacks a large larva, it does not necessarily consume the entire larva. Once satiated, the individual moves on, and may attack the next larva it encounters. Also, with more than one staphylinid adult per chamber, an individual was seen to frequently "join in the fight" when encountering another individual attacking a large larva. These observations suggest that absolute predation rates may be a complex function of A. bilineata adult density and prey density. This relationship needs to be investigated to quantify predation. From this data, predation is assumed to also vary with temperature, and this variation can be predicted within the range of temperatures tested.

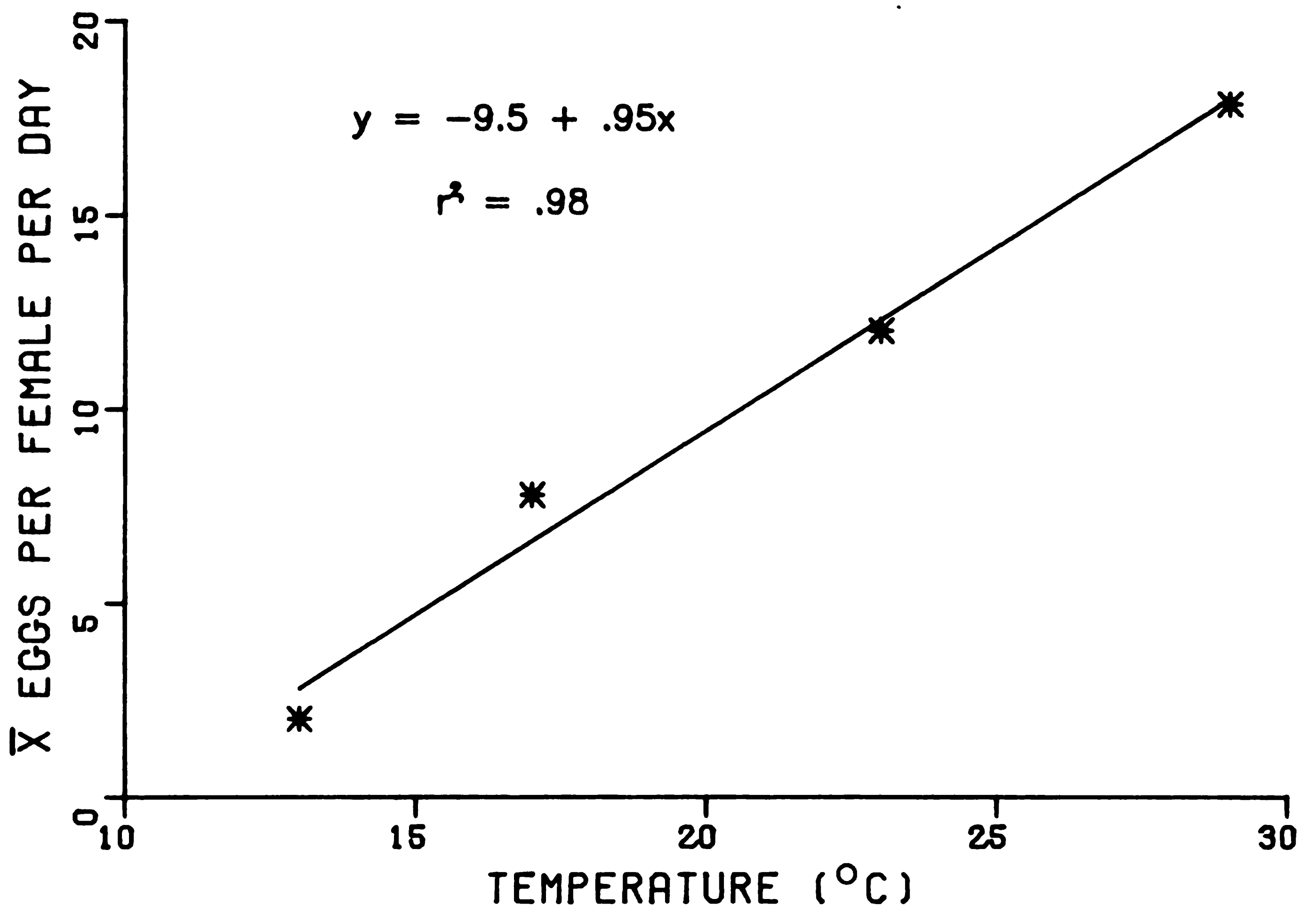


Figure 11. A. bilineata fecundity as a function of temperature.

Table 6. The influence of temperature on the fecundity of *A. bilineata*.

Temperature	Eggs Laid Per Day $\bar{x}$	s	Number of Females	Total Number of Observations
29	17.85	12.02	7	39
23	12.03	9.36	5	36
17	7.80	7.50	7	46
13	2.03	3.95	6	33

Table 7. The influence of temperature on the consumption of third instar onion maggot larvae by *A. bilineata* adults.

Temperature	Larvae Consumed Per Pair Per Day $\bar{x}$	s	Number of Pairs	Total Number of Observations
29	1.69	1.00	8	38
23	1.13	0.85	7	47
17	1.02	0.91	6	43
13	0.77	0.95	6	33

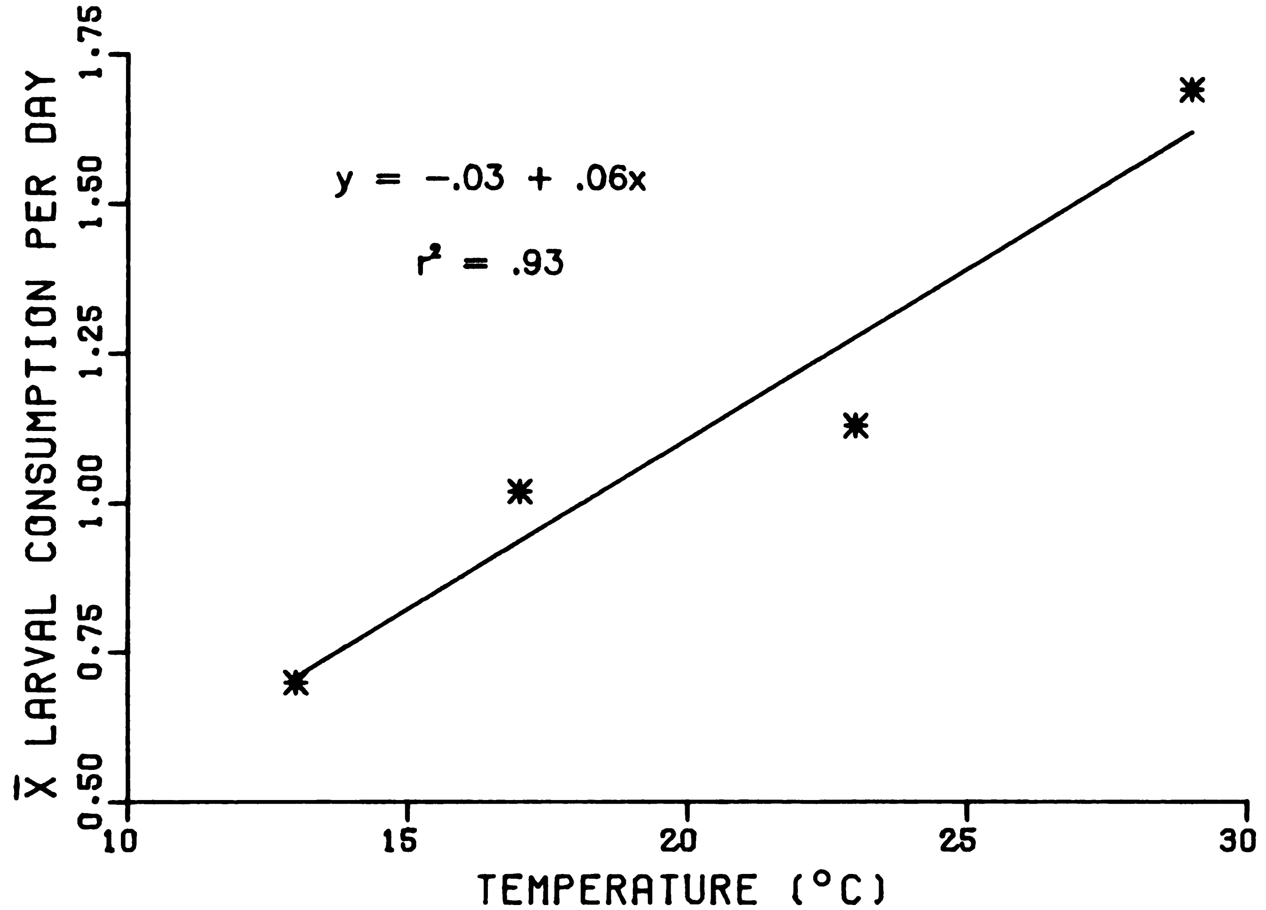


Figure 12. A. bilineata consumption of third instar OM larvae as a function of temperature.

A. BILINEATA OVIPOSITION PREFERENCES

Materials and Methods

An oviposition chamber designed to evaluate preferred choices for oviposition by A. bilineata females was constructed out of four, square, pint-sized, plastic food containers. Two adjacent sides of each container were cut down to 2 cm in height. The short sides of all containers were fastened together and sealed with duct tape to prevent any possible escape. The tall sides of adjacent containers were fastened together and sealed the same way. The bottom of the chamber was then filled just to the height of the inner walls (ca. 2 cm) with moist sand. The resulting four-sectioned chamber permitted free movement throughout the entire arena for A. bilineata adults traveling along the surface of the sand, but limited movement of A. bilineata larvae traveling through the sand to a single section.

Oviposition preferences were evaluated as follows. One of each of the four treatments to be compared was placed in the center of one of the four sections. Four mating pairs of A. bilineata were released into the arena. The top of the chamber was secured with a cotton muslin lid. Adults were free to travel about the chamber for 48 hours, after which they were removed and 25 to 50 OM pupae were added to each of the four sections. (An equal number was added to each chamber in a single trial.) Pupae were gently buried within the sand as to not disturb any of the staphylinid eggs or larvae. The pupae were left in the chamber for six days, after which they were removed and examined for holes indicating A. bilineata larva attack and entry. As the parasitizing larvae could not travel between sections of the chamber in search for pupae, the number of parasitized pupae within a section was considered a relative measure of the number of eggs laid within that section. Hence, the number of parasitoids per section was used as an indirect measure of oviposition activity and was compared between sections to reflect any preference in oviposition with the treatments tested.

The treatments were randomly distributed among the sections for each experiment. The experiments are listed in Table 8.

Results and Discussion

The results of the A. bilineata oviposition preference experiments are presented in Figure 13. In the first experiment, a larger number of eggs (as reflected by successful parasitism) were laid around the control, a moist sponge, than around any of the other treatments. No preference between the other treatments tested (an onion, an onion with host pupae, or a maggot-infested onion) was seen. Preference for the sponge was assumed to reflect a preference for high moisture. The same test was repeated again in experiment 3, only particular attention was paid to maintaining the same high soil moisture in all four sections of the treatments, including the moist sponge. The resulting parasitism indicated no particular preference for any of the treatments, including the moist sponge.

To further test the attraction of A. bilineata to moist areas for oviposition sites, a test was set up to evaluate any preference for oviposition between four levels of soil moisture (Experiment 4). As reflected in the resulting parasitism, preference increases with soil moisture. Twice as many larvae parasitized pupae in the low moisture section than in the dry, and twice again as many in the medium moisture section than the low. Parasitism between the medium and the high moisture levels showed little difference.

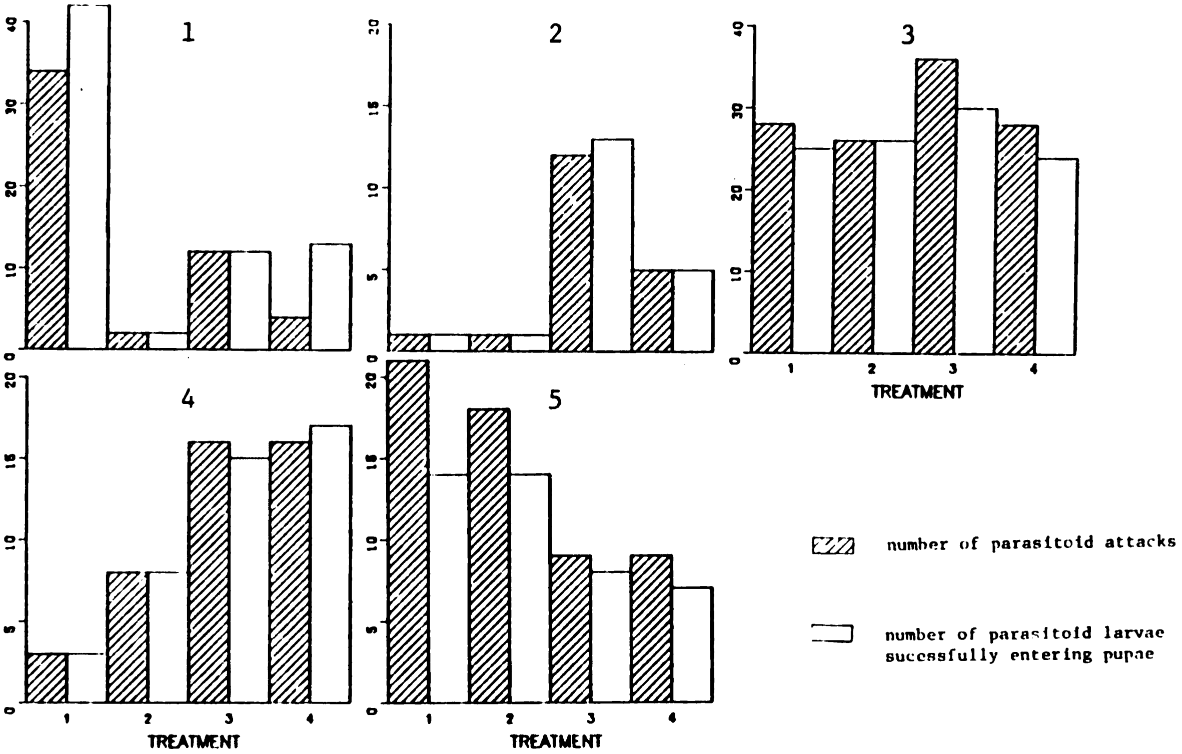


Figure 13.1-13.5. Oviposition preferences of *A. bilineata*.

Table 8, *A. bilineata* oviposition preference experiments.

Experiment	Treatment			
	1	2	3	4
1	control = moist sponge	onion with OM pupae	onion	maggot-infested onion
2	maggot-infested onion	maggot-infested onion	control = no treatment	control = no treatment
3	control = moist sponge	onion with OM pupae	onion	maggot-infested onion
4[1]	no moisture: dry sand	low moisture: 5 ml H_2O/section	medium moisture: 10 ml H_2O/section	high moisture: 15 ml H_2O/section
5	radish	maggot-infested radish with pupae	maggot-infested onion with pupae	onion

[1] For experiment 4, each of the four sections of the chamber were intially filled with dry sand to a depth of ca. 2 cm. The above different volumes of water were added to the sand to create various levels of soil moisture. When the adult staphylinids were removed and the pupae were added, half the initial volume of water recieved by each section was again added.

Alone, this method of evaluating oviposition preferences does not adequately test responses to differing levels of soil moisture. The differences in parasitism may also reflect differing egg and first instar larval survival under different soil moisture regimes. Experiment 1 indicates that A. bilineata females prefer areas of high soil moisture. Experiment 4 probably reflects these differences, but to accurately evaluate this test, egg and larval survival under such conditions must be examined.

Experiment 5 compares A. bilineata preference for ovipositing about radishes and onions, and any added influence of maggots and pupae. Maggots infesting onions and maggots infesting radishes appear not to influence the attractiveness of their host plants as oviposition sites. However, radishes with or without maggots and pupae appeared to be more attractive than onions with or without maggots and pupae. This greater attractivity of radishes could be one factor responsible for the greater staphylinid parasitism in maggot-infected radishes than adjacent maggot-infected onions in the field study plots.

The results of experiment 2 comparing the attractiveness of maggot-infested onions to a control or no treatment are puzzling as there appeared to be a greater response to the control than to the onions. I assumed that, as previous experiments indicated no ovipositional preference about onions with or without maggots or pupae, the greater parasitism in the control section is probably due to random chance, and, given adequate replication, there would be no significant difference between the onions and the control.

MULTIPLE PARASITISM

An experiment was conducted to determine whether A. bilineata larvae searching for OM pupae would distinguish and select against *A. pallipes* parasitized OM pupae.

Materials and Methods

Fifty OM pupae, half parasitized by *A. pallipes* and half healthy, were buried in the sand in the *A. bilineata* colony for 48 hours. The pupae were then removed and examined for attack holes and *A. bilineata* parasitism. The experiment was repeated a second time with 24 OM pupae, half parasitized by *A. pallipes* and half not.

Results and Discussion

During the first trial, ten healthy OM pupae were parasitized by *A. bilineata*, and two healthy pupae showed signs of attack although they were not parasitized. Thirteen of the healthy pupae remained unparasitized. Only one of *A. pallipes* parasitized pupae showed any signs of *A. bilineata* attack, and none were parasitized. Similar results were obtained in the second trial. Seven healthy pupae were parasitized by *A. bilineata*, and five were not attacked. None of the 12 braconid-parasitized pupae were attacked.

These results indicate that *A. bilineata* larvae recognize OM pupae attacked by the larval parasitoid *A. pallipes*. Bromand (1980) reported similar findings regarding *A. bilineata* attack on OM pupae previously parasitized by *Tribliographa rapae*. The mechanisms for detection are not known.

DIET INFLUENCES ON THE ADULT LONGEVITY OF *A. PALLIPES*

A carbohydrate food source for several adult hymenopteran parasitoids significantly increases the longevity and fecundity of the parasitoids (Leuis 1960, 1961, 1963, 1967). Several investigators suggest that the availability of carbohydrates in the form of nectar and pollen sources influence the distribution and abundance of many hymenopteran parasitoids (Symes 1975). The influence of diet in the longevity of adult A. pallipes was investigated to determine if the availability of a food source might influence their distribution and abundance about the onion agroecosystem.

Materials and Methods

Forty-two newly-emerged adult A. pallipes were separated into groups of seven (3 males and 4 females) in rearing dishes covered with a fine cotton muslim cloth secured with an elastic band. The parasitoids were fed and watered every other day by touching a corner of the muslin cloth with the food mixture and moistening the sand in the rearing dish. Each dish of parasitoids was maintained on a different diet. The diets tested included: (1) a 10% honey solution, (2) a 10% sucrose solution, (3) a 10% sucrose solution with brewers yeast, (4) a 10% honey solution with brewers yeast, (5) a cut onion, and (6) a control of distilled water. Parasitoids were monitored daily for mortality.

Results and Discussion

A. pallipes longevity on diets of 10% sucrose or honey with or without brewers yeast was significantly longer ($F_{5,41} = 14.33$) than with either an onion food source or just water (Table 9). There were, however, no significant differences in longevity between the different sugar diets. Adding brewers yeast to the diets did not increase longevity. Over all diets, the average male and female survival did not differ.

The greater than three fold increase in adult A. pallipes longevity with a carbohydrate food source suggests that the availability of this food source in the field could influence the abundance and distribution of this parasitoid.

Table 9. The influence of diet on the adult longevity of *A. pallipes*.

Diet	$\bar{x}$ longevity (days)
10% honey solution	13.29 a
10% sucrose solution	15.43 a
10% honey solution with brewers yeast	14.86 a
10% sucrose solution with brewers yeast	18.14 a
Cut onion	5.00 b
Control (distilled water)	4.57 b

[1] Treatments followed by the same letter are not significantly different at $\alpha = .01$; Duncan's multiple range test.

FIELD INVESTIGATIONS

SPRING EMERGENCE

Materials and Methods

In 1980, overwintering *A. pallipes* and *A. bilineata* parasitized OM pupae were monitored for adult emergence. Parasitized pupae were collected from onion fields in the fall of 1979 and buried at 2.5 cm, 7.5 cm, 12.5 cm, and 17.5 cm depths in plastic buckets filled with muck soil. Each bucket contained ten parasitized pupae and each depth was replicated three times for *A. pallipes* and twice for *A. bilineata*. The buckets were perforated with 1 cm holes to facilitate drainage, and buried in an onion field at the MSU Muck Farm, such that the top of each bucket was flush with soil surface. In late April 1980, emergence traps (Gage and Haynes 1975) were emplaced over the buckets, and the traps were monitored every three days for the emergence of the adult parasitoids. *A. pallipes* adults were easily recognized by the yellow legs and basal antennal segment. No attempt was made to identify *A. bilineata* adults to species; all staphylinids of the appropriate size and color were recorded.

Results and Discussion

First emergence of *A. pallipes* adults occurred on June 2. The mean emergence date was June 10 ($s_{\bar{x}}$=.58 dys.), a week earlier than that of *A. bilineata*. Female *A. pallipes* emerged an average four to five days earlier than male *A. pallipes* (Table 10). The date of emergence varied with the depth at which the pupae were buried. The parasitoids in pupae at the deeper depths emerged later and over a longer span of days than the shallower ones.

A. bilineata emergence did not vary with depth. The first emergence of a

Table 10. Spring emergence of *A. pallipes* adults.

	Emergence Date					
Depth (cm)	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$	$s_{\bar{x}}$	n
2.5	157	.77	16	154	.31	36
7.5	161	-	1	156	.69	23
12.5	166	.99	18	164	.81	31
17.5	172	2.12	7	169	1.52	14

staphylinid adult was June 6 (287 degree days, base 8.6°C). Emergence continued through the first week in July, yet the mean emergence date was June 17 (S_x=.74 dys.; 387 degree days, base 8.6°C). Using the model for A. bilineata spring emergence developed from laboratory data in the literature and MSU Muck Farm soil temperatures monitored at a 10 cm depth, the predicted emergence date for this parasitoid is in exact agreement with the mean observed in the field.

Fifty percent emergence for the OM (Whitfield 1981) averaged 16 days earlier than A. pallipes, and 23 days earlier than A. bilineata. Thus both parasitoids appear well synchronized with the OM life stage they attack.

The spring emergence data was used to estimate a lower threshold for development and accumulated degree days required for emergence of A. pallipes adults. As soil temperatures were monitored at depths intermediate to those at which the pupae were buried, the mean emergence dates from two adjacent depths were calculated to generate estimated emergence dates for three A. pallipes populations to correspond with the three sets of temperature data.

Modifying the method described by Casagrande (1971), hypothetical threshold levels were combined with soil temperature data to predict the accumulated degree days required for emergence. The mean and standard error for the predicted degree days at the different depths was calculated from a range of hypothetical thresholds. These standard errors were plotted against the thresholds (Figure 14), and the threshold corresponding to the lowest point in the parabolic curve was chosen in the best estimate. A lower developmental threshold of 9.0°C with 292 degree days required to complete development was chosen as the best predictor. This model was not validated and requires an

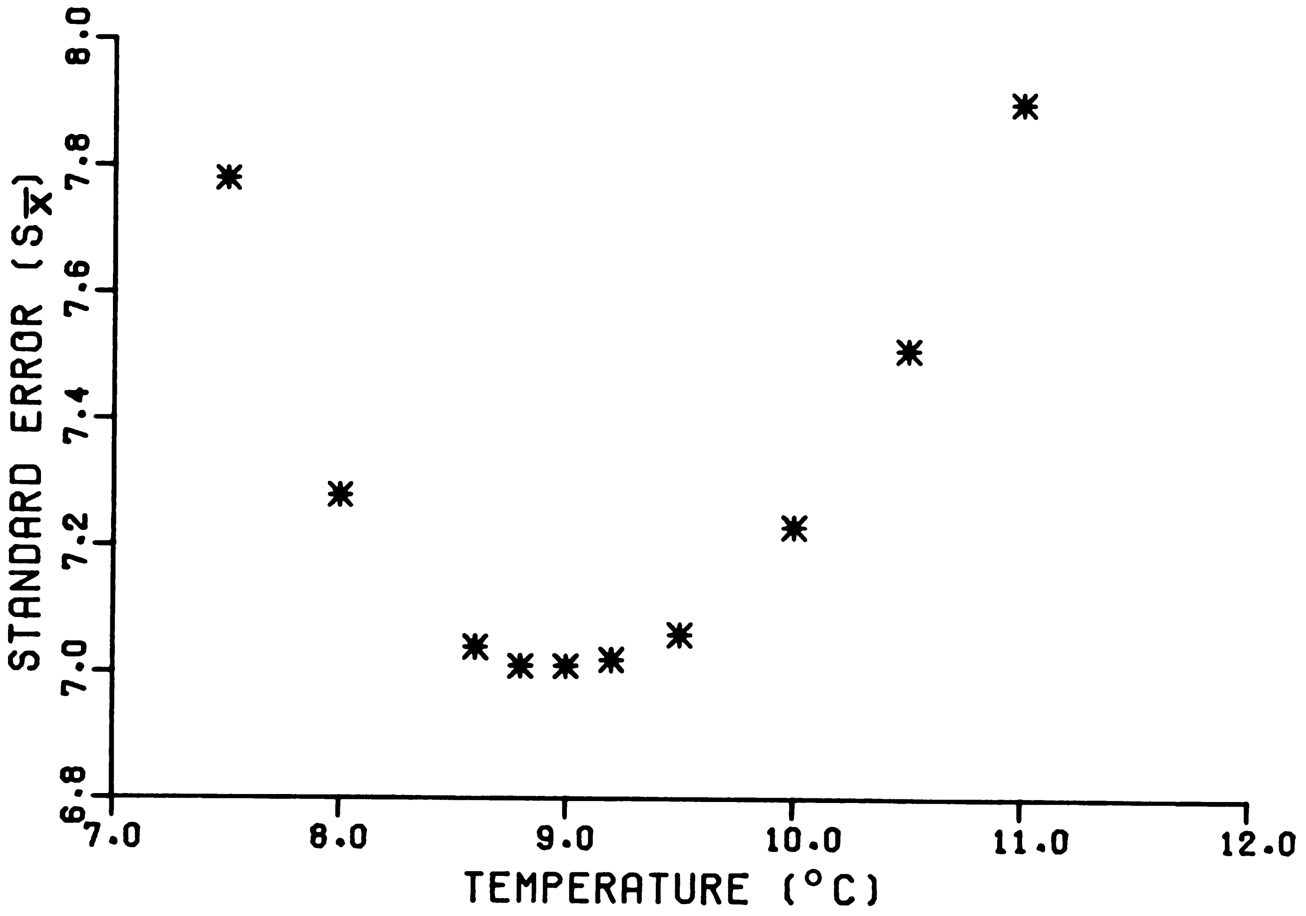


Figure 14. Standard error method for determination of developmental base temperature for overwintering A. pallipes.

independent data set to do so.

SUMMER DYNAMICS

Materials and Methods

Field investigations on the OM and CM parasitoid populations were conducted in three different Michigan onion production regions from the fall of 1979 through 1980 (Figure 15). The two primary study sites were the Michigan State University Organic Soils Research Farm in Laingsburg, Michigan (Bath Township, Clinton County), henceforth referred to as the MSU Muck Farm, and an organic onion production farm near Eaton Rapids, Michigan (Eaton Rapids Township, Eaton County). The research plots at the MSU Muck Farm were a combination of experimental plantings of onions and radishes, some with and some without insecticide inputs. All onion plantings received one or two herbicide treatments, but no fungicides. The radish plantings received neither. The organic onion production farm in Eaton Rapids was maintained free of any chemical inputs including pesticides and commercial fertilizers. The grower culturally controlled (crop rotation, delayed planting, strip planting, cultivation, etc.) insect, disease, and weed pests and soil fertility. Additional population monitoring and post-harvest experiments were conducted in the Rice Lake vegetable production region (Grant Township, Newaygo County) from the fall of 1979 through the fall of 1980. Detailed descriptions of each of the study areas follow. These study sites were utilized by several investigators researching the dynamics of the OM, natural enemies, plant growth, and several other biological parameters of interest in the overall onion agroecosystem project.

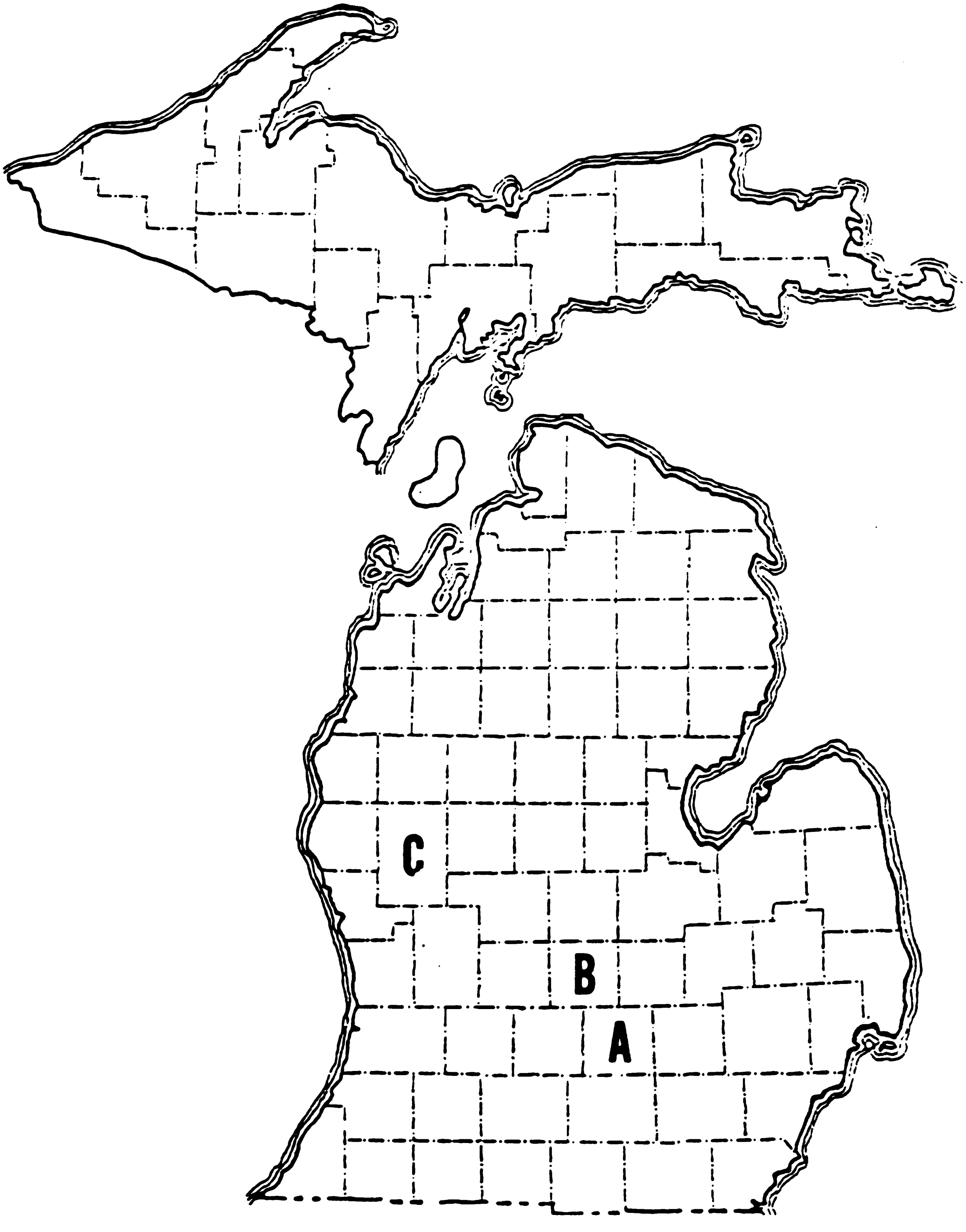


Figure 15. Location of research sites for onion agroecosystem project.

Organic Farm, Eaton Rapids

Description of Study Area

With the cooperation of the grower, Mr. Dale Kunkel, standard production practices at the organic farm were modified to incorporate two beds of radishes adjacent to onion plantings. Otherwise, this research was conducted in fields arranged by the grower (see Figure 16 for a map of the research site). The grower commonly planted crops in long, narrow fields, maximizing the interfacing between different crops. The onion fields were planted the first week of May. With the exception of the fall surveys, most of the OM damage and population monitoring throughout the growing season was conducted in field three, as OM populations in fields one and two were too low to efficiently sample. Two plantings of radishes were sown along the east border of field one. Each planting consisted of three 15 m rows. The first crop was sown in early June (June 6) and the second in mid-July (July 14). The Charlotte weather station provided records of daily maximum and minimum temperatures throughout the year.

Damage and Population Sampling

Onions: Three methods for estimating OM damage were used at different times during the growing season to accommodate the needs of the study and varying OM densities. Initially, damage sampling was conducted as determined optimal for within-field damage estimates by Carruthers (1979). Ten randomly selected 30 m samples of onion row were examined for the number of OM-damaged plants. With experience, OM damage can be recognized by examining the onion leaves for loss of turgor and yellowing (Carruthers 1979). Percent damage was estimated from the number of damaged plants (on that sample date)

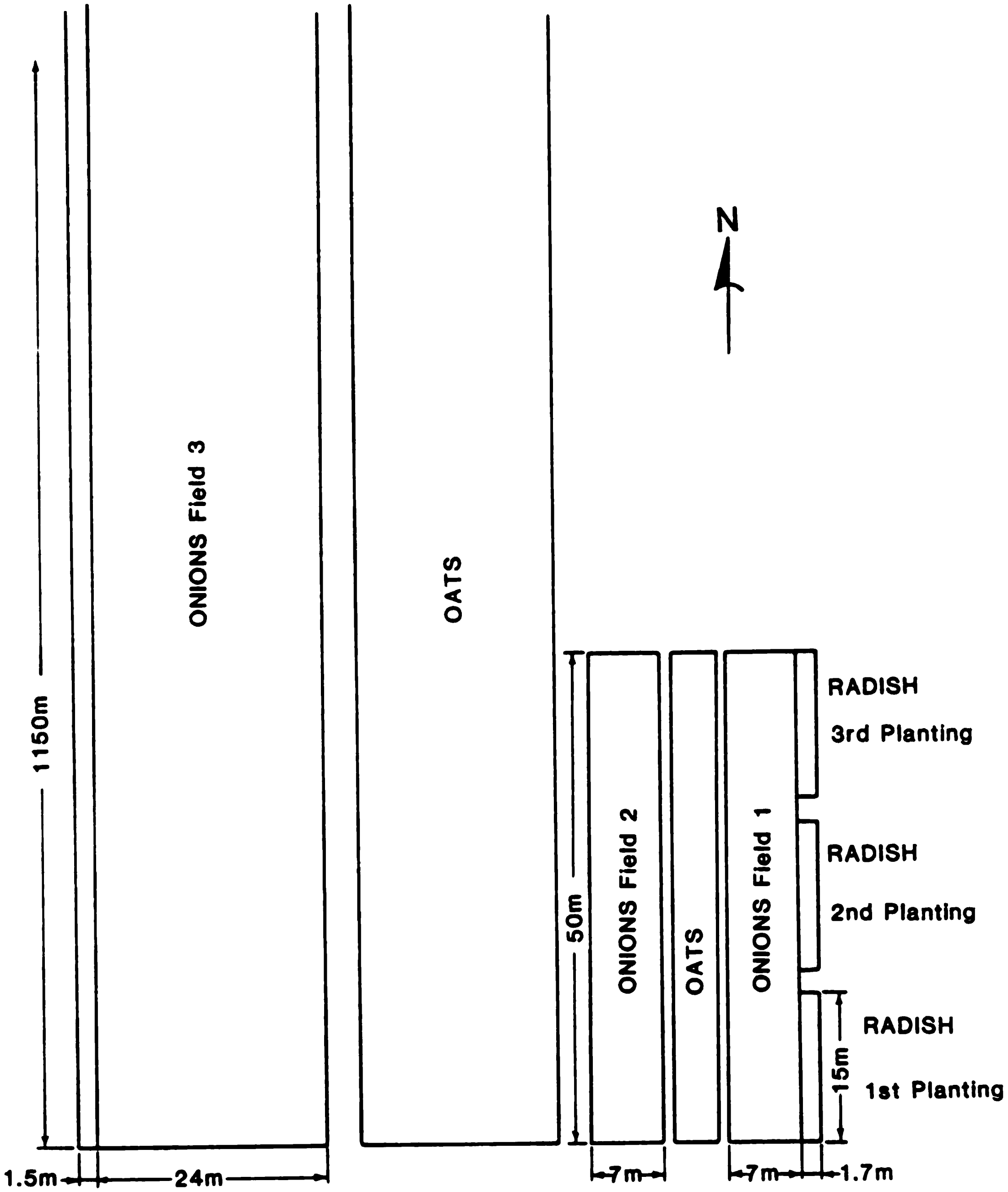


Figure 16. Research fields at organic onion farm in Eaton Rapids, Michigan, 1980.

divided by the average plant density of 725 plants per 30 m. This sampling plan was carried out over three sampling dates from June 6 to June 27. After this time, damage sampling was stratified relative to the distance of the sample from the field's border to coincide with stratified sampling for pupal parasitism. (If the incidence of parasitism differed with distance from the field border, it would be important to know whether or not this spatial pattern was independent of the host's distribution.) Each strata consisted of six single rows (two beds) of onions parallelling the east-west field borders. Seven strata, encompassing the width of the field, were sampled. Five randomly-selected 8 m samples of row were examined per strata to estimate percent damage. Damage estimates were pooled over all strata to determine the field estimate of damage. OM damage was estimated as such from July 4 to July 18.

OM damage and OM pupal density were estimated at the same time due to limited resources. With decreasing OM densities and the intensive efforts required in pupal sampling, a combination of distance and row sampling was the most efficient (see pupal sampling, methods). The distance down a row (north-south direction randomly selected) to the nearest damaged onion from a random point was measured. The number of OM-damaged plants and healthy plants within a .3 m section of row beyond the initially encountered damaged plant was recorded. The percent damage was calculated as:

$$\%\ \text{damage} = (\text{number of infested plants})/(2 \times \text{distance (m)} + .3)\ \ 7.25\ \text{plants/m})$$

Five random samples per strata were collected on four sampling dates from July 18 through August 15. For a comparison of the two methods, row sampling by bed and distance-row sampling by bed were conducted on July 18.

No attempt was made to monitor densities of OM eggs and larvae. Maggots from 10 to 20 damaged plants were sampled routinely and aged to obtain an estimate of the age structure of the population to determine when to initiate first generation pupal sampling.

Initially pupae were sampled by sifting through the soil under randomly selected damaged plants to a depth of ca. 15 cm. Samples were stratified relative to the distance of the sample from the field border. As in the damage sampling, each stratum consisted of six single rows of onions. Five to ten pupae were collected per stratum on four occasions between July 2 and July 11.

Although this sampling method determined the percent parasitized pupae on any one day, estimates of the seasonal incidence of parasitism could not be made without a measure of parasitized and non-parasitized pupal density. Therefore, a pupal sampling strategy based on a measured area sample was developed. As OM pupae are not randomly distributed about a field, and the effort involved in sampling pupae is quite intense, sampling randomly selected unit area plots was too inefficient to be considered. An area with a high probability of containing pupae--usually around a damaged plant--was found. The distance up or down a row from a randomly selected point to the nearest damaged onion was measured, and the soil under a .3 m section of row beyond and including the encountered damaged onion was sampled to a depth of ca. 15 cm for OM pupae. Pupal density was then calculated as:

density = (no. of pupae) divided by (2 x distance (m) + .3 m)

Pupae were examined for signs of parasitism.

<u>Radishes:</u> As at the MSU Muck Farm (see following section: MSU Muck

Farm), the radish beds in Eaton Rapids were sampled for damage and maggot population density by randomly selecting five samples of five adjacent plants per planting and examining these for feeding damage and maggots. The maggots were aged and identified to species. CM pupae were sampled by sifting through the soil to a depth of ca. 12 cm under each five-plant sample of radishes. Sampling of the first planting was initiated on July 18 and was continued once every two weeks through the growing season and the fall. Sampling of the second planting was initiated in mid-August and continued through the fall.

MSU Muck Farm

Description of Study Area

Experimental plots were designed to investigate the effect of (1) the time of planting of onions and radishes, and (2) the use of the soil granular insecticide, Dyfonate, on maggot damage and A. bilineata production. Each plot was 14 m x 15 m large divided into four 6.75 m x 7.5 m sections (Figure 17). Four treatments (onion with Dyfonate, onion without Dyfonate, radish with Dyfonate, radish without Dyfonate) were randomly assigned. Each stratum contained four beds of plants with three single rows per bed. Each planting was bordered on the east and west by a 1.5 m x 15 m strip of oats.

The first planting was sown on May 7, about the time most Michigan onion growers plant. The second planting was sown on May 14; the third planting was sown on May 28; and the fourth planting was sown on June 12. The corresponding degree day accumulations for OM, CM, and A. bilineata on each planting date are presented in Table 11.

The Muck Farm weather station provided daily maximum and minimum temperatures. A three-point thermograph monitored soil temperatures at three

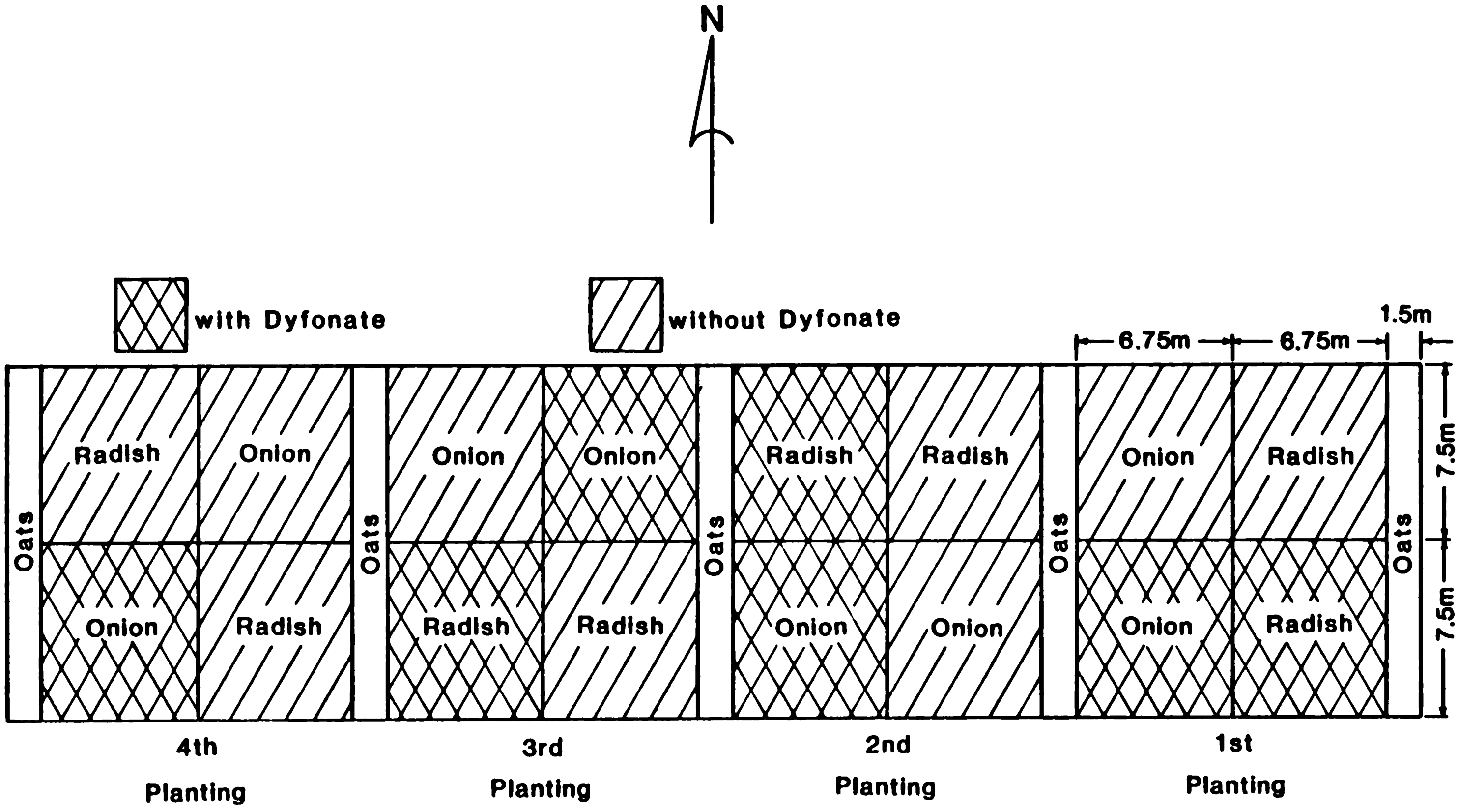


Figure 17. Research plots at the MSU Muck Farm in Laingsburg, Michigan, 1980.

Table 11. Degree day accumulation for OM, CM, and A bilineata on planting dates at MSU Muck Farm, 1980.

		Degree-day Accumulation[1]		
Planting	Date	onion maggot base 4.4 C	cabbage maggot base 6.1 C	*A. bilineata* base 8.6 C
1	May 7	117	86	49
2	May 14	168	125	72
3	May 28	341	275	186
4	June 12	557	465	339

[1] From soil temperatures monitored at a depth of 10 cm.

depths (5, 10, and 15 cm) from November 1979 through July 1980. In August and September, the three-point thermograph monitored the soil temperatures at a depth of 3 cm under the onion canopy, the radish canopy, and the oats.

Damage and Population Sampling

Onions: OM-damaged plant assessments were initiated in each planting when the onion plants reached 3-6 cm in height. This was on May 31 for the first and second plantings, June 23 for the third planting, and June 30 for the fourth planting. From May 31 through June 30, damage assessments were conducted weekly by examining every onion plant in each plot. As the rate of damage decreased, damage assessments were reduced to sampling one row per bed in each of the four beds per plot, once every two weeks.

No attempts were made to obtain density estimates of OM life stages within the plots. Observations of the age structure of infesting maggots in 10 to 20 damaged plants were made routinely to estimate when to initiate pupal sampling. Five to ten pupae were sampled per bed in those plots with OM infestation substantial enough to warrant the intensive effort necessary for sampling pupae. Pupae were examined for the presence of parasitoids.

Radishes: Unlike onions, in most instances, maggot damage to radish was detectable only by pulling up the radish plant and examining the bulb for maggot feeding. Therefore, it was necessary to choose a sample size that would give an accurate estimate of infestation levels, yet would not appreciably change the resource with repeated sampling through time. It was arbitrarily decided that five randomly selected samples of five adjacent plants per plot would meet these criteria. Sampling began on May 24 in the first and second plantings, June 16 in the third planting, and June 30 in the fourth planting. Plots were sampled weekly from May 24 through June 30 and once every two weeks through the rest of the season. Sampled plants were returned to the laboratory where they were examined for feeding damage and the presence of maggots. The maggots were examined for species and age determinations.

As the maggots in radishes began to pupate, samples of fifty pupae were collected in infested plots and examined for parasitism. Pupae were collected four times between June 21 and July 3. At this time, it was decided that infestation levels were high enough that pupal sampling could be combined with the radish plant sampling, giving a measure of pupal density, and still retrieving enough pupae to evaluate parasitism. Therefore, from July 14 through the rest of the growing season, the soil under the 5-plant samples of radishes to a depth of ca. 12 cm was sifted for pupae. These pupae were then examined for symptoms of parasitism.

Grant

In 1980, OM pupae were periodically sampled in a few commercial onion fields in Grant, Michigan, to determine a relative estimate of parasitism. First and second generation pupae were collected from a 10 hectare field which was treated with Dyfonate at planting but received no foliar sprays (field 1), and an adjacent field which was treated with Dyfonate and had seven foliar sprays of either Sevin or parathion throughout the season (field 2). Second generation pupae were also sampled from a small onion field receiving foliar sprays but no Dyfonate at planting (field 3).

On June 3, four double rows of radishes were planted along the west border of field 1. These radish plantings were periodically sampled in the same manner as those at the Eaton Rapids research site. Maggot damage and infestations were monitored and pupae were collected and examined for parasitism. After a portion of the radish plantings were destroyed by the onion grower's cultivation practices in July, new plantings were sown within the older plantings.

Results and Discussion

Evaluating Parasitism

Parasitism of insect populations was frequently evaluated by percent of parasitized individuals in a single sample (usually taken at peak abundance of the attacked life stage). This measure of relative parasitism between comparisons (i.e., fields, habitats, hosts, etc.) can also measure a parasitoid's impact on its host population (if the population is sampled when all parasitized and non-parasitized individuals in a specific life stage are present, as would be during an overwintering stage). However, for multivoltine species and parasitoids attacking non-diapausing life stages, this estimate can be very misleading. Many parasitoids develop at different rates than their hosts, and without considering this, one cannot accurately estimate the proportion of the population actually parasitized. To obtain an unbiased estimate, the total seasonal production of parasitized hosts to the total seasonal production of all hosts (parasitized and non-parasitized) was calculated.

The problem was similiar to that described by Southwood (1966, 1976), Helgesen and Haynes (1972), Kiritani and Nakasujii (1967) and Manly (1976), when estimating age-specific mortality in a population where all age classes occur simultaneously. If the population census is taken frequently, an occurrence curve can be established for each life stage. The total seasonal incidence can then be calculated by (Lampert 1980):

$$TI_i = \sum_{j=1}^{n-1} \left(\frac{D_{ij} + D_{ij+1}}{2}\right) (DD_{j+1} - DD_j)$$

where: TI_i = total seasonal incidence for life stage i

D_{ij} = density of the i^{th} life stage on the j^{th} sample date

DD_j = accumulated degree days on the j^{th} sample date

The total seasonal incidence (TI_i) estimates the stage-degree days. To determine the total seasonal production (TP_i) of the stage, and correct for redundancy in sampling, divide the total seasonal incidence by the developmental time for the stage (DT_i):

$$TP_i = \frac{TI_i}{DT_i}$$

Lampert (1980) evaluated total life stage parasitism of the cereal leaf beetle (<u>Oulema</u> <u>melanopus</u>) larvae by multiplying this host density (D_{ij}) times the sampled proportion parasitized (PP_{ij}) to estimate the parasitized host density (PD_{ij}). He then calculated the total seasonal incidence of parasitized hosts and, by dividing this by the total seasonal incidence of the life stage, determined the proportion of the life stage parasitized as follows:

$$PPar_i = \frac{\Sigma_{ij} \; ((D_{ij}\; PP_{ij}) + (D_{ij+1}\; PP_{ij+1}))/2 \; (DD_{j+1} - DD_j)}{TI_i}$$

If the developmental rates of the parasitoid and its host are synchronized, the ratio between total seasonal incidence of parasitized hosts (as calculated above) to the total seasonal incidence of the host life stage, accurately estimates the proportion of the population parasitized. However, if the developmental rates of the parasitoid and its hosts differ, as with *A. bilineata* and its hosts, the OM and CM, the sampled proportion parasitized on the j^{th} sample date is a biased estimate. To correct for this bias, the total seasonal incidence of parasitized host (TPI_i) must be calculated from the sampled parasitized host density (sPD_{ij}) and accumulated degree days based on the parasitoid developmental thresholds, as follows:

$$TPI_i = \mathop{S_i}\limits_{j=1}^{n-1} \left(\frac{sPD_{ij} + sPD_{ij+1}}{2}\right) (DD_{pj+1} - DD_{pj})$$

The total seasonal production of parasitized hosts (TPP_i) is then calculated by dividing this seasonal incidence of parasitized hosts by the developmental time of the parasitoid:

$$TPP_i = \frac{TPI_i}{DT_p}$$

To calculate the proportion of the life stage $_i$ parasitized, the total seasonal production of non-parasitized hosts (TNP_i) must be calculated based on sampled densities of non-parasitized hosts and the host's developmental thresholds. The proportion parasitized is calculated by:

$$PPar_i = \frac{TPP_i}{TPP_i + TNP_i}$$

This bias, however, can lead to incorrect conclusions. For example, figure 18 shows non-corrected and corrected parasitized pupal densities relative to the total sampled pupal density of CM in the first radish planting at the MSU Muck

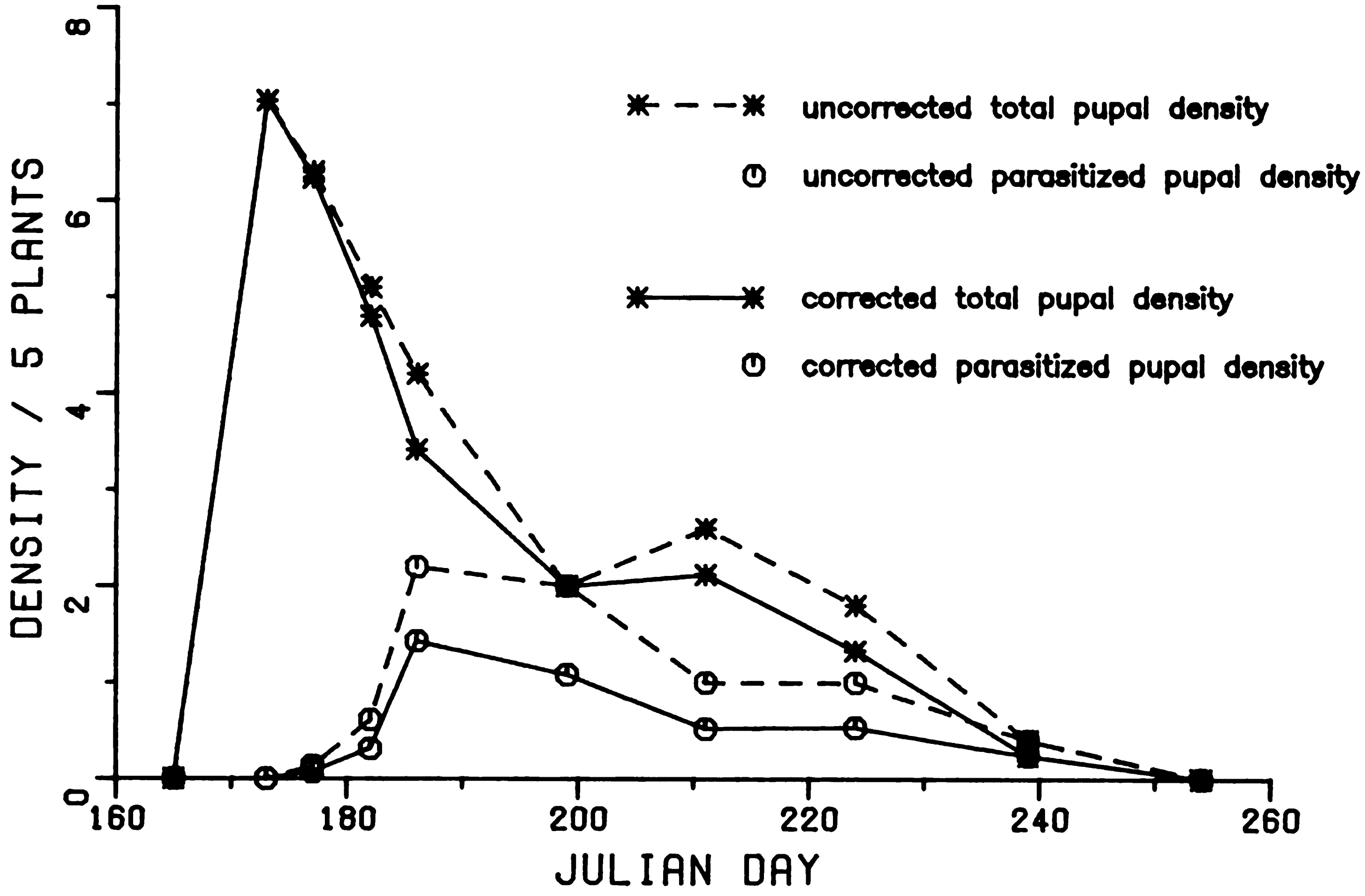


Figure 18. Correcting for redundancy in sampling due to differences in the rates of development of A. bilineata and its host, CM.

Farm. To correct for the bias at each sample date, sampled parasitized pupal density was multiplied by the ratio of A. bilineata developmental time to CM pupal developmental time accumulated between successive sampling dates (j - 1 and j). Without correcting for this bias, the total seasonal proportion CM pupae parasitized was 62%. Yet, with the seasonal temperatures experienced, the parasitoid required 1.6 times as long to develop as its host, and therefore was more likely to be redundantly sampled. Correcting for this difference revealed a true proportion parasitized of 26%.

Organic Farm - Eaton Rapids

Seasonal OM Damage

OM damage in the research field at the organic farm in Eaton Rapids reached 40% of the total crop (Figure 19) during the 1980 growing season. Eighty-one percent of the damage occurred during the first OM generation. This pattern was similar to the pesticide-free plots at the MSU Muck Farm, but differed from the pesticide-dominated commercial onion fields (Whitfield 1981). Most commercial onion growers plant their onions along with the systemic, soil granular insecticide, Dyfonate. Dyfonate reduced the impact of the first generation OM, but lost its effectiveness before second generation damage began. The effectiveness of chemical foliar sprays for second generation adults is questionable (Whitfield 1981), hence a significant portion of crop damage (39 to 79%; Whitfield 1981) happens during the second generation.

Without chemicals, first generation damage was significant, but second generation damage was reduced. This reduction is partially due to the dynamics of the onion plant and OM adult oviposition behavior. As the bulb matures, each individual plant can support more maggots, and because female flies prefer to

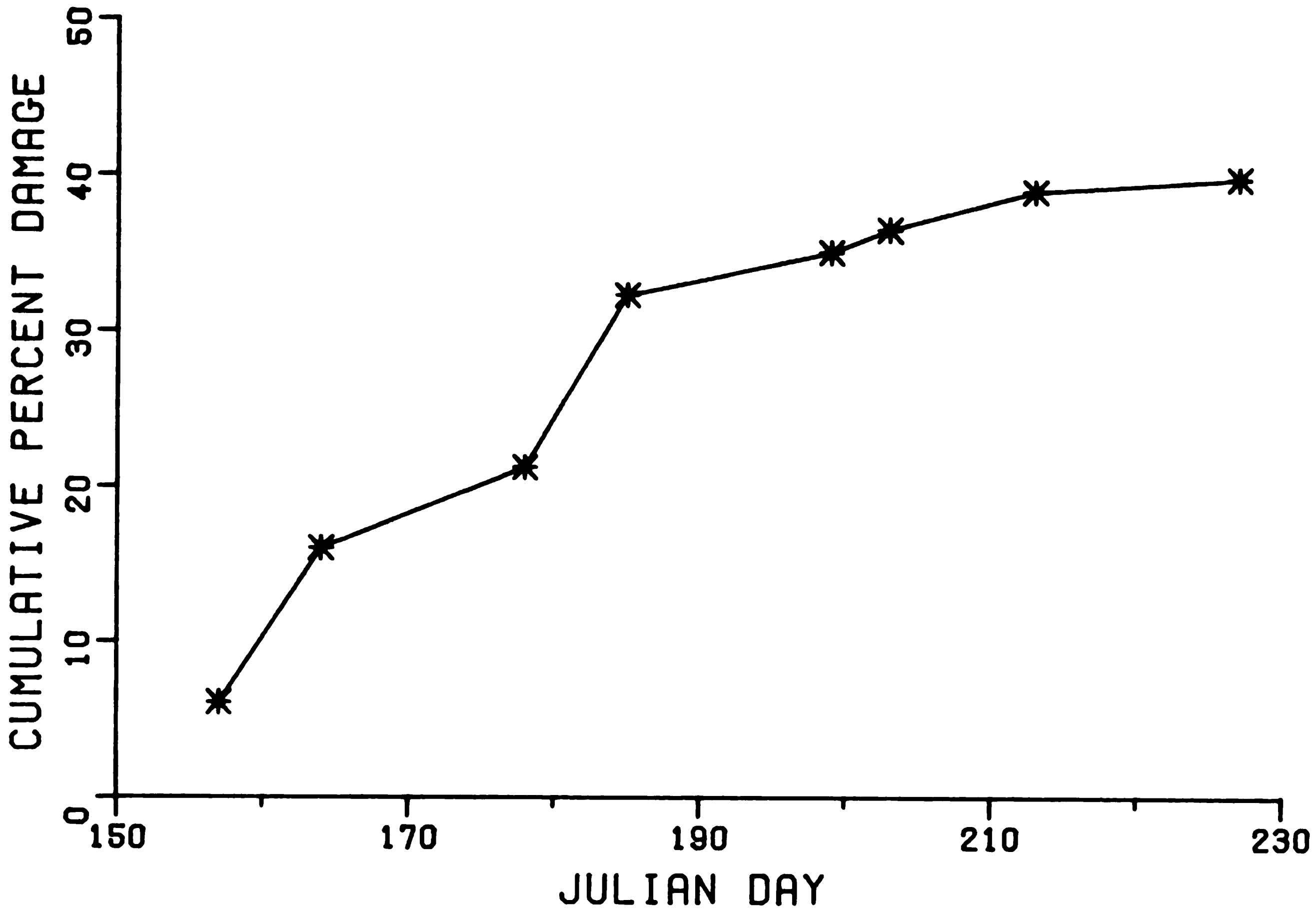


Figure 19. OM damage in Eaton Rapids research field, 1980.

oviposit on previously-infested onions, a loading effect occurs. Hence, the same population density causes less damage later in the season. It is also likely that a build-up of natural enemies in the pesticide-free environment affected OM mortality and hence reduced OM damage.

An analysis of variance for factorial design was performed on the plant damage data to determine differences in OM damage with distance from the field border over time. No significant differences existed in OM damage levels between beds sampled ($F_{6,112}$=.996). OM activity was evenly distributed about the width of the field. Only two out of 180 larvae sampled in Eaton Rapids during the first week of August were SCM; the overwhelming majority were OM. Some of the early season damage probably was caused by SCM, but larvae were not identified to species.

Parasitism of OM

Sampling absolute densities of OM pupae at Eaton Rapids was labor-intensive and did not yield an adequate data set for determining the seasonal incidence of parasitized and non-parasitized pupae. As a result, a relative measure of parasitism corrected for the differences in host and parasitoid developmental times was calculated from numbers of periodically sampled pupae. The ratio of accumulated degree days from one sample date to the next divided by the developmental time of the parasitoid (385 degree day, base 8.6^{0}C) to accumulated OM degree days divided by the developmental time of OM pupae (306 degree day, base 4.4°C) was multiplied by the number of sampled parasitized OM pupae to give the corrected value (n_p^1).

The percentage of sampled OM pupae parasitized by A. bilineata in Eaton Rapids reached 17.0%. After correcting for the developmental times, it decreased to 10.9% (Table 12). The largest proportion of hosts parasitized was sampled during the later part of the first generation of pupae. This might be expected, because the parasitoid continues to attack through this life stage. Also, because it takes longer to complete development, the parasitoid is likely to still be in the soil when healthy flies emerge.

An analysis of variance reveals no significant differences in the proportion of OM pupae parasitized in the different beds around the width of the onion field ($F_{6,24}$=.914). _A._ _bilineata_ activity did not appear to be influenced by the proximity of the field border. The width of the onion field samples in Eaton Rapids is considerably less than most commercial onion fields. This may or may not represent the spatial distribution of parasitoid activity in larger fields.

CM Damage in Radishes

The first radish planting in Eaton Rapids had reached nearly 100% damage by CM by the first sample date (July 18, see Table 13). Seventy-six percent of the sampled radishes were infested with CM larvae, of which 96% showed some signs of feeding damage. Little damage was experienced in either the second or third radish plantings (8% and 4% respectively), and damage was not initiated in these plantings until September. Seven percent of larvae sampled in the radish plantings on July 18 and 1 of the 4 larvae sampled on August 29 were SCM. The majority of the maggots sampled were CM; no other species of radish-infesting maggots were detected.

Unlike onion plants, maggot-infested radishes continued to grow. Plants attacked by CM larvae early in the season continue to attract CM flies for some time. As a result, although the first radish planting by July 18 had 100% damage, the food resource for maggots was not depleted, and these plants were

Table 12. *A. bilineata* parasitism of OM at Eaton Rapids research site.

Date	OM Degree Days	Aleochara Degree days	n	Proportion Parasitized	Corrected Proportion Parasitized[1]
178	746	478	0	0	0
183	823	535	54	.09	.07
185	853	556	69	.07	.04
189	916	602	21	.24	.11
192	969	642	33	.33	.23
199	1098	742	5	.60	.36
203	1176	803	17	.18	.12
213	1337	923	67	.22	.11
226	1555	1086	45	.16	.07
222	1520	1092	12	0	0
Season Total	1570	1097	323	.17	.10

[1] Proportion parasitized corrected for differences in developmental times of the host and parasitoid (see text).

Table 13. CM infestation in radishes at Eaton Rapids research site.

Date	1st Planting		2nd Planting		3rd Planting	
	$\bar{x}$ % Damaged plants	$\bar{x}$ % Infested plants	$\bar{x}$ % Damaged plants	$\bar{x}$ % Infested plants	$\bar{x}$ % Damaged plants	$\bar{x}$ % Infested plants
199	96 (2.0)[a]	76 (7.0)	-	-	-	-
217	80 (6.0)	8 (4.0)	0 (0.0)	0 (0.0)	-	-
227	100 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	-	-
242	76 (5.0)	4 (2.0)	15 (5.0)	4 (2.0)	0 (0.0)	0 (0.0)
255	92 (2.0)	0 (0.0)	8 (4.0)	0 (0.0)	8 (2.0)	0 (0.0)
303	80 (3.0)	0 (0.0)	20 (4.0)	0 (0.0)	8 (2.0)	4 (2.0)

[a] standard error

reinfested.

Parasitism of CM

The ratio of the seasonal incidence of parasitized pupae to the seasonal incidence of all pupae determined the seasonal parasitism of CM pupae in radishes at Eaton Rapids. Corrected for differences in developmental times, an estimated 74% of the CM population was parasitized (Figure 20). Total seasonal production of parasitized pupae was estimated at 2.72 pupae/5 plants, compared with .94 non-parasitized pupae/5 plants. Though parasitoid densities were not directly measured, the A. bilineata population was fairly high. Eighty-one percent of the parasitized pupae were attacked by more than one parasitoid larvae. Parasitoid activity in the radish plot was well synchronized with its host population for the first generation; however, no parasitoid activity was detected in the fall generation.

MSU Muck Farm

OM Damage as Affected by Planting Date and Insecticide Use

OM damage was first detected in plots with Dyfonate and plots without Dyfonate in both the first and second plantings on the same date (June 8, Figure 21). Damage levels were considerably higher in the non-Dyfonate plots and continued to be so through the end of June. After this time, the damage rate for all plots declined, corresponding with first generation pupation. Damage slightly increased during the second generation of OM in the first planting, non-Dyfonate plot. The third planting plots and the Dyfonate fourth planting also had damage. Little additional damage was incurred in either of the second planting plots.

Five percent of the first generation maggots infesting onions at the MSU Muck Farm were SCM. The remainder from the first and subsequent generations

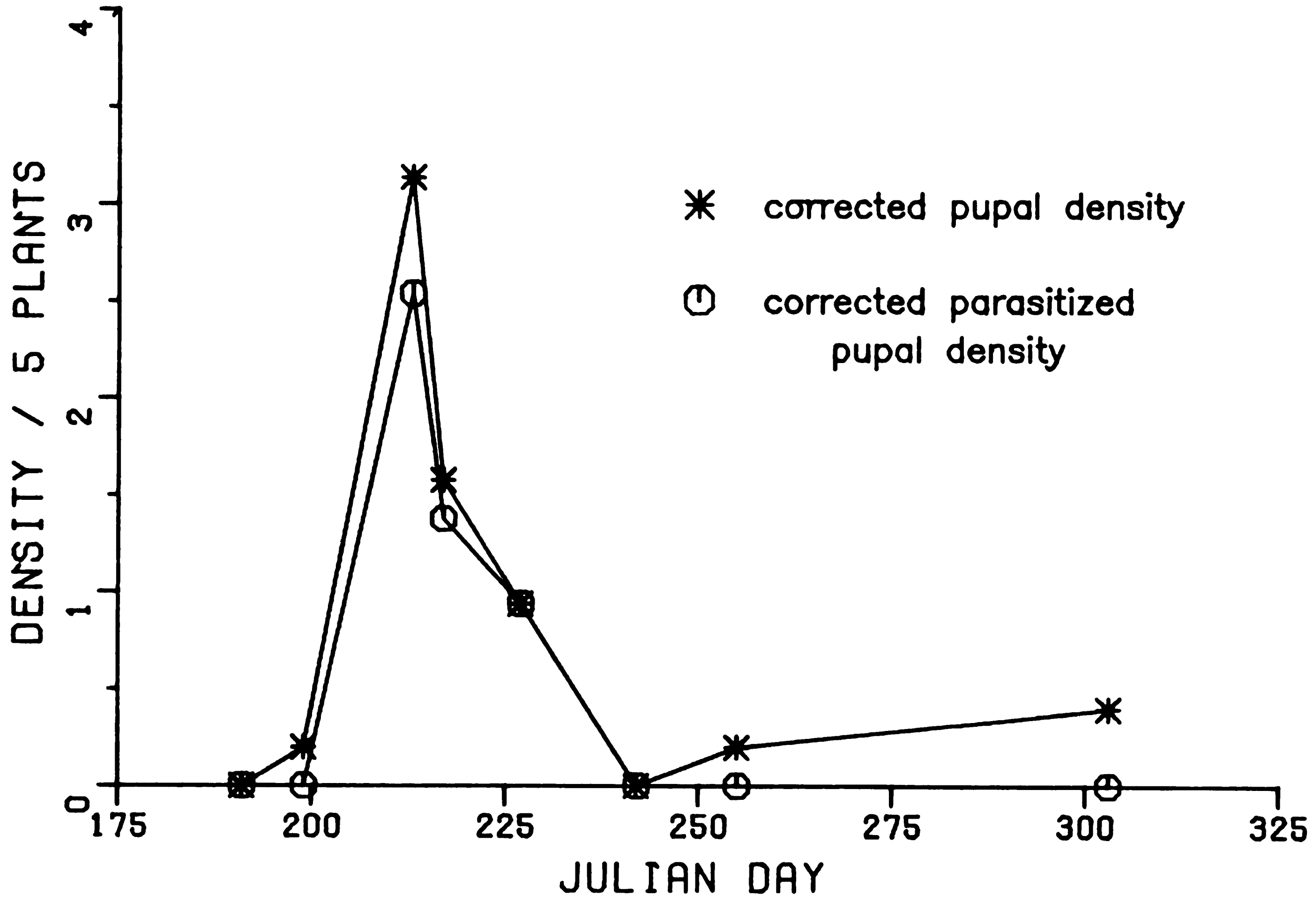


Figure 20. A. <u>bilineata</u> parasitism of CM pupae in radish plots in Eaton Rapids, 1980. Densities are corrected for differences in the rates of development of the host and parasitoid.

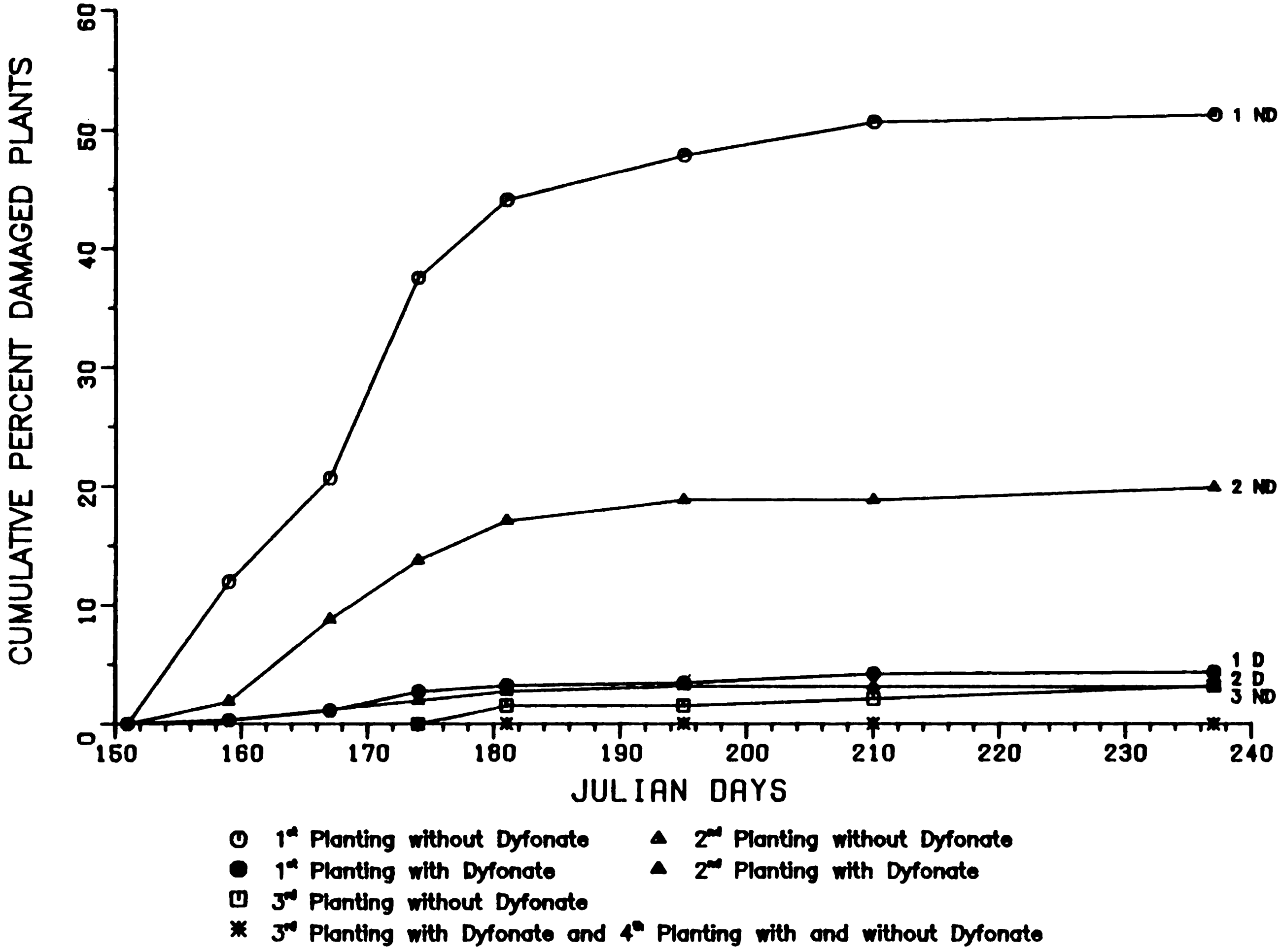


Figure 21. The influence of planting date and the use of Dyfonate® on OM damage at the MSU Muck Farm, 1980.

were OM. OM damage in the different plots was strikingly different between planting dates and the soil granular insecticide, Dyfonate. In the non-Dyfonate plots, seasonal damage experienced in the second planting of onions was 40% of that experienced in the onions planted without Dyfonate seven days earlier. Onions planted three weeks later had 6% damage. This was less than the damage incurred in the first planting Dyfonate plot. The difference in damage levels between Dyfonate plots and non-Dyfonate plots of the same planting date decreased with delay of planting. Though OM damage was slightly higher in the non-Dyfonate plot than in the Dyfonate plot of the third planting, total cumulative damage levels for both over the entire season were still less than 4%. Neither of the fourth planting plots experienced any substantial OM injury. The percent cumulative damage for the Dyfonate plot and non-Dyfonate plot were .003% and 0%, respectively.

Planting date and the use of the soil granular insecticide in early season plantings greatly affected OM damage. Yet, delayed planting alone probably will not reduce OM damage. The presence of a preferred resource in the form of earlier planted, perhaps previously-infested onions (Carruthers 1979) probably affects damage in later plantings. However, this indicated that delayed planting in conjunction with the use of an earlier planted trap crop could be a valuable component of an integrated management strategy for OM (see Discussion).

Parasitism of OM Pupae

OM densities in the experimental plots at the MSU Muck Farm were high enough to repeatedly sample pupae only in the earliest non-Dyfonate onion planting during the first generation. One sample was taken in the second non-Dyfonate onion planting about peak pupation of the first generation. The results of OM pupae sampling are presented in Table 14. Parasitized pupae were very low in number, accounting for only 2.9% of all the pupae sampled.

CM Infestations in Radishes

CM infestations in radishes at the MSU Muck Farm are presented in Figure 22 a-h. CM egg laying was first detected in the earliest non-Dyfonated radish planting on May 30—three weeks after the plants were sown. Within ten days, more than 50% of the plants were infested. Damage was begun in the second and third non-Dyfonated plantings in early June, though the third planting incurred little first generation damage.

Dyfonate delayed damage in the first and second plantings (Figure 22) such that these plantings had little first generation damage. The resulting damage in the Dyfonated plots (Figure 22) was considerably less than the same aged plantings without the insecticide treatment.

Due to the different timed plantings, the CM food resource was continually changing, and as such, a CM incidence curve could not be constructed. However, it appears that the CM completed three generations in radishes at the MSU Muck Farm. The first and second generations attacked the first and second plantings, and a late summer-fall generation was evident in the third and fourth plantings.

More SCM were observed infesting radishes at the MSU Muck Farm than in any other plantings of onions or radishes in the other regions. SCM comprised 25% of the radish-infesting maggots sampled in June, 4% in July, and 25% in August. No SCM were detected in the fall generation.

Ellis et al. (1979) investigated the comparative attractiveness of different aged radish plants to adult CM for oviposition, and discovered two distinct peaks in attractivity. The plants become more attractive as the hypocotyls swell, and

Table 14. Parasitism of OM pupae, MSU Muckfarm, 1980.

Julian Day	Plot	n	number parasitized
184	1st planting; non-Dyfonated	21	0
191	1st planting; non-Dyfonated	30	0
192	2nd planting; non-Dyfonated	36	2
199	1st planting; non-Dyfonated	18	1

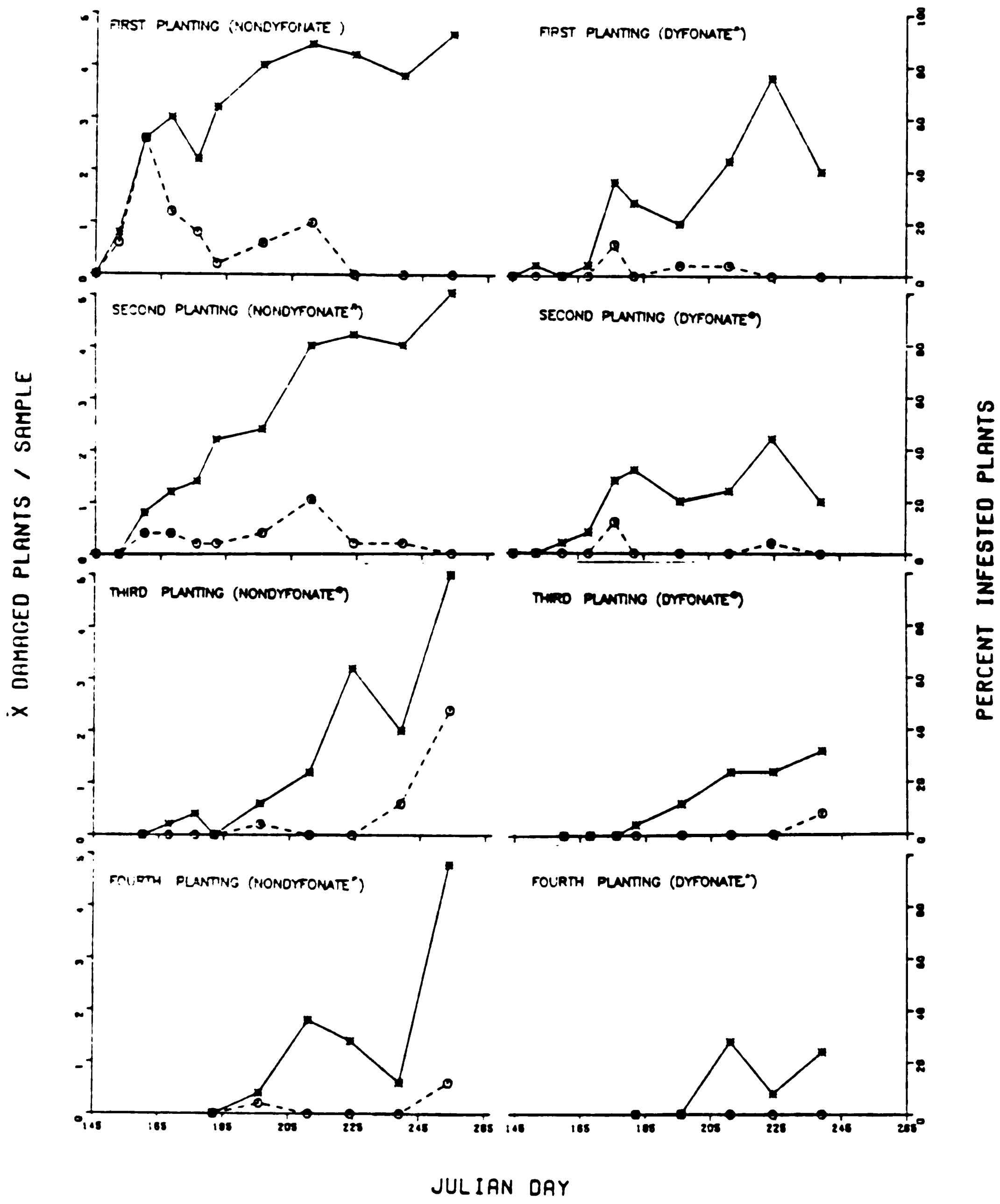


Figure 22. CM damage and infestation in radish plantings at the MSU Muck Farm, 1980.

are most attractive as they reach marketable size. After this stage, the plant's attractivity decreases, but increases again as the plant produces flowering shoots.

Oviposition preference was seen in the MSU Muck Farm plots. CM females were attracted to earlier plantings until the later plantings began to reach marketable size. Infestations then shifted. As the first radish planting was heavily infested before the hypocotyls had begun to swell, it appears that, without a choice CM adults will oviposit in whatever is available. These results indicate that the timing of planting and the use of Dyfonate can influence the timing and levels of CM infestations.

Parasitism of CM

CM pupal samples collected in the first radish planting at the Muck Farm between June 21 and July 3 were not taken per a measured unit area. Absolute densities over these sample dates were estimated from third instar density data. Third instar densities at 97.5 degree days, base 6.1°C (developmental time for third instar CM larvae) prior to each pupal sampling date were used to construct a hypothetical incidence curve for CM pupae (Figure 23). However, as *A. bilineata* parasitoid activity began during the later half of the first generation pupation period, and parasitized pupae require considerably more time to complete development than healthy CM pupae, it is unlikely that the pupal population goes to zero between generations, but rather overlaps generations. To reflect this situation and thereby make pupal density estimates more realistic, a line was fitted by connecting the estimated peak pupation with the first sampled pupal density estimate on July 14th. CM pupal densities for the interim sample dates were drawn off this resulting curve.

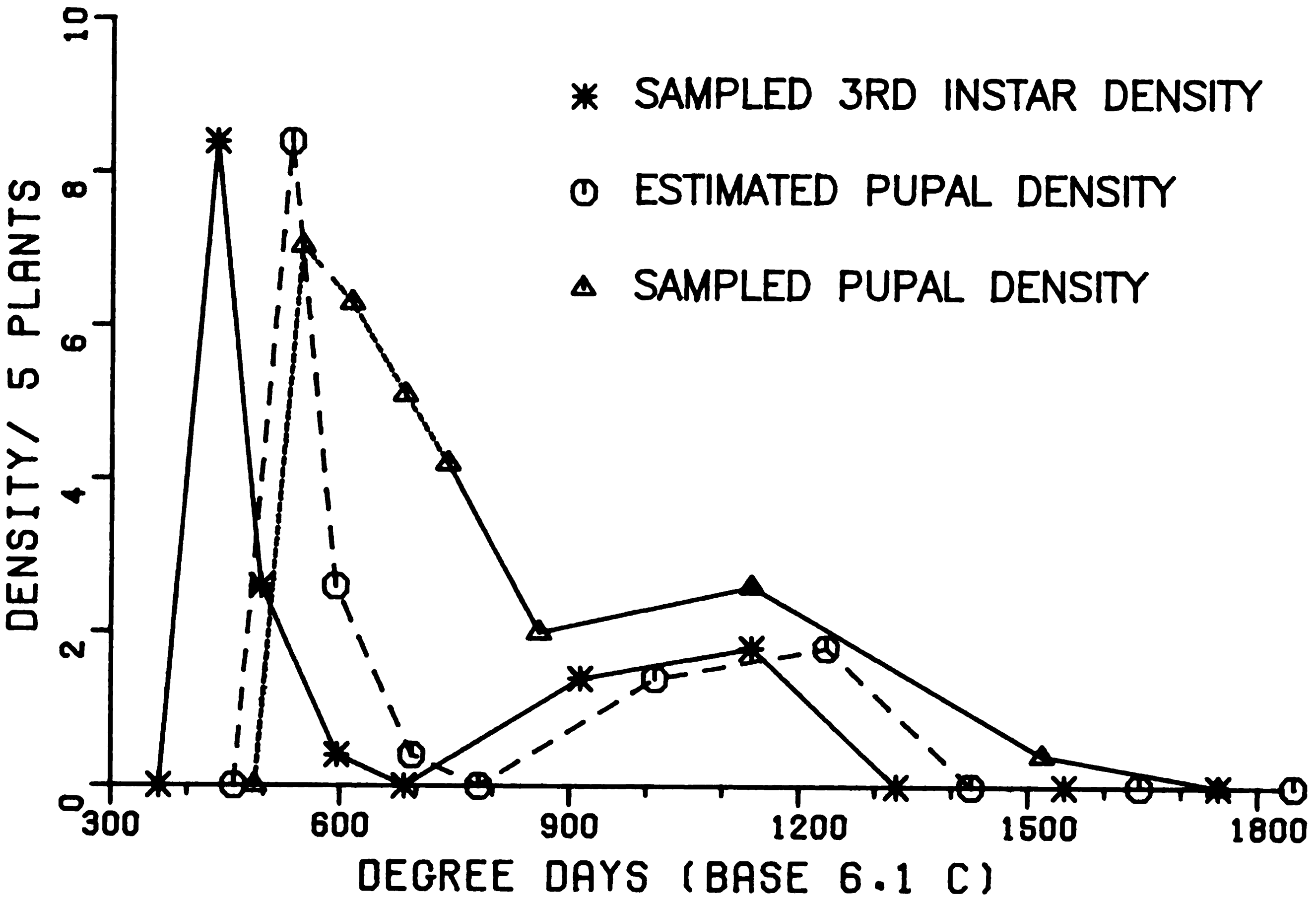


Figure 23. Estimation of early season CM pupal densities from third instar densities.

Seasonal production of A. bilineata parasitized and non-parasitized CM pupae and the resulting proportion parasitized in the infested radish plantings at the MSU Muck Farm are presented in Table 15 and Figures 24 a-f. The first non-Dyfonate planting showed the largest number of parasitized pupae and the largest proportion of parasitized host population. In the second non-Dyfonate planting, parasitoid activity appeared synchronized with the initial incidence of pupation; however, parasitism declined with the first pupal generation and remained low through the second, despite moderate CM pupal density.

The earliest Dyfonate planting was also well synchronized with its host's pupation, and resulted in a relatively high proportion parasitized (.23). However, the CM population in this planting was low, and parasitoid activity was not evident until the second generation, resulting in a low seasonal production of parasitized pupae. The later-planted Dyfonate radish plots produced few CM pupae and no detectable parasitism. The third non-Dyfonate planting produced the largest overwintering CM pupal population, yet only 6.7% were parasitized. The fourth planting produced few CM pupae, and no detectable parasitism.

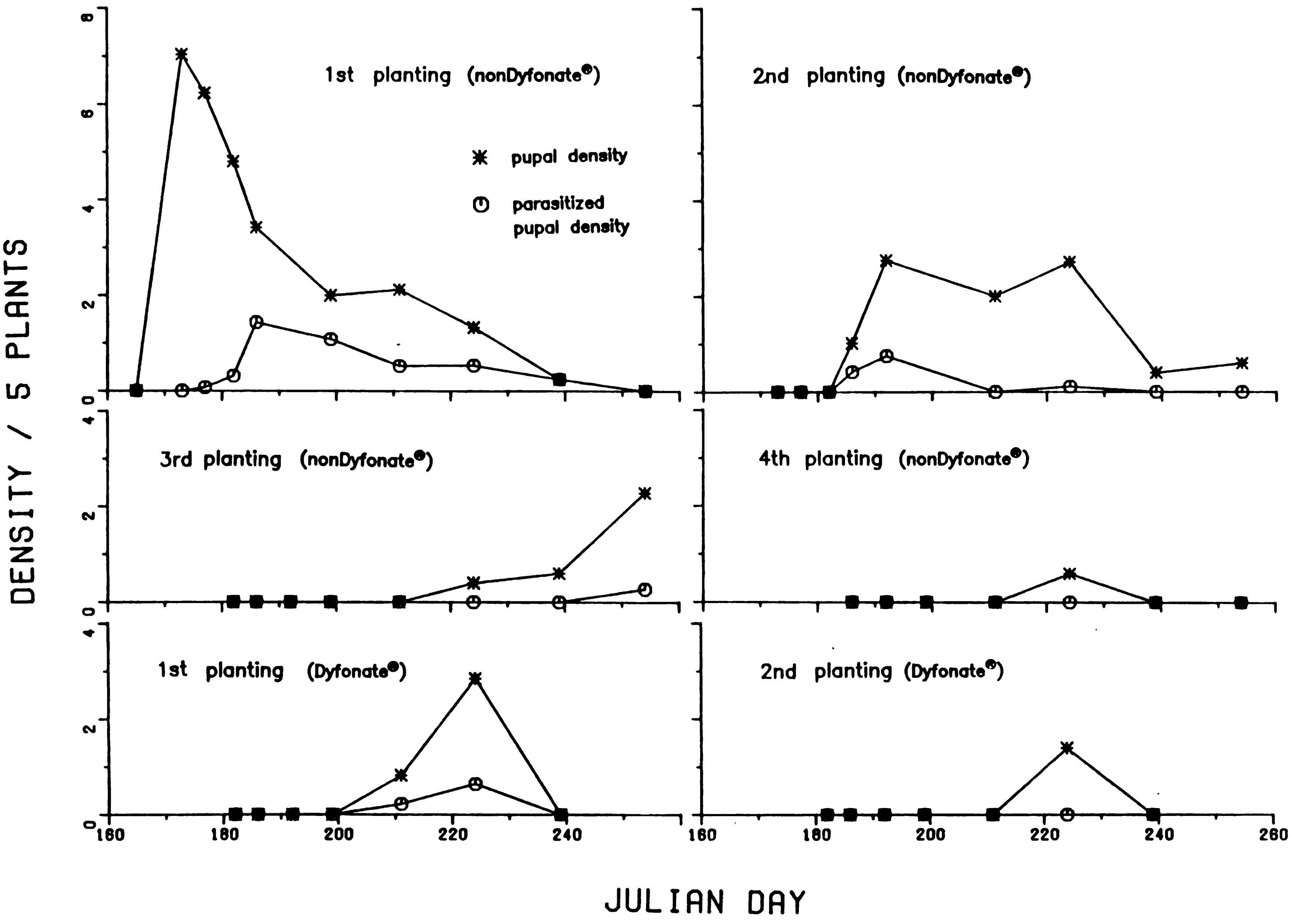
The radish plots were small and close together; therefore, CM distribution between the plots may have been influenced by the presence of a preferred resource, the earlier planted radishes. However, given the resulting CM infestations and A. bilineata parasitism in the radish plots at Eaton Rapids and the MSU Muck Farm, it appeared that the timing of infestations and resulting parasitism was influenced by host plant availability, and thus planting date.

The larval parasitoid of the CM, Trybliographa rapae, was found in pupal samples collected in August and September in the radish plots at the Muck Farm. Nine percent of the pupae collected in August were parasitized by T. rapae, and

Table 15. *A. bilineata* parasitism of CM pupae in radish plots at the MSU Muck Farm, 1980.

Planting	Seasonal production/5 plants CM pupae	 *A. bilineata* parasitized CM pupae	Proportion Parasitized
1 nonDyfonate	10.257	2.661	0.259
2 "	7.348	0.832	0.113
3 "	1.908	0.129	0.067
4 "	.470	0.0	0.0
1 Dyfonate	2.991	.689	.230
2 "	1.098	0.0	0.0

Figure 24 a-f. *A. bilineata* parasitism of CM pupae in radish plantings at the MSU Muck Farm, 1980. Densities are corrected for differences in rates of development between the host and parasitoid.


DENSITY / 5 PLANTS
JULIAN DAY
1st planting (nonDyfonate®)
2nd planting (nonDyfonate®)
3rd planting (nonDyfonate®)
4th planting (nonDyfonate®)
1st planting (Dyfonate®)
2nd planting (Dyfonate®)
✱ pupal density
ⓘ parasitized pupal density
0
2
4
6
8
160
180
200
220
240
260

10% of those collected in September. Bromand (1980) found a lesser percentage of A. bilineata parasitism in T. rapae parasitized H. floralis pupae than in non-parasitized pupae. He concluded that some selection for non-parasitized pupae may exist, but the process of recognition is not understood.

Grant

Parasitism of OM

First generation pupae samples were pooled over fields 1 and 2. The first sample (n=195), collected on July 3, revealed no A. bilineata and less than 1% A. pallipes parasitism. Of the pupae collected on the second sample date, July 16 (n=170), 3.53% (uncorrected) were parasitized by A. bilineata and none by A. pallipes. If parasitism occurred, it should have been more detectable at this time, as July 16 (1064 degree day, base 4.4°C) was just past peak pupation, and healthy flies had already begun emerging, whereas parasitized pupae would still be in the soil.

Table 16 presents the results of the second generation pupal sampling. More parasitism was observed in the field without foliar sprays, though Whitfield (1981) reported no difference in OM infestations between the fields. These results may be slightly biased, as the Dyfonate field with foliar sprays, field 2, was sampled a week prior to the non-sprayed field 1, and during that time, parasitism could have increased. However, the field with no Dyfonate, but with repeated foliar spray applications, was sampled the same day as field 1, and less than 1% parasitism was observed.

Five percent of the first generation pupae sampled were SCM, as were 4% of the second generation. No parasitism of SCM was observed.

Table 16. Parasitism of second generation OM pupae in fields receiving different insecticide treatments.

			Percent parasitism[2]	
Date	Insecticide Use[1]	n	*A. bilineata*	*A. pallipes*
233	Dyfonate plus foliar sprays	417	4.31	.24
240	Foliar sprays only	274	.36	0
240	Dyfonate only	116	19.83	.86

[1] Dyfonate is a soil granular applied at planting, foliar sprays consisted of F-10 applications of Sevin® or parathion throughout the season.

[2] Percentages not corrected for differences in developmental times.

CM Infestations of Radishes and Parasitism

Eighty percent of the sampled radish plants from the plots in Grant showed CM damage by the first sample date, July 24. Seventy-four percent of the sampled plants were infested. The maggot infestation decreased to 5% of the sampled plants on August 13, but increased to 14% by the end of August, and 24% by the end of September. Thus, it appears that there were two generations of CM in the radishes in Grant. An earlier generation was probably missed due to the late planting date.

A. bilineata parasitism of CM pupae is presented in Table 17. Parasitism levels were corrected for differences in the developmental times of the host and parasitoid by multiplying the number of sampled parasitized pupae times .53 (the mean ratio of physiological time calculated for different sample dates during July and August at the MSU Muck Farm and Eaton Rapids). (This ratio only varied between .51 and .54 over this time period.) No T. rapae parasitism was observed in Grant. SCM accounted for 12% of the radish-infesting larvae in July 24, and 3% of the pupae on August 13. Otherwise, all other radish-infesting maggots were CM.

Superparasitism

The corrected numbers of A. bilineata parasitized pupae in the different non-Dyfonated radish plots at the MSU Muck Farm were examined in relation to the host densities. A least squares regression revealed a fairly exact linear relationship (r^2=.980; Figure 25). This indicates that with increases in host densities, the proportion of pupae parasitized by a single A. bilineata population remains fairly constant. Examining the attack behavior of the first instar parasitoid larvae reveals a possible explanation for this relationship.

Table 17. *A. bilineata* parasitism of CM pupae in Grant radishes.

Date	n	percent parasitized	corrected percent parasitized
205	36	25.00	15.01
225	131	75.57	62.14
240	5	40.00	26.11

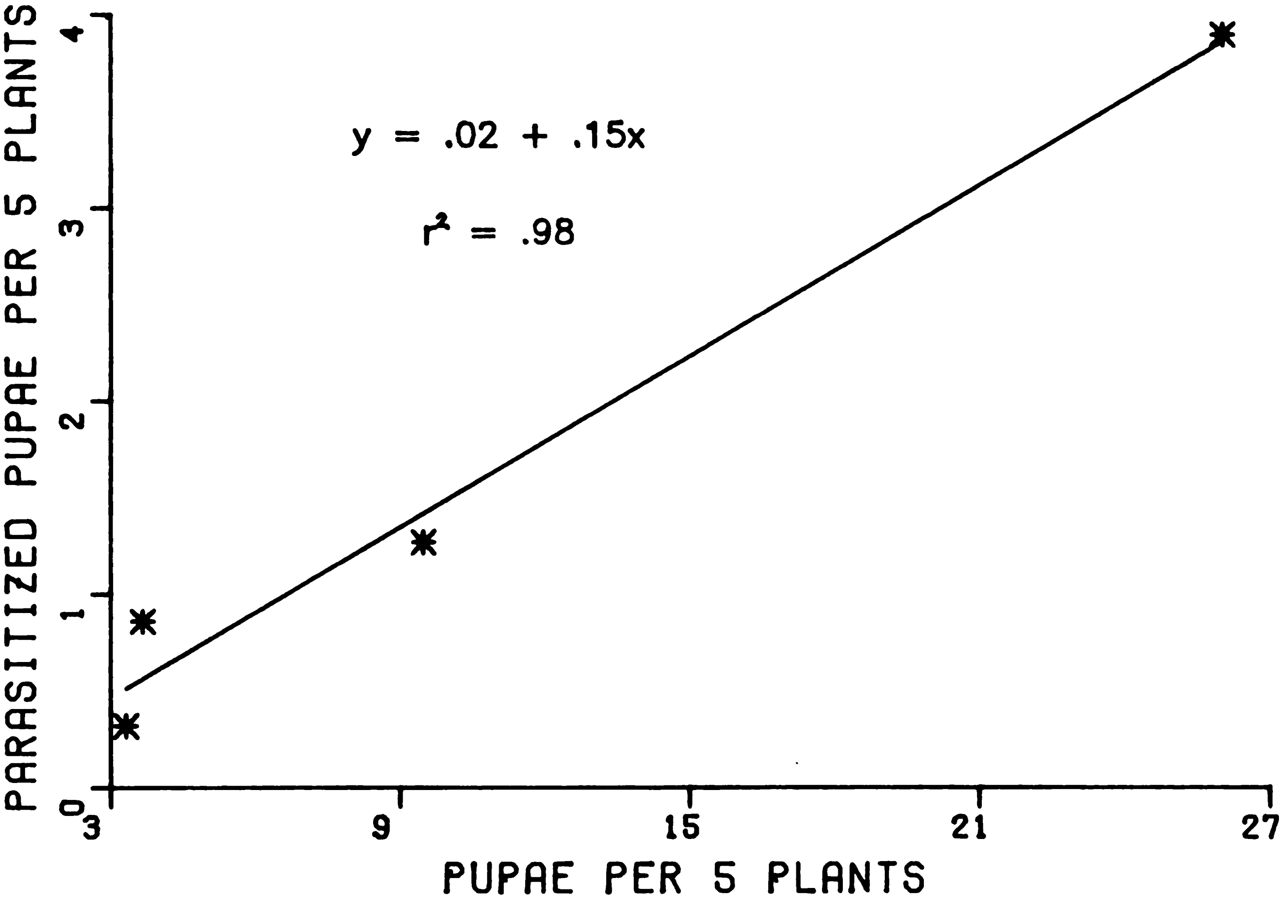


Figure 25. *A. bilineata* parasitism at different host densities.

Bromand (1980) reported that under laboratory conditions, the maximum depth through which a parasitoid larva would burrow in sand to parasitize a pupa was 9.5 cm; in the field, parasitized pupae are not found below 20 cm. He also noted that if two host-pupae are placed in close proximity, one directly above the other, the lower one is seldom parasitized. Even with several parasitoid larvae present, the upper pupa is reattacked. Superparasitism or multiple attacks of the same pupae occurs on both CM (Bromand 1980) and OM (Whitfield 1981), and was prevalent on both hosts in this study. More than a single larva per pupa was much less common.

With the inclusion of two years of data from Bromand (1980) on A. bilineata superparasitism of CM in swede fields in west Jutland, Denmark, and the data from radish plantings at the different research sites in this study (for each site data were pooled over all plots and sample dates), a least squares regression was performed to examine the relationship between the proportion of the host population parasitized and the proportion of the parasitized pupae superparasitized. The same analysis was performed in OM parasitism data for the Eaton Rapids research site and three different fields in the Grant data. (All values represented uncorrected numbers of parasitized individuals sampled.) If the proportion of host parasitized is constant at a given A. bilineata density irrespective of host density, we can assume the differences in the proportion of individuals parasitized represent relative differences in the A. bilineata density. With both hosts, increases in the proportion of pupae parasitized correlated with an increase in superparasitism (CM $r^2=.74$; OM $r^2=.88$; Figures 26 and 27). The regression equation predicted that for CM, the percentage of parasitized pupae superparasitized increased with the percentage of the host population parasitized

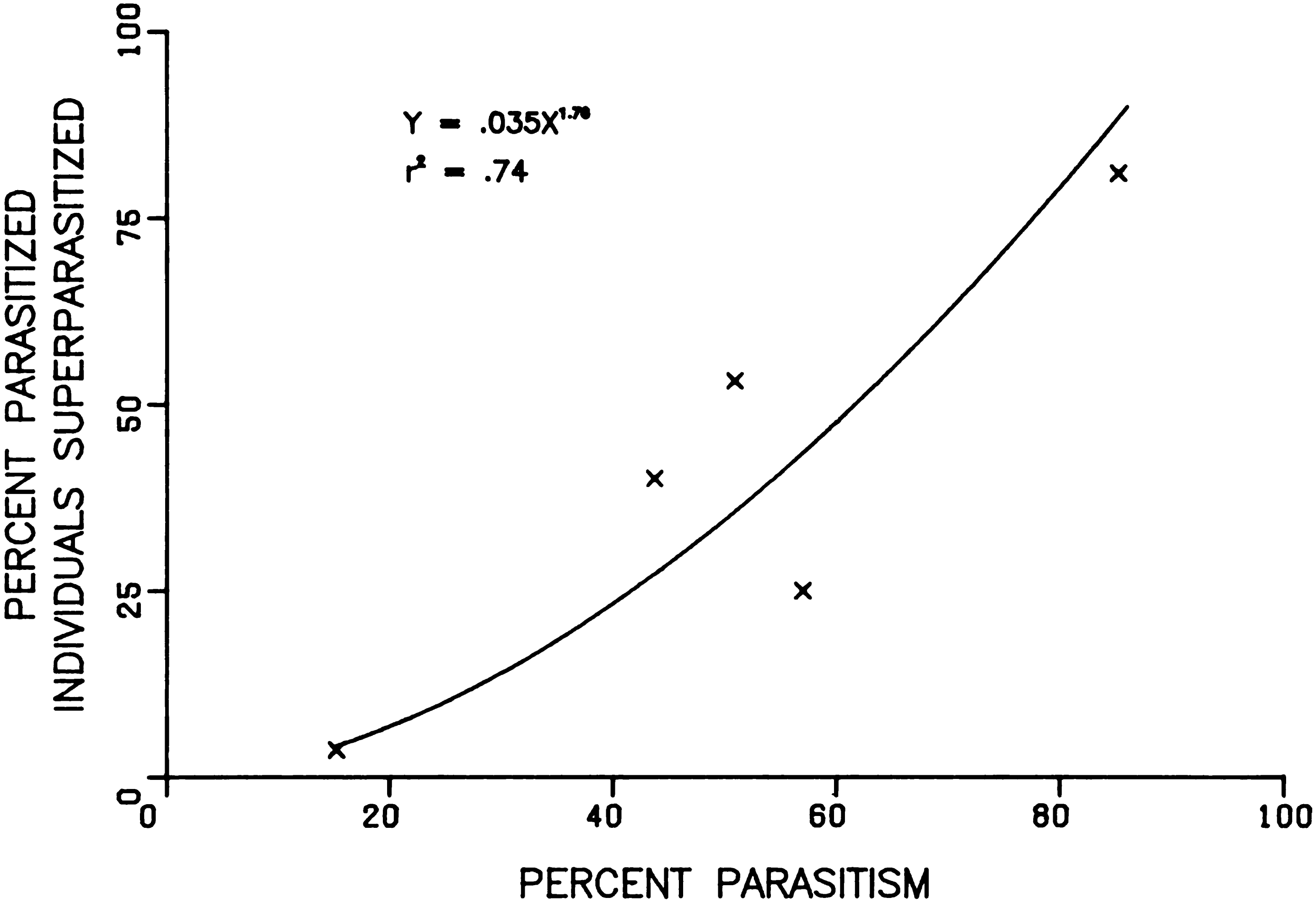


Figure 26. A. bilineata superparasitism of CM pupae.

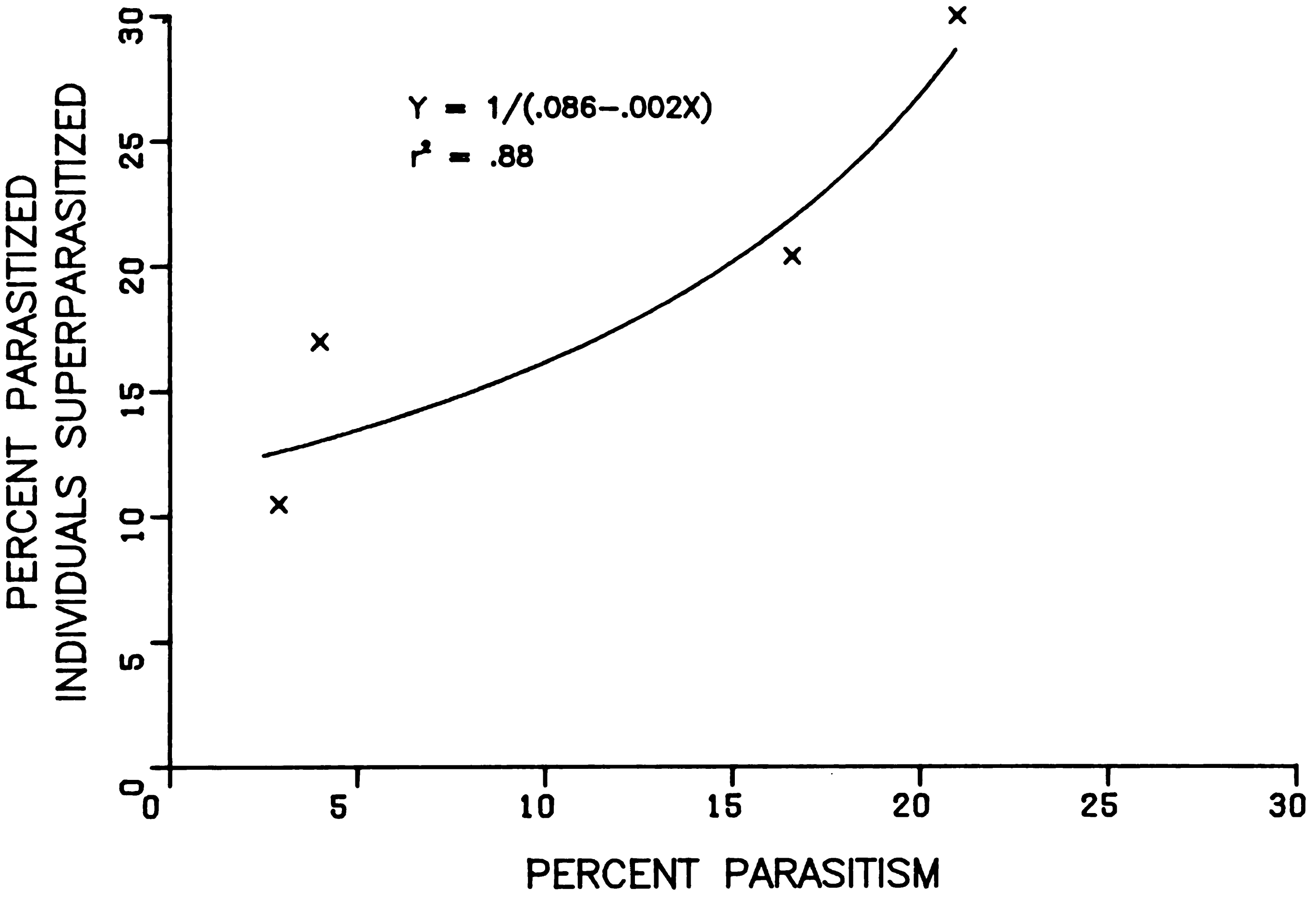


Figure 27. A. bilineata superparasitism of OM pupae.

(A. bilineata density), and at 100% parasitism, 92% of the parasitized pupae would be superparasitized. The relationship between proportion of OM pupae parasitized and percent superparasitism is best described by a curvilinear function, in which at 31% parasitism 100% of the parasitized pupae would be superparasitized. Whitfield's findings (1981) agree with this model. He reported 29% A. bilineata parasitism of OM in a research field in Grant and noted that most of the attacked pupae were superparasitized.

The vertical distributions of CM (Harris et al. 1967) and OM (Carruthers, 1979) pupae in the soil (Figure 28) differ considerably; more CM larvae pupate within the top 2 inches (5.08 cm.) of soil than do OM larvae. Within this shallow zone, pupae are more often attacked by A. bilineata larvae. As a larger proportion of the OM population pupates at a greater depth, a larger proportion is less likely to be attacked, and as A. bilineata populations increase, superparasitism of shallower pupae is more likely to occur.

Read (1962) suggests that parasitoid larvae prefer unparasitized pupae, and that larvae will search the soil for unparasitized rather than enter a previously attacked puparium. However, his experiments were performed in the laboratory with CM pupae buried at a uniform depth. He also examined superparasitism concerning the number of larva entering the puparium--not the multiple attacks on a host puparium. As stated previously, few multiply-attacked pupae had more than one parasitoid within the puparium. Hence, once the larvae gnaws through the puparium, it may detect the presence of the previous attacker.

Multiple attacks result in reduced parasitoid survival. Bromand (1980) found that only 22% of the superparasitized pupae produced A. bilineata adults, whereas in 52% of the singly-attacked pupae parasitoid adults emerged. The

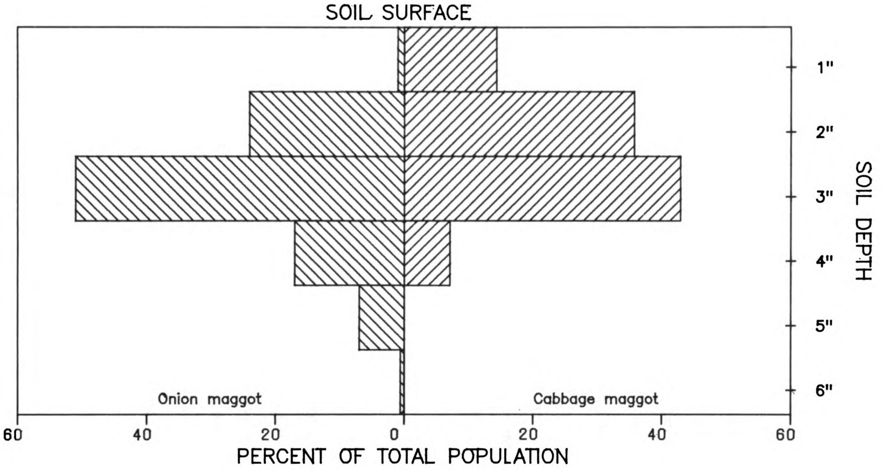


Figure 28. The vertical distributions of OM and CM pupae in the soil. (Data from Carruthers 1979 and Harris et al. 1967.)

increased punctures in the puparium may increase the potential for ingress of fungi or other disease-causing organisms.

More data are necessary to exactly define the curves and limits of parasitism and superparasitism for both host populations. Unless the parasitoid larvae are more adapted than OM pupae to locating CM pupae at the deeper depths, one would expect the relationship between the percentage of the CM population parasitized and the percentage of the parasitized individuals superparasitized, to follow the same trend as that of the OM, and reach 100% superparastism at some limit of parasitism less than 100%. These dynamics are most likely also influenced by soil type and moisture and other factors that impact parasitoid and maggot survival and distribution in the soil. However, these findings indicate that the parasitoid's attack behavior imposes a somewhat dynamic upper limit of parasitism.

FALL DYNAMICS

Materials and Methods

In the late summer and fall of 1979, OM pupae were collected weekly or every other week from onion fields in Eaton Rapids and Grant. Sampling was initiated in Eaton Rapids in early August and continued through mid-October. In Grant, sampling was initiated in mid-September and continued through early November.

In the first week of September, 1980, after harvest, plots of onion culls were monitored for all populations of predators and parasitoids. Experiments were constructed at all three research sites: Grant, Eaton Rapids, and the MSU Muck Farm. Plot of 3m x 5m areas of the fields were cleared of any existing onion culls, and replaced with fresh, non-infested culls, such that any observed OM or natural enemy activity would reflect only the fall dynamics.

In Grant, cull plots were set up in field 1 at varying distances away from the west field border. Three replicates each were placed along the field border abutting the radish plantings, and 75m and 150m into the field from this border. The onion cull types distributed in these plots included whole onions, smashed onions, and cut onions buried for sprouting. Culls were distributed to maintain uniform densities between plots.

In Eaton Rapids, three replicates of cull plots were set up in this same manner in each of the three different onion fields at the research site. Field 1 plots abutted the radish plantings; field 2 plots abutted the oat planting; and field 3 plots were placed in the middle of the field.

At the MSU Muck Farm, the cull plots were designed to examine the effect of different cull types on OM infestations and predator densities. The areas of the first and second summer plantings of Dyfonated radishes and onions were harvested and cleared of debris, but the non-Dyfonate plantings were not disturbed. The 3m x 5m plots consisted of (1) unharvested onions (the non-Dyfonate plantings), (2) unharvested radishes with smashed cull onions, and (3) a harvested area with smashed cull onions. In a harvested onion planting separated from the radish plantings by a windrow of pine trees and considerable distance, another set of plots comparing smashed culls with whole culls were constructed. Each set of comparisons at the Muck Farm was replicated twice.

Square barriers 20 cm deep with sides .5 m in length were constructed out of sheet metal for sampling predator densities in the cull plots. X, Y-coordinates were designated for two adjacent sides of each plot, and numbers were drawn from a random numbers table to determine a random location for each sample. The barrier was placed at each location to define the sample and area, and to trap any predators within this area. Each plot was sampled six times, and the number of culls and number of infested culls per sample were recorded.

The Eaton Rapids plots were sampled on September 19. In the field, the soil within each sample was sifted to a depth of ca. 7 to 8 cm and the number of Carabidae and Staphylinidae were recorded. All culls were replaced after sampling.

The MSU Muck Farm plots were sampled on September 22, and the Grant plots on September 26. The Grant radish plantings were also sampled. At both Grant and the MSU Muck Farm, rather than sifting through the soil in the field, ca. 7 to 8 cm of soil for each sample was collected and returned to the laboratory, where it was held at 5^{o}C until it could be examined. Before examination in the laboratory, each sample was held at 23^{o}C for four to six hours to increase the soil temperature and insect activity, as the insects were more easily located when active. Carabidae and Staphylinidae densities were recorded. No attempts were made to identify predators beyond family.

On October 13, all plots in Grant were examined and the location of OM infested culls within each plot were marked for subsequent pupal sampling. At this time 20 randomly selected onions per plot were examined for A. pallipes and staphylinid adults. (A. pallipes adults searching a cull onion would continue their search as the onion was examined.) Infested onions within the plots at Eaton Rapids were also located and marked in mid October for subsequent pupal sampling, but adult predators and parasitoids were not counted. OM pupal sampling was conducted in all the plots in early November.

Analyses of variance were performed to compare predator and parasitoid densities, cull densities and infestation levels between the treatments at each research site. Kruskal-Wallis non-parametric test was used where variance stabilizing transformations could not be found.

Results and Discussion

Predator and Parasitoid Surveys

Surveys of the onion cull plot in Grant revealed no significant differences in the densities of culls ($F_{3,48}$ = .94) nor the densities of infested culls ($F_{3,48}$ = .78) between the plots at different distances into the onion field. Carabidae densities sampled on September 26 did not differ significantly ($F_{3,52}$ = 1.45) between the plots in the onion field or the radish plantings (Table 18). The mean ground beetle density over the field was .42 beetles per .5 m^2 s_x = .11.

The adult Staphylinidae densities between the different treatments, however, did differ significantly ($F_{3,63}$ = 8.95). The density averaged 2.94 adults per .5 m^2 ($S_{\bar{x}}$ = .47) in the radishes, considerably higher than in any of the onion field plots. The density decreased to a mean of .94 (S_x= .70) adults per .5 m^2 in the adjacent onion culls. Though there was no significant difference in the staphylinids densities between the border onion cull plots and those at 75 and 150 m into the field, the decrease in the mean density with distance from the border may indicate a trend. It is difficult to ascertain whether this trend represents an increase in staphylinid densities with proximity to field borders or infested radishes.

The results from the October survey of the relative abundance of adult staphylinids in the cull plots reflect the same phenomenon (Table 19). Signifi-

Table 18. Predator densities in post harvest cull plots in Grant.

		Density/.5m^2 [1]	
Habitat	Distance from field border (m)	Carabidae Adults	Staphyllinidae Adults
Radishes	0	.60a	2.94a
Onion culls	1	.69a	.94b
Onion culls	75	.25a	.44b
Onion culls	150	.59a	.13b

[1] Those treatments followed by the same letter are not significantly different at the $\alpha = .05$ (Kruskal-Wallis Rank Multiple Comparison Test).

Table 19. The relative abundance of Staphyllinidae and _A_. _pallipes_ adults in post harvest cull plots in Grant.

Distance from border (m)	Staphyllinids x/cull[2]	 x/infested[2] cull	A. pallipes x/plot[1]	 x/infested[1] cull/plot
1	1.03a	.18a	3.00a	.47a
75	.50b	.05b	.67b	.19a
150	.25b	.04b	1.00b	.19a

[1] Treatments followed by the same letter are not significantly different at α = .05 (Duncan's Multiple Range Test).

[2] Treatments followed by the same letter are not significantly different at α = .05 (Kruskal-Wallis Rank Multiple Comparison test).

cantly more staphylinid adults were encountered in the cull plots adjacent to the border than those at 75 m and 100 m into the field. The observed densities did not differ significantly between 75 m and 100 m, but the decreasing means with distance follow the same trend as that of the previous survey.

The relative number of A. pallipes adults per plot was also significantly larger ($F_{2,5}$ = 6.76) in the plots adjacent to the field border than those at 75 and 100 m. However, when analyzed relative to the number of infested onions per plot, this difference is not significant ($F_{2,5}$ = .75), though the same trend of increased density with proximity to the field border is indicated.

The predator survey in Eaton Rapids resulted in too few insects recovered to warrant analysis. The total infested culls encountered from 18 samples per treatment ranged from two to seven. The total staphylinids recovered ranged from five to eight per treatment, and total carabids ranged from three to six. It is possible that delaying the survey until later in the fall may have yielded greater densities if more OM oviposition occurred. However, considerable OM oviposition was observed prior to the sample date on cull onions in an adjacent grower's field.

In the plots in field 1 at the MSU Muck Farm representing different strategies for cull management (smashed culls within radishes, smashed culls in a harvested onion planting, and unharvested onions), no significant differences in staphylinid ($F_{2,13}$ = .45) or carabid ($F_{2,13}$ = .81) densities were detected between the treatments. There were no differences in cull densities or infested cull densities between treatments either. The mean staphylinid density over all treatments was 1.68 per .5 m^2 ($S_{\bar{x}}$ = .55), and carabid densities averaged .57 per .5 m^2. The plots designed to test differences between these treatments may have been too small and too close to one another to reflect differences in predator densities as a result of the cull management strategies. OMs and predators drawn to the vicinity of one habitat type may have increased the densities in the adjacent habitats.

When comparing predator densities between the plots associated with radishes (field 1) and those not (field 2), no significant differences between staphylinid densities emerge. Significantly more carabids were found in field one than field two ($F_{1,55} = 4.3$). However, the number of OM infested culls is also significantly higher ($F_{1,63} = 11.25$) in field 1 plots. The carabid density per infested cull is greater in field 2 plots (2.10 per infested cull) than those in field 1 (.73 per infested cull).

It is difficult to ascertain whether the difference in OM densities between the two areas at the Muck Farm reflects any influence of the radish planting or summer OM infestations in these areas. OM damage reached 50% in the first non-Dyfonate planting in field one. The field 2 planting was not sampled throughout the growing season for OM damage (it was treated with Dyfonate at planting and received several foliar spray applications throughout the season), and it is doubtful that it supported an OM population equivalent to field 1.

Parasitism

From the OM pupae collected in the late summer and fall of 1979, only 2 out of 105 pupae collected on September 21 in Eaton Rapids were parasitized by A. pallipes, and 5 out of 107 collected in Grant on October 26. However, a considerable number of A. bilineata parasitized pupae were collected through the sampling period (Table 20).

Table 20. *A. bilineata* parasitism of fall collected OM pupae in 1979.

	Eaton Rapids		Grant	
Collected	n	% parasitism	n	% parasitism
Aug 1 - Aug 15	93	1	-	
Aug 16 - Aug 31	160	5	-	-
Sept 1 - Sept 15	73	5	-	-
Sept 16 - Sept 30	132	11	66	32
Oct 1 - Oct 15	100	27	126	35
Oct 16 - Oct 31	-	-	224	21

Of the 300 OM pupae collected from the fall cull plots in the three research sites in 1980, only three were parasitized by A. bilineata. A. pallipes predominated fall parasitism. In Grant, OM pupae were collected in the soil samples for the predator survey in September 26 and November 15. The total A. pallipes parasitism pooled over the two sample dates was 30%.

The pupae collected on September 26 were recovered from six randomly selected soil samples in each plot. Percent parasitism was calculated for each sample with pupae. The mean percent parasitism over each treatment (distance from the border) was then calculated.

The pupae collected on November 15 originated from infested onions located in mid October. The total pupae recovered per plot were pooled while sampling. The mean percent parasitism per treatment was calculated over the percentages per plot. A. pallipes parasitism of OM did not differ significantly with distance from the field border in the early fall sample (Table 21). However, in the November sample, significantly more parasitism occurred in the cull plots adjacent to the field border than in those at 75 or 100 m into the field.

Some of the OM pupae collected in late September represent parasitoid dynamics occurring preharvest. In September, temperatures were not high enough to allow individuals to develop from oviposition to pupation in the three weeks during which the cull plots were established. The ground cover afforded by mature onions preharvest is considerably different from that available after harvest. This may partially explain why this earlier sample did not represent the spatial trends in A. pallipes activity observed in later and previous surveys.

Of the 89 post-harvest OM pupae collected in Eaton Rapids in November, 15% were parasitized by A. pallipes. There were no significant differences in

Table 21. *A. pallipes* parasitism of OM in post harvest cull plots.

Distance from field border (m)	September 26 % parasitized n	$\bar{x}$	$s_{\bar{x}}$	November 15 % parasitized n	$\bar{x}$	$s_{\bar{x}}$
1	13	32.9	.75	78	37.8	3.0
75	13	12.5	3.47	27	9.5	1.7
150	29	26.2	.41	24	10.2	1.9

parasitism levels between the three fields sampled, and no significant correlation between parasitism and pupa density per plot. A. bilineata parasitism was not detected.

OM pupae at the MSU Muck Farm were sampled coincidental with the predator survey in September 22. Only 19 pupae were recovered, of which 9 (47%) were parasitized by A. pallipes, and 2 by A. bilineata. Sixteen out of the 19 pupae (84%) were recovered from plots in field 1. Only three pupae (no parasitized individuals) were collected in the plots in field 2.

A. PALLIPES ACTIVITY IN AND ABOUT PASTURES AND ONION FIELDS

A. pallipes' activity on fresh dung in two active cow pastures in close association with onion production was monitored periodically throughout the growing season. One pasture in the Eaton Rapids research area was several acres in size and supported only six beef cows. The other pasture in Grant was of comparable size but supported 17 beef cows. Parasitoid activity was monitored once or twice a month from June through September by observing the number of A. pallipes adults searching a fresh pat during a three minute period. Five fresh pats per pasture were examined on each sample date. All observations were made during clear warm weather about mid day. Searching A. pallipes adults were aspirated from fresh dung at both sites and sent along with parasitoids emerging from OM pupae to Dr. L. E. Caltagirone, Division of Biological Control, University of California, Berkeley.

Little A. pallipes activity was observed in onion fields throughout the growing season; however, these parasitoids were active on maggot-infested culls left in the field after the onion harvest. Therefore, A. pallipes field experiments were conducted after harvest.

Materials and Methods

In the fall of 1979 in Grant, Michigan, plots of five maggot-infested onions placed within a 1 x 1 m area were used to monitor parasitoid ovipositional activity in an active cow pasture and at varying distances into an adjacent onion field. Plots were also placed in the center of two other onion fields: one with weed cover, the other without. Maggot-infested onions were collected in August from a commercial onion field and held at 10°C for 3 weeks to retard development. When set out for this experiment, most maggots had developed to 2nd and 3rd instars. No attempt was made to manipulate the number of maggots per onion, so as not to disrupt the within-onion distribution of maggots. Onions with about the same level of infestation were chosen for the study. Forty maggot-infested onions were held at 23°C in the laboratory for a control. At pupation, the pupae were examined for a base parasitism level.

Three replicate plots of five onions were placed in the pasture, within the weedy border separating the pasture and the adjacent onion field, at 15, 30, 60 m (50, 100 and 200 ft) into the field from the border edge, and in the center of the other two fields. The onions were left for 10 days, after which they were collected with ca. 0.1 x 0.1 m (0.33 ft^3) volume of soil immmediately under the onion. The samples were held for 5 days at 23°C after which time it was assumed that all maggots originally placed in the field had pupated; however, any OM eggs would not have completed development. Samples were sifted for pupae and the pupae were examined for parasitism. Percent parasitism was then determined for each plot. An analysis of variance was performed to determine any differences in parasitism levels between the different areas tested.

In 1980, A. pallipes post-harvest activity was monitored and compared between different onion field border habitats and one active cow pasture. Of the five field borders monitored, four represented the outer borders of the Grant Swamp onion-growing area, two of which abutted active cow pastures, and two abutted wooded areas. The remaining field border was in the center of the Grant Swamp, separating two adjacent onion fields.

The methodology for obtaining a relative measure of parasitoid activity used the previous year was used for sampling activity between the borders. However, for this study, OM eggs were collected from culls in a commercial onion field after harvest in early September. The eggs were held at 23°C for two and a half weeks, by which time most of the maggots had developed to 2nd and 3rd instars. Three replicate plots of five maggot-infested onions were set in each of the five field borders and the pasture in late September and were collected seven days later with the soil immediately under the onion. The samples were held at 23°C for five days before the pupae were extracted and examined for parasitism. An analysis of covariance (arc sine transformation) was performed with OM density per onion as the covariate to determine any difference in percent parasitism between borders.

Results and Discussion

Given the infrequency of sampling and the tremendous difference in the densities of dung pats, the abundance of the parasitoids in the two pastures cannot be estimated. However, it is important to note that A. pallipes was active on fresh dung in both the Eaton Rapids and the Grant pastures throughout the sample period (Table 22). Parasitoid activity dramatically increased in the Grant pasture in September. Turner et al. (1968) reported the greatest

Table 22. *A. pallipes* activity in fresh dung in pastures abutting onion fields, 1980.

Month	A. pallipes adults[1] per 3 minutes Eaton Rapids	 Grant
June	1.8 (.73[2])	3.1 (.71)
July	2.6 (.51)	--
August	1.3 (.42)	3.0 (.77)
September	2.4 (.87)	45.2 (8.62)

[1] Mean number of parasitoid adults searching a fresh pat during a three minute period; n=5.

[2] Standard error

emergence of parasitoids attacking Ravinia species in Virginia to occur at the end of September; it probably occurs a bit earlier in Michigan.

Parasitoids collected from the pasture habitat and the onion habitat were identified as A. pallipes by Dr. Caltagirone, based on the key developed by Dr. Robert Wharton (1977) and comparisons with museum type specimens.

In 1979, base parasitism determined from 385 pupae held in laboratory was less than 0.5%. Figure 29 depicts the levels of parasitism found in the field abutting the pasture. The highest level of parasitoid activity was observed in the field border adjacent to the cow pasture, averaging 75%, but going as high as 96%. Parasitoid activity in the border differed significantly from the other treatments. Relatively high levels of parasitoid activity were also observed in the pasture and in the field within 30 m (100 ft) of the field border. Beyond 30 m, parasitism levels dropped. Significantly higher levels of parasitism were observed than in the other fields devoid of weeds (Table 23).

The 1980 results comparing percent A. pallipes parasitism of OM in different field borders suggest no differences in parasitoid activity between the field borders or the pasture (Figure 30). With a mean of 130 pupae recovered per border (ranging from 50 to 200), parasitism ranged from 7.22 to 22.5%. Unlike the results from the previous year, parasitism in the 1980 experiment did appear to vary with OM densities.

Table 23. Parasitism by A. pallipes on trap crop planted in different habitat types (post-harvest).

Habitat Type	% Parasitism
Pasture border	75.00
Pasture	32.00
Center of onion field: no cover	5.67
Center of onion field: cover	22.00

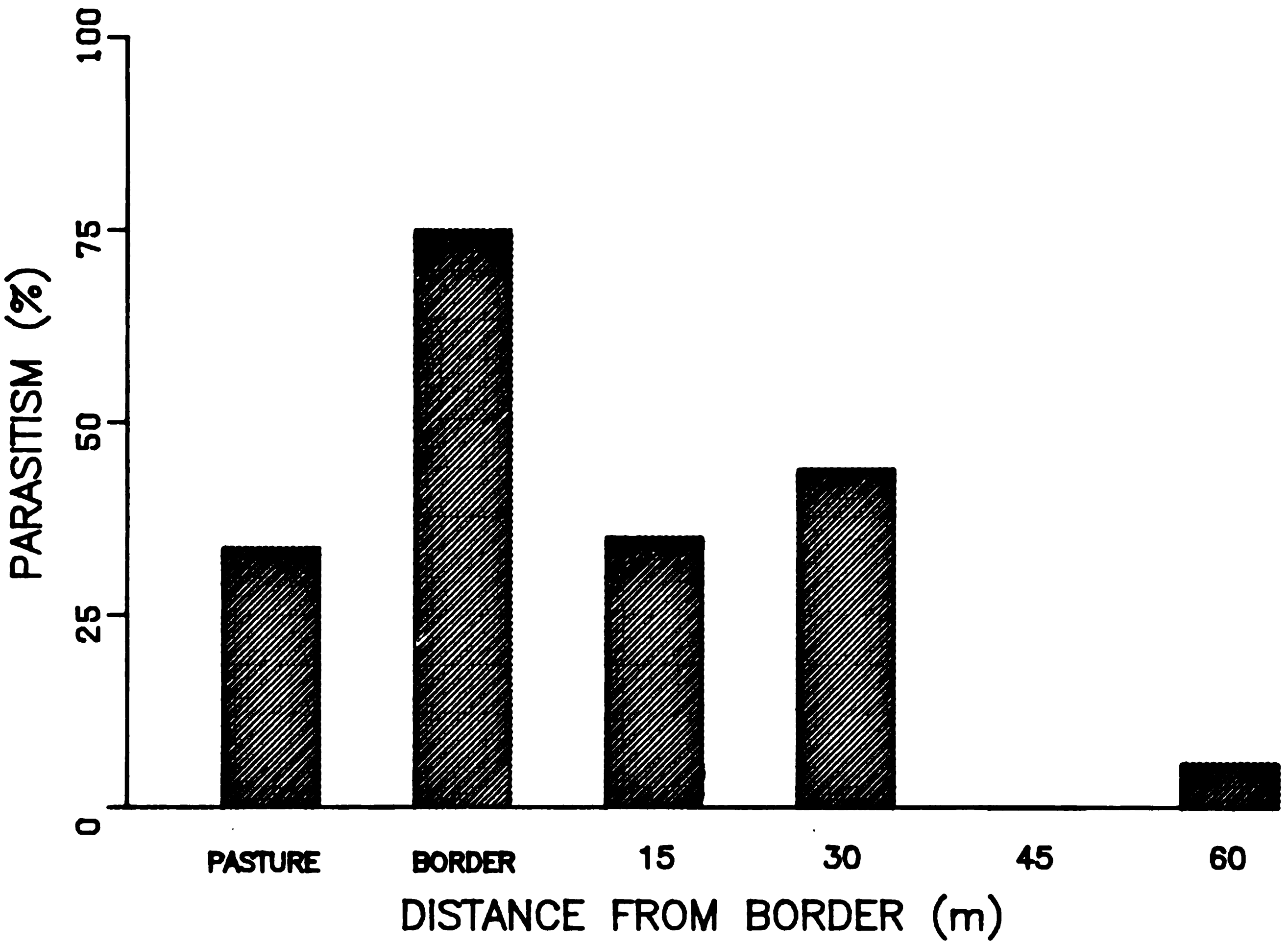


Figure 29. A. pallipes post-harvest activity in relation to the onion field border.

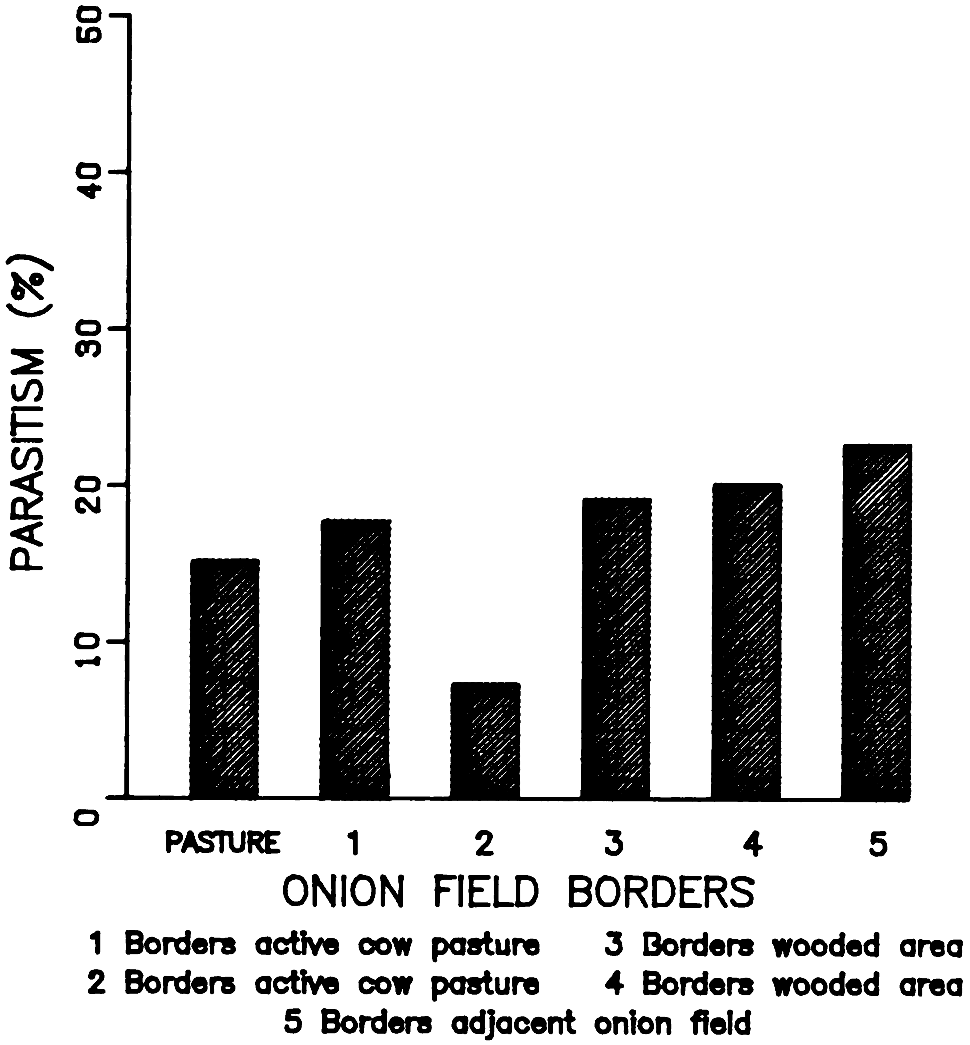


Figure 30. A. pallipes post-harvest activity in different onion field borders in Grant, 1980.

DISCUSSION

THE INFLUENCE OF PLANTING DATE ON ROOT MAGGOT INFESTATIONS

Planting date greatly influenced OM infestations. OM damage decreased significantly with each weeks' delay of planting. Gary (1922) showed that early sown onions are most heavily infested, and later-sown onions are not damaged until the end of the first generation. However, the meaning of early and late planting is not clear from this report, nor if the early planting was in the vicinity of the later.

First generation OM oviposition continued in the Muck Farm onion plots through late June. Due to the late planting date, the third and fourth onion plantings missed the major portion of the OM oviposition period. The second planting, however, was at a susceptible stage when OM damage was initiated, yet the flies appeared to prefer the earlier planting. Threherne and Ruhmann (1922) reported that OM are more attracted to the more vigorously growing plants. With the greater leaf tissue of the earlier planted onions, growth was likely more vigorous. Once damage was initiated, as flies were attracted to previously damaged onions, the earlier plants continued to accumulate most of the egg load. This pattern continued through the second generation.

As the plants were susceptible, without the earlier planting the second onion planting probably would have experienced a heavier OM infestation. It cannot be concluded that delayed planting alone (unless delayed through most of the OM oviposition period) will reduce OM damage. Yet early-planted onions may be extremely valuable as a trap crop.

The research plots used for this study were very small relative to a commercial onion field. As any point attractant for the adult fly is limited by the range of fly dispersal, before early sown onions can be used as a trap crop for OM, more research must be focused on the scale where this method would be effective.

CM infestations in radish plantings also varied with planting date, reflecting a known preference for older plants (Ellis et al. 1979). Yet, it can be seen from the heavy infestations of CM in late sown radishes in both Eaton Rapids and Grant that delayed planting alone does not reduce infestations. Planting date, however, does influence the timing of CM infestations, and hence its availability to parasitoids.

A. BILINEATA SYNCHRONY WITH ITS HOSTS

Aleochara adults emerged about mid to late June. With a preoviposition period of two to three days (Colhoun 1953) and five days to egg hatch, parasitizing larvae usually are not active until late June and early July. Peak pupation of first generation CM in the earliest radish planting occurred about June 23 (degree day, base 6.1° C). A. bilineata parasitism was not detected in this plot until June 27.

Parasitoid activity appeared to be better synchronized with pupation of CM in the second radish planting. The seasonal proportion of individuals parasitized and total production of parasitoids was greater in the first than second planting. Yet without the influence of the earlier planting, infestation levels and parasitism may have been greater in the later, as they were in Eaton Rapids and Grant.

When examining the synchrony of parasitoid activity with the CM population, it is important to address the temporal distribution of the target host, the OM (Figure 31). The OM with peak pupation in early July is well synchronized with Aleochara parasitoid activity. Emerging adult Aleochara seek a food source in the form of dipteran eggs and larvae and randomly deposit their eggs in the process. As the OM pupate, the food source declines. The timing of CM infestations at the Muck Farm indicate that second generation oviposition activity in radishes begins about this time. The temporal distributions of these organisms is dynamic as development is tied to temperature. Yet in 1980, second and third generation CM oviposition in radishes roughly synchronized with first and second generation OM pupation (Figure 32). Interplanting radishes with onions may increase the food supply for adult Aleochara and hence increase the parasitoid abundance in onions.

Aleochara females are long lived (average 45 to 50 days in the laboratory) (Colhoun 1953, Bromand 1980) and produce eggs during their entire life. Overlapping generations of Aleochara most likely occur, and dependent on host availability more than on the parasitoid availability. With CM pupation occurring between that of the OM (Figure 33), a continuous supply of hosts would be available to parasitizing larvae, resulting in a greater production of Aleochara in the system.

General predator populations were greater within the radish plantings than the onions. This may reflect a more favorable microhabitat afforded by the radishes. Temperatures were cooler and fluctuated less within the radish canopy than within the onions (Figure 34). The broad leaves and growth habit of the radish provides greater protection from solar radiation and maintains higher

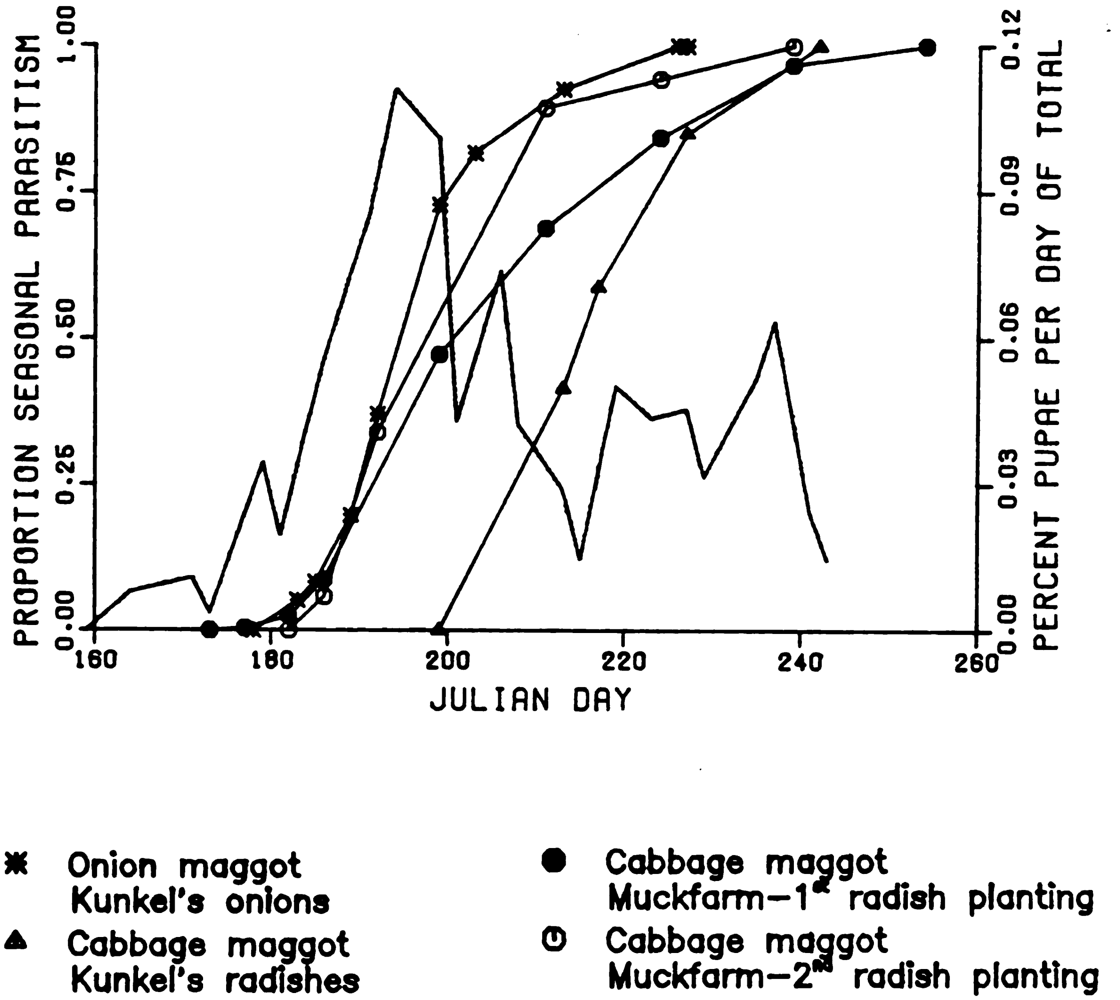


Figure 31. The rate of A. bilineata parasitism of CM and OM in reference to the seasonal abundance of OM pupae.

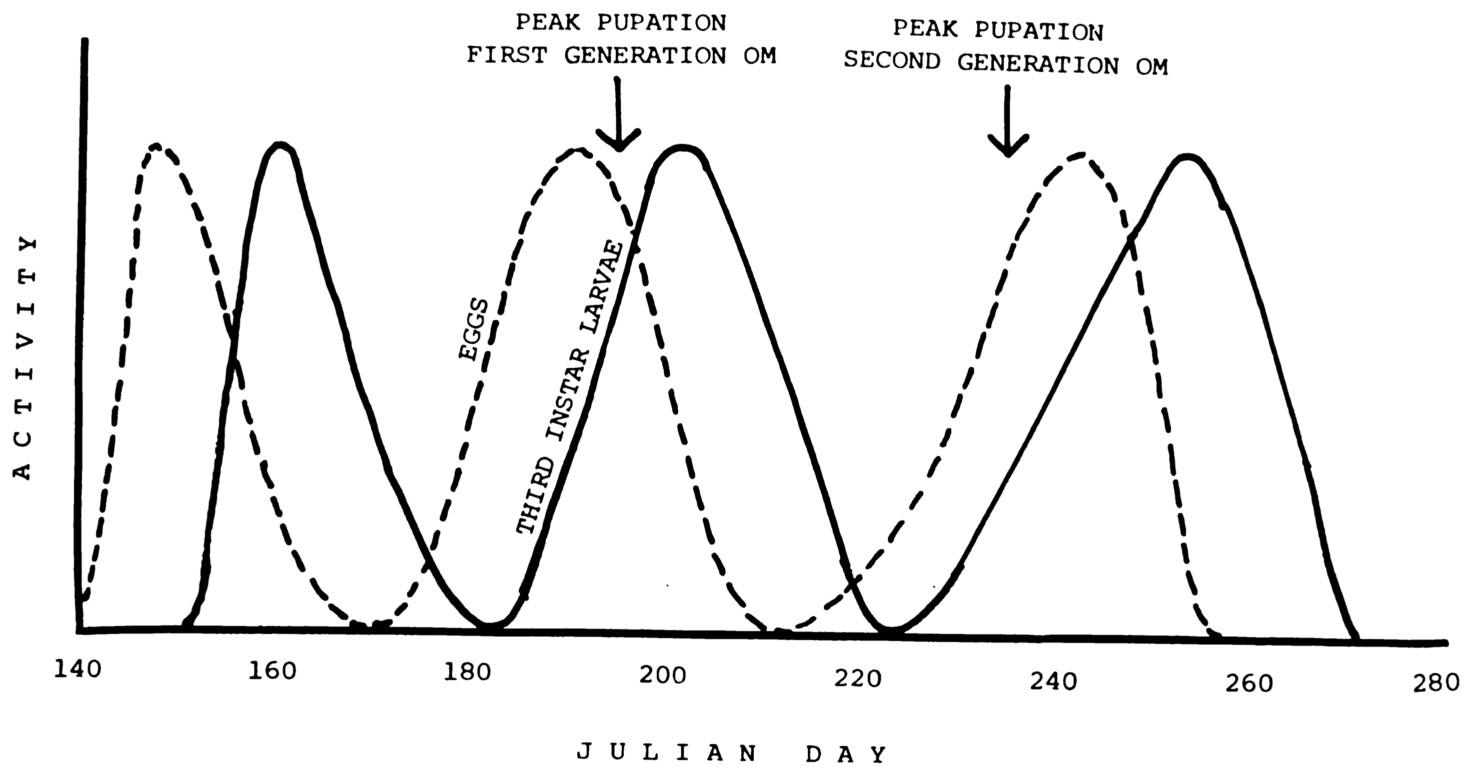


Figure 32. Seasonal CM egg and larval activity on radishes relative to OM pupation.

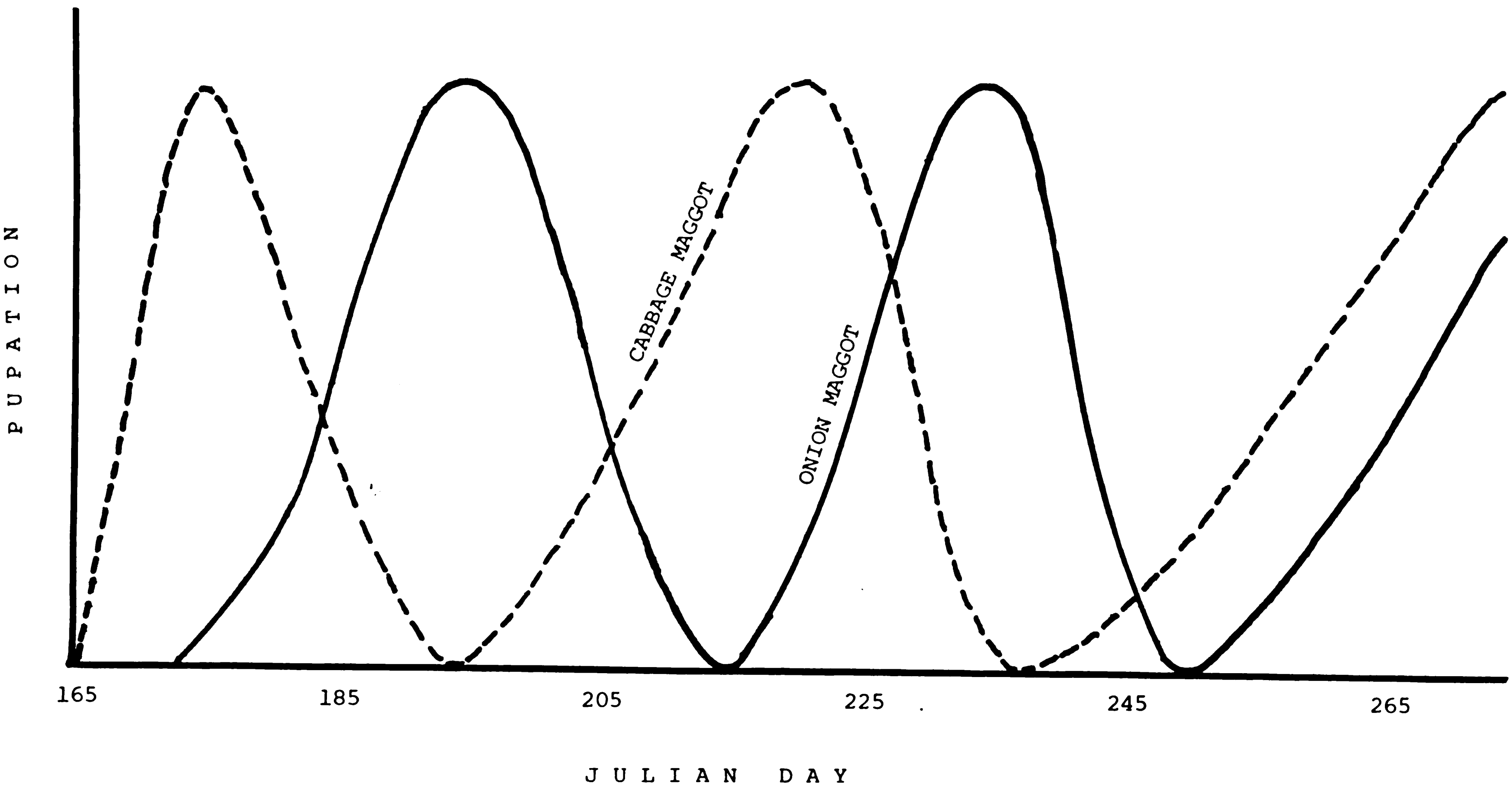


Figure 33. Timing of CM pupation relative to OM pupation.

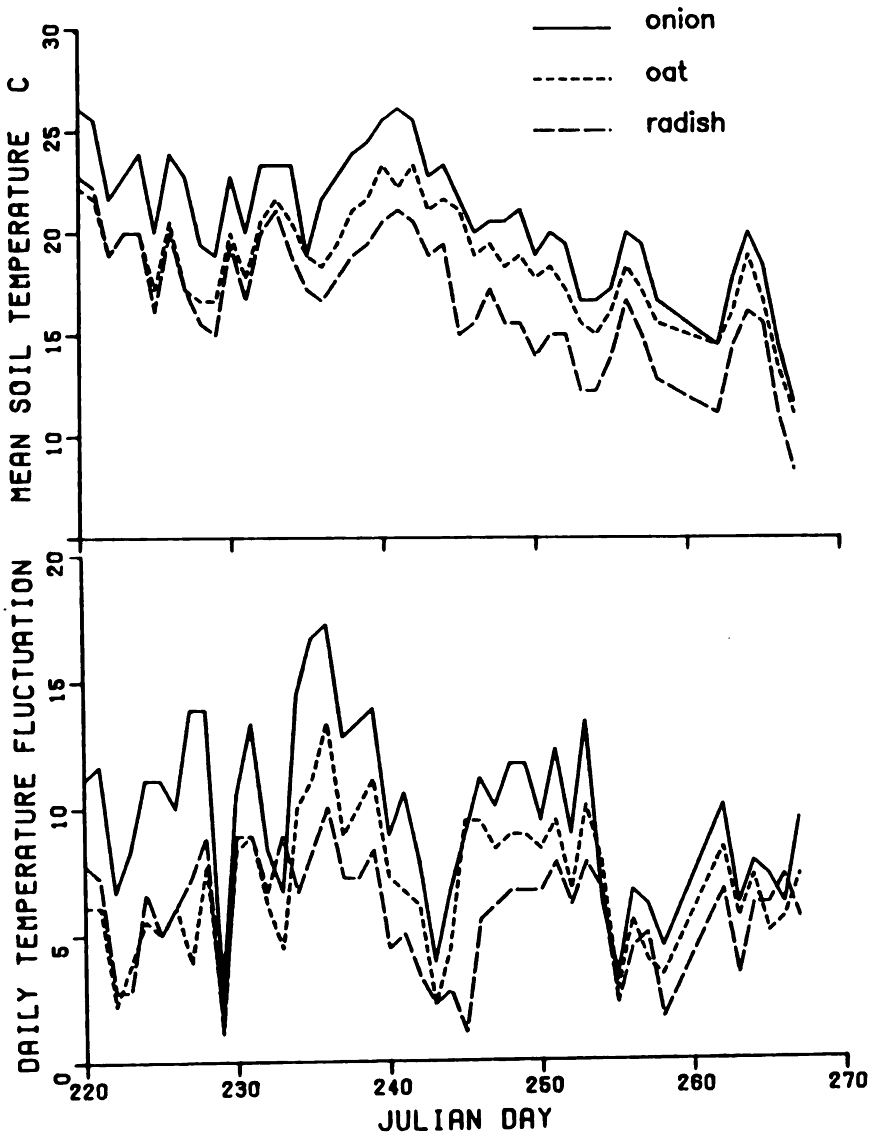


Figure 34 a-b. Soil temperatures at a depth of 3 cm under the onion, radish and oat canopies.

moisture conditions than the onion plant. Oviposition preference experiments indicated that A. bilineata may be attracted to radishes (perhaps all crucifers) by some chemoattractant. If this is true, strip planting of radishes with onions may not increase A. bilineata abundance in onions. A more effective strategy may be to interplant radishes with onions in a 5% radish to 95% onion mixture. With this design radishes could be weeded out of the field before the onion harvest.

LIMITATIONS ON A. BILINEATA PARASITISM

Foliar applications of insecticides significantly reduced parasitism by A. bilineata. Parasitoids may not be significantly affected by a soil granular insecticide at planting due to their late emergence. However, a soil granular would reduce alternate host infestations in radish.

Superparasitism and the refuge afforded OM pupae in depth appear to limit Aleochara parasitism. Yet, A. bilineata's potential for biological control of the OM in an integrated management program should not be underestimated. Aleochara exerts a double mortality factor on the OM through predation by adults and parasitism by the larvae. Maximizing both these interactions should be the focus of any management program for this species.

FALL DYNAMICS

The pupae collected in the fall plots in 1980 represented the dynamics of individuals pupating after October 1. The plots were cleared of infested culls in early September, and the degree days required to complete larval development for individuals oviposited after this time would not have accumulated until the end of September.

The October 1979 pupal samples represent parasitoid activity in October combined with that occurring earlier. As the proportion of individuals parasitized increased through mid-October, and no healthy flies were emerging at this time, it can be assumed that the parasitoids were still active.

The fall of 1979 in Michigan was particularly warm. From mid-September to mid-October, 104 degree days (base 10^{o} C) accumulated in 1979, whereas only 84 degree days accumulated over the same time period in 1980. The rate of degree day accumulation in the last week in September 1980 was 2.77 per day, less than half the rate during that week the previous year. A. bilineata eggs laid in the last week in September 1980 would not accumulate enough degree days to hatch by November 1, whereas those laid at the same time in 1979 would hatch by the end of the first week in October. As the parasitoid larvae live an average of 8.7 days under optimal laboratory conditions, it is unlikely that much A. bilineata parasitoid activity occurred in the fall of 1980, as the pupal samples reflect. In 1979 percent parasitism began declining by the second week in October. At this time, the rate of degree day accumulation had dropped to less than one per day. The impact of A. bilineata parasitism in the overwintering generation of OM is probably associated with the temperatures in late September and October.

As Aphaereta activity in onion fields increases dramatically after harvest, warm years leading to a lengthened period of Aleochara activity may increase interference between these two species of parasitoid. Not enough is understood about the association between the two parasitoids. Preliminary studies indicate that Aleochara may select against Aphaereta-parasitized OM. During most years there may not be much overlap in the temporal distributions of the two parasitoids in onions. In 1979 and 1980 little A. pallipes activity was detected within onion fields until after harvest. A. pallipes is highly susceptible to several herbicides, insecticides, and fungicides used in onion production (Carruthers 1981). Yet the braconid's activity was not detected in the research sites in Eaton Rapids receiving no pesticide inputs through most of the growing season.

A. pallipes may be limited by the inaccessibility of the maggots throughout the growing season. A. pallipes abundance in onion fields post harvest could also be related to the dynamics of its alternate hosts in dung pats. A. pallipes' two major hosts in dung overwinter as adults (Hammer 1941, Mohr 1943), and it has been shown that later in the season A. pallipes adults are incapable of emerging from Ravinia species, the two common hosts that overwinter as pupae (Turner et al. 1968). Selection pressure may favor dispersal of A. pallipes from the pasture habitat in the late season to increase overwintering survival. The temporal dynamics of A. pallipes and its hosts in fresh dung requires more investigation to understand any association it may have with the onion agroecosystem.

SPATIAL DISTRIBUTION OF A. PALLIPES AFTER HARVEST

In both 1979 and 1980 A. pallipes was more abundant in the vicinity of the field borders. One hypothesis is that the tall, dense border vegetation affords refuge for these parasitoids from higher temperatures, lower relative humidity, and greater air movement than would be experienced in the center of a field. The significantly higher parasitism levels observed in the center of the weedy field when compared with that of non-weedy fields may reflect the same relationship. Townes (1957) suggests the same hypothesis for most parasitoids in cultivated areas.

As abiotic stresses, particularly temperature and relative humidity, may not be critical in the fall in Michigan, perhaps a more important factor influencing the spatial distribution of A. pallipes is the availability of food for adult parasitoids in non-cultivated field borders. The study on different diets in the longevity of A. pallipes revealed a three-fold increase in adult longevity with a carbohydrate source. These parasitoids were not able to obtain carbohydrates from onions--the only source available within commercial onion fields--either during the growing season or after harvest. Hence, parasitoid activity in and about onion field borders may result from their necessity to find food.

Nearness to an active cow pasture did not influence parasitism in onion field borders. This does not necessarily indicate the lack of importance of the pasture habitat as a reservoir for the parasitoids. It may reflect the parasitoid's ability to disperse throughout the Grant onion growing area. A. pallipes was not active in onion fields throughout the growing season, yet post harvest parasitism reached 30% in Grant, which means the population must be maintaining itself on an alternate host.

CROP DIVERSITY AND PEST MANAGEMENT

Historically, most research has been directed at intercropping and crop diversity in agricultural systems as it affects insect pests and their natural enemies (Cromartie 1981). However, intercropping is rarely practiced. Recent research addressing the ecological factors responsible for increased insect pest outbreaks in monocultures versus polycultures have lead to the development of two separate hypotheses: the "Enemies Hypothesis" and the "Resource Concentration Hypothesis" (Risch 1981). The former states that the increased abundance of predators and parasitoids in a diverse ecosystem can better control herbivore populations (Pimentel 1961). Habitat diversity provides nectar and other food sources for natural enemies, enhances cover from abiotic stresses, and alternate hosts to aid in the synchrony and build up of natural enemy populations for target pests.

The later hypothesis concerns differences in the herbivores' ability to colonize and exploit diverse versus uniform food resources. The diverse habitat interferes with the visual (Kennedy et al. 1959a,b, Smith 1969, 1976) and chemical orientation (Feeny 1976, Tahranainen and Root 1972, Root 1973) to their host plants, as well as sometimes providing a physical barrier. The behavior of herbivores in pure stands is altered such that they are less likely to emigrate (Risch 1981).

The research regarding the behavior of herbivores orienting and utilizing polycultures and monocultures has tremendous implications for designing more stable agroecosystems. However, due to the varying results of natural enemies on pests in these research studies, the tendency has been to devalue this factor in support of the "Resource Concentration Hypothesis."

When evaluating the influence of natural enemies within different cropping patterns, the scale of agricultural systems must be kept in perspective. Most studies, concluding that natural enemy populations do not differ significantly with different cropping patterns (Smith 1969, Theunissen and den Ouden 1980, Tahvanainen and Root 1972, Root 1973, Risch 1981) were conducted on extremely small scales relative to most current agricultural systems. Microhabitat requirements influence the spatial distribution of predators and parasitoids. The availability of hosts also governs spatial distribution. Therefore, the dispersal ability of natural enemies and their daily range of activity must be understood before these studies can be used to interpret natural enemy dynamics in agricultural systems.

A. pallipes adults demonstrated a definite affinity for field borders, yet parasitoid activity did not significantly decrease with the range of 30 m from the border. In small experimental plots, this may not be detectable, but in the average one acre onion field it limits parasitoid activity. The spatial aspects of natural enemy distributions about agroecosystems and the factors influencing these distributions must be understood if we are to design more stable systems utilizing all the ecological constraints on pest populations.

SUMMARY

Overwintering OM parasitoids emerged as adults after most of the early season OM damage had occurred. OM damage was, however, dramatically reduced with delayed planting. The early plantings probably acted as a trap crop, drawing flies away from the later plantings.

A. bilineata was the most important parasitoid of the OM throughout the growing season in each of the research areas. A. bilineata was also the predominant parasitoid of CM in radish plantings. Radishes were readily infested by CM, resulting in 100% damage in most plantings. Second and third generation CM oviposition was roughly synchronous with first and second generation OM pupation. Interplanting radishes with onions may provide a continuous food source for A. bilineata adults and hosts for parasitizing larvae.

A. bilineata parasitoids required more time to complete development than either of its hosts. Parasitized pupae remained in the soil longer and were more likely to be redundantly sampled. It was important to correct for the bias this imposed on the data before interpreting the impact of this parasitoid on the host population. The seasonal incidence of parasitized pupae was computed relative to the parasitoid's developmental time and the non-parasitized pupae relative to that of the host. The ratio of parasitized and non-parasitized pupae gave the corrected proportion parasitized for the host population.

The proportion of A. bilineata parasitized pupae did not appear to vary with host density. It was hypothesized that as parasitoid activity was greatest in the first 5 to 7 cm of soil a constant proportion of the host population pupating at deeper levels usually escaped attack. As OM generally pupated deeper than

CM, this protected portion of the population would be larger for this species. *A. bilineata* superparasitism was common in radish plantings with a high density of parasitoids relative to hosts. It was predicted that superparasitism increased with increased parasitoid densities reaching 100% at some level of parasitism less than 100% due to the refuge afforded the host in depth.

A. bilineata parasitism of overwintering third generation OM pupae varied greatly from 1979 to 1980. This was attributed to a sharp decline in the rate of degree day accumulation in the end of September 1980 as compared to 1979. Low temperatures could have reduced *A. bilineata* egg hatch, accounting for the reduction in *A. bilineata* parasitoid activity. Hence, late September and October temperatures may determine the impact *A. bilineata* parasitoids have on overwintering OM.

A. pallipes activity about onion fields in all three research sites was minimal throughout most of the growing season. Yet its post-harvest activity about cull onions resulted in up to 30% parasitism of overwintering OM pupae. *A. pallipes* activity on fresh dung was observed from June through September. It was hypothesized that during the growing season this habitat may serve as a reservoir for these parasitoids which then diapause into onion fields after harvest. There was no difference in *A. pallipes* parasitism of a trap crop in onion field borders abutting active cow pastures and those abutting wooded areas. This may reflect the ability of this parasitoid to disperse.

The distribution of *A. pallipes* post-harvest activity about onion fields showed a strong association with grassy field borders. Parasitoid activity decreased significantly beyond 30 m into the onion field from the field border. Staphylinid adults reflected the same trend.

Laboratory experiments demonstrated that *A. pallipes* adult longevity increased significantly with a carbohydrate food source. *A. pallipes* abundance about the border habitat may reflect their necessity to frequent these areas for food.

CONCLUSIONS

From this study, insight was gained on several aspects of root maggot-parasitoid interactions, some of which (along with understandings gained by others contributing to the onion agroecosystem project) can be used for the development of an integrated management program for the OM. Such a program would entail:

1) Utilize strips of early-planted onions and volunteers (Whitfield 1981) as a trap crop to absorb most of the early season OM damage. Maximize the interfacing of this trap crop with grassy border habitats to encourage the interaction between diseased and healthy flies and favor a build-up of Entomophthora muscae (Carruthers 1981).

2) Interplant radishes with onions in a 5% radish / 95% onion seed mixture to encourage the build-up of A. bilineata populations in the onion agroecosystem.

3) As most of the overwintering OM develop on culls left in the field after harvest, management of this food resource could decrease damage the subsequent spring. Flies prefer ovipositing in sprouting onions in the fall (Drummond). Thus plowing under a narrow strip of onions prior to harvest would force sprouting and act as a trap crop for third generation OM flies. Interfacing this trap crop with grassy borders would maximize the impact of predators, parasitoids, and the disease, E. muscae, on the OM population.

Drummond (1982) reported that the major portion of OM eggs laid in the fall are laid in the soil rather than on the cull onions. Raking the culls into the borders at or just after peak oviposition would result in mortality of most of the hatching larvae and maximize the interactions with natural enemies for those maggots remaining in the culls.

This management program is based on attracting the OM flies to areas that maximize natural mortality, particularly that due to natural enemies. A greater understanding of dispersal capabilities and daily ranges of activity of the fly and its predators and parasitoids is necessary to determine at what scale such a program would be effective.

LITERATURE CITED

Abeles, J.R. and M. Shepard. 1974. Hymenopterous parasitoids associated with poultry manure. Environ. Entomol. 3(5):884-6.

Armstrong, T. 1924. Onion maggot studies in the district of Montreal, Quebec, 1924. Ann. Rpt. Entomol. Soc. Ont. 1923. 54:42-45.

Beglyarov G.A. and A.I. Smetnik. 1977. Seasonal colonization of entomophages in U.S.S.R. In: R.L. Ridgeway and S.B. Vinson (eds.), Biological Control by Augmentation of natural enemies. Plenum Press, New York. 283-328

Benson, O.L., and C.W. Wingo. 1963. Investigations of the face fly in Missouri. J. Econ. Entomol. 56(3):251-8.

Blickle, R.L. 1961. Parasites of the face fly, Musca autumnalis, in New Hampshire. J. Econ. Entomol. 54(4):802.

Bromand, B. 1980. Investigations on the biological control of the cabbage rootfly (Hylemya brassicae) with Aleochara bilineata. West Paleoarctic Regional Section Bulletin, Volume 3, No. 1.

Carruthers, R.I. 1979. Population sampling and spatial distribution of the immature life stages of the onion maggot, Hylemya antiqua (Meigen). M.S. thesis, Mich. St. Univ., E. Lansing. 197 pp.

Carruthers, R.I. 1981. The biology and ecology of Entomophthora muscae (Cohn) in the onion agroecosystem. Ph.D. thesis, Mich. St. Univ., E. Lansing. 238 pp.

Casagrande, R.A. 1971. An approach to alfalfa weevil management in Michigan. M.S. thesis, Mich. St. Univ., E. Lansing.

Coaker, T.H. 1965. Further experiments on the effect of beetle predators on the number of cabbage root fly, Erioischia brassicae (Bouche), attacking brassica crops. Ann. Appl. Biol. 56:7-20.

Colhoun, E.H. 1953. Notes on the stages and biology of Baryodma ontarionis Casey (Coleoptera: Staphylinidae), a parasite of the cabbage maggot, Hylemya brassicae Bouche (Diptera: Anthomyiidae). Can. Entomol. 85(1):1-8.

Cromartie, W.J., Jr. 1981. The environmental control of insects using crop diversity. In: D. Pimentel (ed.), CRC Handbook of pest management in agriculture, Vol. I. CRC Press Inc., Boca Raton, Florida. 223-51.

Doane, J.F. and R.K. Chapman. 1962. Oviposition preference of the cabbage maggot. J. Econ. Entomol. 55:137-142.

Doutt, R.L., and J. Nakata. 1973. The Rubus leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. Environ. Entomol. 2(3):381-6.

Drummond, F.A. 1982. Post-harvest biology of the onion maggot, Hylemya antiqua (Mg.). M.S. thesis, Mich. St. Univ., E Lansing.

Eckenrode, C.J. 1971. Effect of various temperatures upon the cabbage maggot under artificial conditions. Ann. Entomol. Soc. Amer. 64:1079-1083.

Eckenrode, C.J. and R.K. Chapman. 1971. Observations on cabbage maggot activity under field conditions. Ann. Entomol. Soc. Amer. 64:1220-30.

Eckenrode, C.J. 1972. Seasonal adult caggage maggot populations in the field in relation to the thermal-unit accumulations. Ann. Entomol. Soc. Amer. 65:151-56.

Eckenrode, C.J., E.V. Vea and K.W. Stone. 1975. Population trends of onion maggots correlated with air thermal unit accumulations. Envir. Entomol. 4(5):785-89.

Edens, T. and D.L. Haynes. 1982. Closed system agriculture: resource constraints, management options, and design alternatives. Ann. Rev. Phytopathol. 20:363-95.

Ellington, J.J. 1963. Field and laboratory observations on the life history of the onion maggot, Hylemya antiqua (Meigen). Ph.D. thesis, Cornell Univ. 124 pp.

Ellis, P.R., C.J. Eckenrode, and G.E. Harman. 1979. Influence of onion cultivars and their microbial colonizers on resistance to onion maggot. J. Econ. Entomol. 72:512-15.

Ellis, P.R., J.A. Hardman, P. Crisp, and A.G. Johnson. 1979. The influence of plant age on resistance of radish to cabbage root fly egg-laying. Ann. Appl. Biol. 93:125-131.

Esberg, P. and B. Bromand. 1977. Labelling with radioisotopes, release and dispersal of the rove beetle, Aleochara bilineata Gyll. (Coleoptera: Staphylinidae) in Danish cauliflower field. Tidsskr. f. Planteavl. 81:457-468.

Feeney, P.P. 1976. Plant apparency and chemical defense. In: J. Wallace and R. Mansell (eds.), Biochemical interaction between plants and insects. Recent Advances in Phytochemistry 10. Plenum, New York, New York. 1-10.

Finlayson, D.G. and C.J. Campbell. 1976. Carabid and staphylinid beetles from agricultural land in the Lower Fraser Valley, British Columbia. J. Entomol. Soc. Brit. Columbia. 73:10-19.

Finlayson, D.G., J.R. Mackenzie, and C.J. Campbell. 1980. Interactions of insecticides, a carabid predator, a staphylinid parasite and cabbage maggots in cauliflower. Environ. Entomol. 9(6):789-97.

Fitch, A. 1867. Noxious, beneficial and other insects of New York. New York Agric. Soc. R. 11:31-8.

Gage, S.H. and D.L. Haynes. 1975. Emergence under natural and manipulated conditions of Tetrastichus julis, an introduced larval parasite of the cereal leaf beetle, with reference to regional population management. Environ. Entomol. 4:425-34.

Garry, C.E. and C.W. Wingo. 1971. Factors affecting parasitism of the face fly by Aphaereta pallipes in laboratory studies. J. Econ. Entomol. 64(1):104-7.

Gary, H.E. 1924. The onion maggot in Alberta. Ann. Rep. Entomol. Soc. Ontario. 54:36-8.

Gross, A. and V. Clark. 1975. Survival distributions: reliability applications in the biomedical sciences. New York, Wiley.

Hammer, O. 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. Vidensk. Medd. Naturhist. Foren. Kobenhavn. 105:141-393.

Hammond, G.H. 1924. The onion maggot in the Ottawa district. Rep. Entomol. Soc. Ontario. 54:39-40.

Harris, C.R., H.J. Svec, and M.K. Mukerji. 1967. A new look at old problems-the need for a modern evaluation of old soil insect problems. Proc. N. Cent. Br. Entomol. Soc. Amer. 22:47-52.

Haynes, D.L., R.L. Tummala, and T.L. Ellis. 1980. Ecosystem management for pest control. BioSci. 30(10):690-96.

Helgeson, R.G. and D.L. Haynes. 1972. Population dynamics of the cereal leaf beetle, Oulema melanopus (Coleoptera: Chrysomelidae): model for age-specific mortality. Can. Entomol. 104:797-814.

Houser, E.C. and C.W. Wingo. 1967. Aphaereta pallipes as a parasite of the face fly in Missouri, with notes on laboratory culture and biology. J. Econ. Entomol. 60(3):731-3.

Hsiao, T.H. and F.G. Holdaway. 1966. Seasonal history and host synchronization of Lydella grisescens (Diptera: Tachnidae) in Minnesota. Ann. Ent. Soc. 59:125-33.

Kennedy, J.S., C.O. Booth, and W.J.S. Kershaw. 1959a. Host finding by aphids in the field. I. Gynoparae of Myzus persicae (Sulzer). Ann. Appl. Biol. 47:410-23.

Kennedy, J.S., C.O. Booth, and W.J.S. Kershaw. 1959b. Host finding by aphids in the field. II. Aphis fabae Scop. (Gynoperae) and Brevicoryne brassicae L.; with a reappraisal of the role of host finding in virus spread. Ann. Appl. Biol. 49:1-21.

Kiritani, K. and F. Nakasuji. 1967. Estimation of the stage-specific survival rate in insect population with overlapping stages. Res. Popul. Ecol. 9:143-52.

Kirknel, E. 1978. The influence of diazinon, trichloronate, carbofuran and chlorfenvinphos on parasitism capacity of the rove beetle, Aleochara bilineata (Gyll.). Tidsekr. Planteavl. 82:117-29.

Lampert, E.P. 1980. Endemic ecology of the cereal leaf beetle (Oulema melanopus (L.). Ph.D. thesis, Mich. St. Univ., E. Lansing. 526 pp.

Leuis, K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. Can. Entomol. 92:369-76.

Leuis, K. 1961a. Influence of food on fecundity and longevity of Itoplectis conquisitor (Say) (Hymenoptera: Ichneumonidae). Can. Entomol. 93:771-80.

Leuis, K. 1961b. Influence of various foods on fecundity and longevity of adults of Scambus buolianae (Htg.) (Hymenoptera: Ichneumonidae). Can. Entomol. 93:1079-84.

Leuis, K. 1963. Effects of pollens on fecundity and longevity of adult Scambus buolianae (Htg.) (Hymenoptera: Ichneumonidae). Can. Entomol. 95:202-7.

Leuis, K. 1967. Influence of wild flowers on parasitism of tent caterpillar and codling moth. Can. Entomol. 99:444-6.

Loosjes, M. 1976. Ecology and genetic control of the onion fly, Delia antiqua (Meig.). Ag. Res. Rpt. 857 P, Wageningen. 179 pp.

Manly, B.F.J. 1976. Extensions to Kiritani and Nakasuji's method for analyzing insect stage-frequency data. Res. Popul. Ecol. 17:191-199.

McComb, C.W. 1958. New synonymy in the genus Aphaereta with a redescription of Aphaereta pallipes (Say). Proc. Ent. Soc. Wash. 60(5):223-4.

Merritt, R.W. 1974. A review of the food habits of the insect fauna inhabiting cattle droppings in north central California. Pan-Pacific Entomol. 52:13-22.

Merritt, R.W. and J.R. Anderson. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. Hilgardia. 45(2):31-71.

Miller, L.A. and R.J. McClanahan. 1960. Life history of the seed-corn maggot and of H. liturata (Mg.) in southwestern Ontario. Can. Entomol. 92:210-21.

Mohr, C.O. Cattle droppings as ecological units. Ecol. Monogr. 13:275-309.

Moore, I. and E.F. Legner. 1971. Host records of parasitic staphylinids of the genus Aleochara in America (Coleoptera: Staphylinidae). Ann. Ent. Soc. Amer. 64:(5)1184-85.

Nair, K.S.S. and F.L. McEwen. 1975. Ecology of the cabbage maggot, Hylemya brassicae (Diptera: Anthomyiidae), in rutabaga in southwestern Ontario, with some observations on other root maggots. Can. Entomol. 107:343-54.

Newsom, L.D. 1974. Pest management: history, current status and future progress. In: F.G. Maxwell and F.A. Harris (eds.), Proceedings of the summer institute on biological control of plant insects and diseases. Univ. Press of Mississippi, Jackson. 1-18.

Perron, J.P. 1972. Effects of some ecological factors on populations of the onion maggot, Hylemya antiqua, under field conditions in southewestern Quebec. 17(1):20-47.

Pimentel, D. 1961. The influence of plant spatial patterns on insect populations. Ann. Entomol. Soc. Amer. 54:61-69.

Poorbaugh, J.H., J.R. Anderson, and J.F. Burger. 1968. The insect inhabitants of undisturbed cattle droppings in northern California. Calif. Vector Views. 15:17-35.

Ravlin, F.W. 1980. Development of management concepts in parasite systems. Ph.D. thesis, Mich. St. Univ., E. Lansing. 186 pp.

Read, D.C. 1962. Notes on the life history of Aleochara bilineata (Gyll.) (Coleoptera: Staphylinidae) and on its potential value as a control agent for the cabbage maggot, Hylemya brassicae (Bouche) (Diptera: Anthomyiidae). Can. Entomol. 94:417-24.

Risch, S.J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology. 62(5):1325-40.

Root, R.B. 1973. Organization of a plant arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleraceae). Ecol. Monogr. 43:95-124.

Salkeld, E.H. 1959. Notes on anatomy, life history and behavior of Aphaereta pallipes (Say) (Hymenoptera: Braconidae), a parasite of the onion maggot, Hylemya antiqua (Meig.). Can. Entomol. 91:93-97.

Scott, D.R. 1969. A selected bibliography of the onion maggot, Hylemya antiqua (Meigen). Bull. Entomol. Soc. Am. 15:345-54.

Shenefelt, R.D. 1974. Pars 11. Braconidae 7. Alysiinae. *In*: van der Vecht, J. and R.D. Schenefelt (eds.), Hymenopterorum Catalogus (nova editio). 937-1113. Dr. W. Junk B.V.'s-Gravenhage.

Sleesman, J.P. and H.L. Gui. 1931. The onion maggot. Ohio Ag. Exp. Sta. Bimon. Bull. 149:35-41.

Smith, J.G. 1969. Some effects of crop background on populations of aphids and their natural enemies on brussel sprouts. Ann. Appl. Biol. 63:326-330.

Smith, J.G. 1976. Influence of crop background on natural enemies of aphids on brussel sprouts. Ann. Appl. Biol. 83:15.

Smith, K.M. 1922. A study of the life-history of the onion fly (*Hylemya antiqua*, Meigen). Ann. Appl. Biol. 9:177-84.

Southwood, T.R.E. 1978. Ecological methods with particular reference to the study of Insect Populations. 2nd Edition. Chapman and Hall, London. 524 pp.

Symes, P.D. 1975. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. Environ. Entomol. 4:337-46.

Tahranainen, J.O. and R.B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia. 10:321-46.

Theunissen, J.A. 1976. Aspects of gametogenesis and radiation pathology in the onion fly, *Hylemya antiqua* (Meigen). Wageningen, The Netherlands. Veenmand and Zonen. 163 pp.

Theunissen, J. and H. den Ouden. 1980. Effects of intercroping with *Spergula arvensis* on pests of brussel sprouts. Ent. Exp. and Appl. 27:260-8.

Thomas, G.D. 1967. Natural Enemies of the face fly, *Musca autumnalis* DeGeer in Missouri. Ph.D. thesis, Univ. of Missouri, Columbia. 131 pp.

Thomas, G.D. and C.W. Wingo. 1968. Parasites of the face fly and two other species of dung-inhabiting flies. J. Econ. Enotmol. 61(1):147-52.

Townes, H. 1958. Some biological characteristics of Ichneumonidae (Hymenoptera) in relation to biological control. J. Econ. Entomol. 51(5):650-2.

Turner, E.C., Jr., R.P. Burton, and R.R. Gerhardt. 1968. Natural parasitism of dung-breeding Diptera: a comparison between native hosts and an introduced host, the face fly. J. Econ. Entomol. 61(4):1012-5.

Wadsworth, J.T. 1915. On the life history of *Aleochara bilineata* Gyll., a staphylinid parasite of *Chortophila brassicae* Bouche. J. Econ. Biol. 10:1-26.

Weseloh, R.M. 1972. Spatial distribution of the gypsy moth (Lepitoptera: Lymantridae) and some of its parasitoids. Entomophaga. 17:339-51.

Weseloh, R.M. 1979. Comparative behavioral responses of three *Brachymeria* species and other gypsy moth parasitoids to humidity and temperature. Environ. Entomol. 8:670-5.

Wharton, R.A. 1977. New world *Aphaereta* Species (Hymenoptera: Braconidae: Alysiinae), with a discussion of terminology used in tribe Alysiini. Ann. Entomol. Soc. Amer. 70(5):782-803.

Whitfield, G.H. 1981. Spatial and temporal population analysis of the onion maggot (*Hylemya antiqua* (Meigen)), in Michigan. Ph.D. thesis, Mich. St. Univ., E. Lansing. 379 pp.

Wishart, G. 1957. Surveys of parasites of *Hylemya* spp. (Diptera: Anthomyiidae) that attack cruciferous crops in Canada. Can. Entomol. 89:450-54.

Wishart, G., J.F. Doane and G.E. Maybee. 1956. Notes on beetles vs. predators of eggs of *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae). Can. Entomol. 88:634-39.

Wishart, G. and E. Monteith. 1954. *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae), a parasite of *Hylemya* spp. (Diptera: Anthomyiidae). Can. Entomol. 86:145-54.

Workman, R.H., Jr. 1958. The biology of the onion maggot, *Hylemya antiqua* (Meigen), under field and greenhouse conditions. Ph.D. thesis, Oregon St. Coll. 82 pp.

APPENDIX A

A. BILINEATA REARING

A colony of *A. bilineata* was maintained in a covered 35 x 22 x 7 cm plastic box. Small holes were punctured in the bottom and a portion of the cover was replaced with a fine mesh nylon screen to facilitate drainage and air flow. The box was filled to a depth of ca. 3 cm. with a mixture of moist sand and vermiculite. Adults were supplied with maggots on cut onions, which provided cover for the insects.

Healthy OM pupae were buried in the sand, exposing them to *A. bilineata* larvae for in 48 hours. After this time, the pupae were removed and kept in a separate petri dish with moist vermiculite. When adults emerged, they were returned to the colony. Pupae left in the colony for much more than 48 hours usually suffered repeated attacks from parasitoid larvae resulting in reduced survival. With adequate food and moisture, *A. bilineata* were fairly long lived and easy to maintain. Bromand (1980) describes a more efficient method for mass rearing *A. bilineata*.

APPENDIX B

REARING *A. PALLIPES*

Field-collected A. pallipes emerged in rearing dishes consisting of a 20 cm glass lantern globe in a dish of moist sand. The top of the globe was covered with a fine cotton muslim cloth through which distilled water and sucrose solutions were fed. Sufficient moisture in the sand assured parasitoid survival.

The sex ratio of emerging A. pallipes was 2 males to 5.5 females; an average of 8.3 parasitoids emerged from a single OM pupa. From a small percent of the field-collected pupae, only males emerged, indicating that the female had not mated.

The size of the parasitoids depended on the number of parasitoids per pupa and probably the age of the onion when attacked. The average length was about 2 mm. Males were usually smaller than females and could be easily distinguished as the females ovipositor was visible without magnification. Mating was observed almost immediately on emergence, but the preoviposition period averaged 2.25 days.

OM larvae on slices of onion were placed in the bottom of the rearing dish for exposure to A. pallipes adults. The parasitoids became excited with the introduction of the onion, and frequently mature females would approach within a few minutes. Females crawled between the leaves of the onion bulb in search of OM, often becoming matted with onion juice, resulting in their mortality. A. pallipes oviposited in both second and third instars of OM.

OM pupae were sifted from the moist sand. Parasitized pupae were usually smaller than healthy pupae and frequently misshapen. The developing parasitoids were easily recognized through the fly puparium under a 40X magnification dissecting microscope. By the time the host pupated, the parasitoid larvae had hatched and occupied most of the space in the puparium. A detailed description of the parasitoid life stages is given by Salkeld (1959).

Though never quantified, it was observed that the oviposition process of A. pallipes frequently killed OM larvae. Dead larvae were often found in onions exposed to the parasitoids. Mortality due to A. pallipes oviposition on the face fly, Musca autumalis was reported (Thomas 1967). This phenomenon should receive further investigation. This mortality could result from multiple attacks of a single OM larvae in a caged situation which may not be as frequent in nature.

APPENDIX C

PRECISION OF OM DAMAGE SAMPLING AT EATON RAPIDS RESEARCH SITE

The precision of the different strategies for sampling within-field OM damage at the organic farm in Eaton Rapids was calculated to evaluate whether changes in observed plant damage actually reflected trends in the OM population or changes in the sampling strategies.

Using the field level variance-to-mean relationships estimated by Carruthers (1979) for sample unit sizes of 100 ft (30 m) and 35 ft (10.5 m), and solving for a, precision, in Karandinos' (1976) equation for calculating optimal sample size, levels of precision can be estimated.

$$a = \frac{3.84s^2}{\bar{x}^2 n}$$

where a = precision, s^2 = sample variance, and $\bar{x}$ = sample mean. With the relationship between the sample mean and variance determined as

$$S^2 = a\bar{x}^b$$

and substituting,

$$a = \frac{3.84a\bar{x}^b}{\bar{x}^2 n}$$

The precision levels for the first two sampling stategies for OM damage were calculated with $\bar{x}$ equal to the mean percent damage over the time period that sample unit size was utilized. The results are presented in Table C1 in comparision with Carruthers' (1979) recommended strategy of twenty 200 ft^2 samples per field.

The initial sampling technique of 10-100 ft^2 samples, is, as one would expect, not as precise as Carruthers' recommended twenty samples of 100 ft of row, at the densities sampled. However, the stratified sampling technique, using

Table C1. Precision of onion maggot damage sampling.

Sample Unit Size (ft. of rows)	n	a[1]	b[1]	Precision[2] (expressed as proportion of x)
100	20	4.48	1.35	.5176
100	10	4.48	1.35	.7320
25	35	3.78	1.29	.3228

[1] From Carruthers, 1979

[2] Calculated with x equal to the mean percent damage observed over the time period that the sample unit size was utilized.

35 samples of 25 ft of row was more precise. A comparative precision level cannot be calculated for the third sampling technique which was a combination of distance and unit sampling. However, with confidence in the precision of the stratified unit sampling, we can compare the percent damage levels calculated from data called on the same date (July 18) using both stratified unit sampling, and the combination distance and unit sampling. With stratified unit sample, or damage a July 18 is estimated at 2.74 ^{5} .80%, and with combination distance unit sampling, 1.87 ^{5} 1.78.

Given knowledge of the distribution of OM damage (Carruthers 1979, Whitfield 1981), the combination distance-unit sampling could underestimate damage[1], yet when comparing the results of the two different methodologies on one sample date this did not occur.

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[1] As OM distribution about a field is highly clumped (Carruthers 1979), this sampling strategy of walking distance of row until encountering a damaged plant and then sampling .3 m of row beyond that point, may underestimate damage if the clump continues beyond the .3 m sampled. A more accurate methodology would entail measuring the size of the clump or increasing the sampled unit to a size that would most likely encompass the largest clump encountered.

APPENDIX D

Coenosia tigrina, PREDATOR OF THE ADULT ONION MAGGOT

APPENDIX D

Coenosia tigrina, predator of the adult onion maggot

Adults of the tiger fly, C. tigrina, have been reported as important predators of the OM fly (Perron and LaFrance 1952, Perron et al. 1956, LeRoux et al. 1960) and the SCM fly (Miles 1948, Miller and McClanahan 1960) in Canada and Europe. The tiger flies have also been noted as an important predator of muscoid flies associated with fresh dung (Thomas 1967). Hobby (1931, 1934) published a list of prey species reported for C. tigrina in Europe, which includes many anthomyiids.

All life stages of the tiger fly have been found in onion fields in Canada. C. tigrina lays its eggs loosely on or beneath the soil surface (LeRoux and Perron 1960). This species completes only one larval instar from egg hatch to pupation. Mature larvae overwinter in compost soils and pupate in the early spring (LeRoux and Perron 1960). Adults have been reported in fields in southwestern Ontario from early May to late October, their period of activity roughly coinciding with that of the OM (LeRoux and Perron 1960).

Detailed descriptions of the immature life stages and adult C. tigrina are given by LeRoux and Perron (1960) and Perron et al. (1956).

Tiger fly predation on adult onion maggots has been observed in caged situations (LeRoux et al. 1960), and C. tigrina adults reduced the subsequent prey generation by 50%. To date, further field and laboratory investigations have been curtailed by a lack of information on the food habits of C. tigrina larvae. Attempts to rear the larvae to maturity on various vegetable and animal diets were unsuccessful (Perron and LeRoux 1956). Recently, however, C. tigrina larvae were observed in the field feeding on the earthworm, Eisenia rosea (Yahnke and George 1972). Subsequent sampling supported this original observation and the larvae were successfully reared to pupation on earthworms in the laboratory. Yahnke and George (1972) observed the survival of C. tigrina larvae reared on E. rosea in the laboratory to be significantly greater on bisected prey than live intact worms. However, these authors found that with the presence of the cluster fly, P. rudis, also a predator of E. rosea, C. tigrina survival on live worms increased dramatically. The association of P. rudis and C. tigrina under field conditions is not known.

During preliminary sampling of commercial onion fields in the Great Swamp area this past year, C. tigrina were found in very low levels. However, these flies were relatively abundant (densities approaching that of the adult onion maggot) in monitored fields where no chemical pesticides were used (Carruthers 1979). It is known that earthworms are extremely susceptible to fungicide poisoning. In apple orchards, earthworms have been reduced by 90% following two years of standard fungicide spray programs (Stringer 1974). As earthworms are an important food source for immature C. tigrina, fungicide applications in commercial onion fields may be reducing earthworm populations to levels unable to support high predator populations.

Hobby, B. M. 1931. The prey of Coenosia tigrina F. Proc. Entomol. Soc. London 6:13-15.

Hobby, B. M. 1934. Prey of Coenosia tigrina F. (Diptera: Anthomyiidae). J. Entomol. Soc. S. Engl. 1:69-77.

LeRoux, E. J., and J. P. Perron. 1960. Descriptions of immature stages of Coenosia tigrina (F.) (Diptera: Anthomyiidae). With notes on hibernation of larvae and predation by adults. Can. Ent. 93:264-96.

Miles, M. 1948. Field observations on the bean seed fly (seed corn maggot), Chortophila cilicrura Rond., and C. trichodactyla Rond. Bull. Ent. Res. 38:559-74.

Miller, L. A., and R. J. McClanahan. 1960. Life history of the seed corn maggot, Hylemya cilicrura Rond. and H. liturata (Mg.) (Diptera: Anthomyiidae) in southwestern Ontario. Can. Ent. 42:210-21.

Perron, J. P., and J. LaFrance. 1952. A note on a Dipterous predator of the onion maggot, Hylemya antiqua (Mg.). Can. Ent. 84:112.

Perron, J. P., J. LeRoux, and J. LaFrance. 1956. Notes on Coenosia tigrina (F.) (Diptera: Anthomyiidae) mainly on habits and rearing. Can. Ent. 88:608-11.

Stringer, A., and C. H. Lyons. 1974. The effect of benomyl and thiophanate-methyl on earthworm populations in apple orchards. Pestic. Sci. 5:189-96.

Thomas, G. D. 1967. Natural enemies of the face fly, Musca autumnalis DeGeer, in Missouri. Ph.D. thesis, Univ. of Missouri, Columbia. 131 pp.

Yahnke, W. E., and J. A. George. 1972. Earthworms as prey for larvae of Coenosia tigrina. J. Econ. Entom. 65:1478-79.