

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

5-1972

Host-Parasite Relationship Studies of the Larval Alfalfa Weevil and the Ichneumonid Parasite *Bathyplectes curculionis* (Thomson)

Yeboa A. Duodu
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Biology Commons](#)

Recommended Citation

Duodu, Yeboa A., "Host-Parasite Relationship Studies of the Larval Alfalfa Weevil and the Ichneumonid Parasite *Bathyplectes curculionis* (Thomson)" (1972). *All Graduate Theses and Dissertations*. 7943.
<https://digitalcommons.usu.edu/etd/7943>

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



HOST-PARASITE RELATIONSHIP STUDIES OF THE LARVAL
ALFALFA WEEVIL AND THE ICHNEUMONID PARASITE
BATHYPLECTES CURCULIONIS (THOMSON)

by

Yeboa A. Duodu

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Entomology

Approved:

Major Professor

Committee Member

Committee Member

Committee Member

Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1972

ACKNOWLEDGMENTS

I am grateful to my major professor, Dr. Donald W. Davis, for his advice and critical review of this dissertation. My thanks are also due to other members of my dissertation committee, Dr. Keith L. Dixon, Professor of Zoology; Dr. Wilford J. Hanson, Associate Professor of Entomology; Dr. Ting H. Hsiao, Associate Professor of Entomology; and Dr. Frederic H. Wagner, Professor of Wildlife Resources and Associate Dean of the College of Natural Resources, for their valuable suggestions.

I am indebted to my wife, Florence, for her cheerful company, her laboratory and field assistance, and for typing the preliminary manuscript.

Yeboa A. Duodu

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES	vi
LIST OF FIGURES	ix
ABSTRACT	xi
INTRODUCTION	1
REVIEW OF LITERATURE	4
The Alfalfa Weevil in North America	4
Introduction and spread	4
Life history of <u>Hypera postica</u> in the United States	6
Other differences between the eastern and western United States forms of the alfalfa weevil	7
The Alfalfa Weevil Parasite, <u>Bathyplectes curculionis</u> (Thomson)	10
Classification	10
Colonization and establishment in the United States	11
Life history of <u>Bathyplectes curculionis</u>	12
Host defense reactions against <u>B. curculionis</u>	14
Hyperparasites of <u>B. curculionis</u>	17
<u>Bathyplectes curculionis</u> in Integrated Control of <u>Hypera</u>	20
Miscellaneous Literature on <u>B. curculionis</u>	21
Parasites of <u>Hypera</u> , other than <u>Bathyplectes curculionis</u>	25
<u>Bathyplectes</u> spp., other than <u>B. curculionis</u>	25
<u>Tetrastichus incertus</u> (Ratzeburg) (Hymenoptera: Eulophidae)	27
<u>Microctonus</u> spp. (Hymenoptera: Braconidae)	28
Parasites of the prepupae and pupae of <u>Hypera</u>	29
Egg parasites of <u>Hypera</u>	31
Miscellaneous parasites of <u>H. postica</u>	32

TABLE OF CONTENTS (Continued)

	Page
MATERIALS AND METHODS	34
General Rearing Techniques	34
Rearing of parasite-free <u>Hypera postica</u> larvae	34
Rearing of adult <u>Bathyplectes curculionis</u>	36
Determination and Calculation of Percentage Parasitism	37
Determination of parasitism	37
Calculation of percentage parasitism	39
Studies Aimed at Identifying Parasitized Larvae	40
Color segregation of field-collected larvae	40
Transmission of light through larvae	40
Separation of larvae with lesion-like areas	41
Host Instar Parasitization and Survival Studies	41
Separate parasitization of different instars	41
Simultaneous exposure of host instars to parasites ...	43
Individual host "stinging" and survival studies	44
Larval Development and Activity Studies	44
Development of parasitized and unparasitized larvae ..	44
Activity of parasitized and unparasitized larvae	45
Growth and the Consumption and Utilization of Food Studies ...	45
Food consumption and utilization	47
Analysis of Data	52
RESULTS	53
Studies Aimed at Identifying Parasitized Larvae	53
Color segregation of field-collected larvae	53
Transmission of light through larvae	53
Separation of larvae with lesion-like areas	53

TABLE OF CONTENTS (Continued)

	Page
Host Instar Parasitization and Survival Studies	54
Separate parasitization of different instars	54
Simultaneous exposure of host instars to parasites	55
Individual host "stinging" and survival studies	58
Larval Development and Activity Studies	63
Development of parasitized and unparasitized larvae	63
Activity of parasitized and unparasitized larvae	65
Growth and the Consumption and Utilization of Food Studies	65
Growth	65
Food consumption and utilization	72
DISCUSSION	86
Studies Aimed at Identifying Parasitized Larvae	86
Host Instar Parasitization and Survival Studies	87
Levels of parasitism	87
Host instar survival following parasitization	89
Ovipositional behavior of <u>B. curculionis</u>	91
Larval Development and Activity Studies	91
Development of parasitized and unparasitized larvae	91
Activity of parasitized and unparasitized larvae	92
Growth and the Consumption and Utilization of Food Studies	93
Growth	93
Food consumption and utilization	94
SUMMARY AND CONCLUSIONS	106
LITERATURE CITED	111
VITA	121

LIST OF TABLES

Table	Page
1. Fresh and dry weights of 6.5 mm leaf discs from equivalent positions of opposite leaflets of alfalfa trifoliolates	48
2. Fresh and dry weights of 6.5 mm leaf discs from equivalent positions of opposite halves of middle leaflets of alfalfa trifoliolates	48
3. Rates of parasitism of the instars of <u>H. postica</u> larvae after being separately exposed to <u>B. curculionis</u> females	55
4. Survival of the instars of <u>H. postica</u> larvae after being separately exposed to <u>B. curculionis</u> females	56
5. Rates of parasitism of the instars of <u>H. postica</u> larvae after being simultaneously exposed to <u>B. curculionis</u> females	57
6. Survival of the instars of <u>H. postica</u> larvae after being simultaneously exposed to <u>B. curculionis</u> females	59
7. Survival of first instar <u>H. postica</u> larvae after being "stung" by <u>B. curculionis</u> females	60
8. Survival of second instar <u>H. postica</u> larvae after being "stung" by <u>B. curculionis</u> females	61
9. Developmental periods at 25-26 C of parasitized and unparasitized <u>H. postica</u> larvae from the beginning of each instar to the cocoon stage	64
10. Activity scores of parasitized and unparasitized <u>H. postica</u> larvae from the beginning of the second instar to the cocoon stage	66
11. Activity scores of parasitized and unparasitized fourth instar <u>H. postica</u> larvae	66

LIST OF TABLES (Continued)

Table	Page
12. Comparison of mean fresh weight gains by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the day preceding the cocoon formation	68
13. Comparison of mean fresh weight gains by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	68
14. Comparison of mean dry weight gains by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	69
15. Comparison of fresh and dry weight gains by unparasitized <u>Hypera postica</u> larvae reared at 22.2 C and 30 C	69
16. Comparison of fresh and dry weight gains by parasitized <u>Hypera postica</u> larvae reared at 22.2 C and 30 C	71
17. Weight comparisons of <u>Bathyplectes curculionis</u> larvae reared at 22.2 C and 30 C and removed from weevil larvae after cocoons were spun	71
18. Comparison of total food consumption by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	78
19. Comparison of food consumption per larva per day by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	79
20. Comparison of consumption indices (C.I.) by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	79
21. Comparison of approximate digestibility by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	80
22. Comparison of the net efficiency of conversion of ingested food to body matter (E.C.I.) by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	80

LIST OF TABLES (Continued)

Table	Page
23. Comparison of the net efficiency of conversion of digested food to body matter (E.C.D.) by parasitized and unparasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage	83
24. Comparison of food consumption and utilization by unparasitized <u>Hypera postica</u> larvae from the beginning of the third star to the cocoon stage in larvae reared at 22.2 C and 30 C	83
25. Comparison of food consumption and utilization by parasitized <u>Hypera postica</u> larvae from the beginning of the third instar to the cocoon stage in larvae reared at 22.2 C and 30 C	84
26. Comparisons of dry weight-fresh weight consumption indices (C.I.) for different insects	97
27. Comparisons of the approximate digestibilities (A.D.) of food by different insects	98
28. Comparisons of the net efficiency of conversion of ingested food to body substance (E.C.I.) by different insects	101
29. Comparisons of the net efficiency of conversion of digested food to body substance (E.C.D.) by different insects	102

LIST OF FIGURES

Figure	Page
1. Adult alfalfa weevil	5
2. Fourth instar (last stage) alfalfa weevil larva	5
3. Adult <u>Bathyplectes curculionis</u>	13
4. Cocoons of <u>Bathyplectes curculionis</u>	13
5. An ovipositional cage used in rearing field-collected adult alfalfa weevils	35
6. Equipment used for the emergence of adult <u>Bathyplectes curculionis</u>	38
7. Cage used in parasitization of alfalfa weevil larvae by <u>Bathyplectes curculionis</u>	42
8. Survival of first and second instar <u>Hypera postica</u> larvae after being "stung" by <u>Bathyplectes curculionis</u> females	62
9. Mean growth of parasitized and unparasitized <u>Hypera postica</u> larvae at 22.2 C (A) and 30 C (B)	67
10. Mean daily food consumption by parasitized and unparasitized <u>Hypera postica</u> larvae at 22.2 C (A) and 30 C (B)	74
11. Mean daily weight gains and mean daily food consumption by parasitized and unparasitized <u>Hypera postica</u> larvae reared at 22.2 C	75
12. Mean daily weight gains and mean daily food consumption by parasitized and unparasitized <u>Hypera postica</u> larvae reared at 30 C	76
13. Mean cumulative food consumption by parasitized and unparasitized <u>Hypera postica</u> larvae at 22.2 C (A) and 30 C (B)	77

LIST OF FIGURES (Continued)

Figure	Page
14. The relationship with age of the approximate digestibility by parasitized and unparasitized <u>Hypera postica</u> larvae at 22.2 C (A) and 30 C (B)	82

ABSTRACT

Host-Parasite Relationship Studies of the Larval

Alfalfa Weevil and the Ichneumonid Parasite

Bathyplectes curculionis (Thomson)

by

Yeboa A. Duodu, Doctor of Philosophy

Utah State University, 1972

Major Professor: Dr. Donald W. Davis

Department: Zoology

The parasitic effects of the ichneumonid Bathyplectes curculionis (Thomson) on the larval alfalfa weevil, Hypera postica (Gyllenhal), were studied.

Results of experiments on the rates of parasitism of the four host larval instars indicated that the first three are either preferred by the parasite over the fourth instar larvae or are more susceptible to the parasite's attack. Survival of the younger weevil larvae after their exposure to female parasites was markedly poorer than that of unparasitized larvae. Premature death of host larvae was probably from both the puncturing by the parasite's ovipositor and the feeding and other activities of parasite larvae within the hosts. The incidence of premature mortality of host larvae following oviposition by Bathyplectes increased with multiple "stinging" and decreased with host age.

The effects of parasitism on host development and activity were studied at 25-26 C. Larvae of each instar were parasitized and the number of days required for development to the cocoon stage was compared with that of unparasitized larvae of the same age. The development time for larvae parasitized during the third or fourth instar was significantly longer than that for unparasitized larvae. No significant difference existed between the length of development time for larvae parasitized during the first or second instar, and that for unparasitized larvae. There was no significant difference in the activity of unparasitized and parasitized larvae.

The influence of parasitism on growth, food consumption and food utilization by H. postica larvae during the third and fourth instars was studied at 22.2 C and 30 C. At both temperatures, total growth was significantly higher with unparasitized than with parasitized larvae. At 22.2 C, the total food consumption by unparasitized larvae was significantly higher than that by parasitized larvae. At 30 C, there was no significant difference between the total food consumption by unparasitized and parasitized larvae, although unparasitized larvae consumed more food. The food consumption per larva per day was significantly higher for unparasitized larvae at both temperatures. There was, however, no significant difference in the dry weight-fresh weight consumption index between parasitized and unparasitized larvae at either temperature.

No significant difference existed, at either 22.2 C or 30 C, in the approximate digestibility of alfalfa by parasitized and unparasitized larvae. The efficiency of food digestion by both types of larvae decreased with age,

the decline being more pronounced at 30 C than at 22.2 C. The net efficiency of conversion of ingested food to body matter was higher for parasitized than for unparasitized larvae at 22.2 C. The difference was marginally significant at the 5 percent level. At 30 C, there was no significant difference between the net efficiencies of conversion of ingested food to body matter by parasitized and unparasitized larvae. Also no significant difference existed between the net efficiencies of conversion of digested food to body matter by parasitized and unparasitized larvae at either temperature.

Efforts to discover a practical method to distinguish parasitized from unparasitized larvae without dissection were unsuccessful.

(134 pages)

INTRODUCTION

The alfalfa weevil, Hypera postica (Gyllenhal) (Coleoptera: Curculionidae), is the most important pest of alfalfa in the United States (USDA, 1969; Miller, 1970a). It was first found in the U.S.A. at Salt Lake City, Utah, in 1904 (Titus, 1909, 1910). The weevil is apparently a Palearctic species (Titus, 1910, 1911, 1913; Yakhontov, 1934) and was thought to have arrived in Utah from Europe (Davis, 1967). From its initial introduction, H. postica spread to other states in the western United States (Sorenson, 1934b). In 1951 the weevil was discovered in Maryland, its first appearance in the eastern United States (Poos and Bissell, 1953). The eastern and western weevils are probably separate introductions which apparently originated from different ecological areas within the weevil's native distribution (Blickenstaff, 1965; Davis, 1967).

A number of biological, behavioral and other differences have been observed between the eastern and western United States forms of the alfalfa weevil (Koehler and Gyrisco, 1963; Blickenstaff, 1965; Davis, 1967; Pienkowski, Hsieh, and LeCato, 1969; Armbrust, White, and Roberts, 1970b). Studies by van den Bosch (1964a) and by Puttler (1967) showed the larvae of the eastern weevil to possess a higher degree of ability to encapsulate the eggs of the parasite Bathyplectes curculionis (Thomson) than the larvae of the western weevil. Blickenstaff (1965) thought the two forms of the weevil should be considered at least as subspecies.

The obvious damage to alfalfa by H. postica is caused by the larvae which feed in the growing tip, on the leaves, buds and even flowers. The adult weevils feed on the stems, buds and leaves (Titus, 1909). In 1966 H. postica caused an estimated loss of \$56,136,850 to the alfalfa industry in 30 states in the United States (USDA, 1967). The economic importance of the weevil is reflected in the large number of publications dealing with its biology and control (Cothran, 1966, 1968).

Efforts at biological control of the weevil were initiated in 1911 when its natural enemies were imported into Utah from Europe. The parasite Bathyplectes curculionis (Thomson) (Hymenoptera: Ichneumonidae) alone became established at that time (Chamberlin, 1924a, 1926; Clausen, 1956). The parasite was later colonized elsewhere in western United States and natural spread was extensive (Clausen, 1956). B. curculionis has been successfully colonized on the alfalfa weevil in the eastern United States (Puttler, Jones, and Coles, 1961; Brunson and Coles, 1968). The parasite also attacks the Egyptian alfalfa weevil, Hypera brunneipennis (Boheman), in Arizona and southern California (Clausen, 1956; van den Bosch and Dietrick, 1959).

B. curculionis is an endoparasite of the larvae of the alfalfa weevil. The parasitized weevil larvae usually are killed after they have spun their cocoons, thus completing their larval feeding activities.

There are only scattered references on the actual effects of the parasite on the biological processes of the alfalfa weevil larvae. The major components of this work are studies on the biological differences between

parasitized and unparasitized larvae of the western United States form of the alfalfa weevil as expressed in the consumption and utilization of food, growth, larval activity and time required for development.

The objectives of the study are: (1) to determine the effect of parasitism by B. curculionis on growth, food consumption and food utilization by alfalfa weevil larvae; (2) to determine the effect of parasitism on larval development and activity; (3) to study the relationship of larval age to parasitism; and (4) to determine a practical method to distinguish between parasitized and unparasitized larvae.

REVIEW OF LITERATURE

The Alfalfa Weevil in North AmericaIntroduction and spread

The alfalfa weevil, Hypera postica (Gyllenhal) (Figures 1 and 2), is an Old World species which was first observed in the United States in 1904 on a farm on the east side of Salt Lake City, Utah (Titus, 1909, 1910). Titus (1909) points out that the weevil might have been present for several years before its discovery. The exact point of origin of this introduction is unknown but Davis (1967) speculated that the weevil probably originated from southern Europe near the border of France and Switzerland from where many immigrants and their livestock arrived in Utah about 1900. The livestock were bedded in alfalfa straw.

The weevil spread to other parts of Utah and to parts of many surrounding states (Sorenson, 1934b). By 1940, H. postica was present in 11 states in the western United States (Hamlin et al., 1949a; Hamlin, McDuffie, and Lieberman, 1949b).

The alfalfa weevil appeared in the eastern United States in 1951 when specimens were collected in Maryland (Poos and Bissell, 1953). From Maryland the weevil spread to other eastern states and westward to Minnesota, Nebraska, Kansas, Oklahoma and Texas. By 1970 the weevil was known to exist in all 48 contiguous states of the United States (USDA,



Figure 1. Adult alfalfa weevil.



Figure 2. Fourth instar (last stage) alfalfa weevil larva.

1971). It has also been reported from parts of Canada (Hobbs, Nummi, and Virostek, 1959; MacLachlan, 1967).

Crossbreeding experiments by Blickenstaff (1965) between eastern and western United States weevils showed the two to be partially intersterile. Blickenstaff concluded from his studies that the eastern and western weevils originated from different ecological areas in the weevil's native home.

In addition to the alfalfa weevil, H. postica, a closely-related species, Hypera brunneipennis (Boheman), the Egyptian alfalfa weevil, also occurs now in the United States. H. brunneipennis was discovered in Arizona in 1939 (Wehrle, 1940) and has since spread to southern California (Armitage, 1949; van den Bosch and Dietrick, 1959).

Life history of Hypera postica in the United States

The seasonal history of the alfalfa weevil in the western United States differs from that in the East (Titus, 1910, 1913; Newton, 1933; Hamlin et al., 1949a; Manglitz and App, 1957; Evans, 1959; Campbell, Bowery, and Jester, 1961; Prokopy and Gyrisco, 1965; Davis, 1967, 1970).

Life history in the western United States. In the western United States, H. postica overwinters in the adult stage and egg laying begins in the spring. The first eggs are laid in old alfalfa, weed and grass stems but as the new alfalfa stems become large enough they are preferred for oviposition. The larval population in northern Utah usually becomes most abundant about mid-June, approximately the time for the cutting of the first

alfalfa crop. New adults begin to appear in June and leave the fields in late summer and autumn. They pass the winter in hiding, then return to the fields in the spring. There is thus only one generation a year (Titus, 1910, 1913; Newton, 1933; Hamlin et al., 1949a; Davis, 1967, 1970).

Life history in the eastern United States. The alfalfa weevil in the eastern United States overwinters in both the adult and egg stages. Oviposition starts in the autumn but ceases in cold weather and resumes in the spring. In warmer areas, egg laying may continue throughout the winter on warm days. Major weevil damage in the warmer eastern areas occurs about a month before the first alfalfa crop is harvested. In most parts of the eastern United States, the alfalfa weevil leaves the fields at about the time the first crop is cut, usually in June. The weevil remains in hiding in a diapausing state until late summer when it returns to the fields. Many of the new generation adults appear before the first alfalfa crop is cut (Manglitz and App, 1957; Evans, 1959; Campbell et al., 1961; Prokopy and Gyrisco, 1965; Davis, 1967). H. postica apparently also has one generation a year in the East, but Evans (1959) mentions a partial second generation in Virginia during years of favorable autumn weather. White et al. (1969) also presented evidence of a second generation of the weevil in southern Illinois.

Other differences between the eastern and western United States forms of the alfalfa weevil

In addition to the partial intersterility between the eastern and western weevils (Blickenstaff, 1965) and the differences in their seasonal

histories, behavioral and other differences between the weevils have been reported.

The weevils in the eastern United States are reported to spin their cocoons in the terminal parts of the alfalfa plant (Poos and Bissell, 1953; Manglitz and App, 1957). In contrast, western weevils spin their cocoons on the ground (Titus, 1909, 1910). According to Manglitz and App (1957), the difference may be due to the higher relative humidity in the eastern states. These workers suggested that the habit of spinning cocoons on the ground in the drier West was an attempt at moisture conservation. Davis (1967), however, believed the difference in the placement of cocoons resulted from the time of cutting of the alfalfa. In the western states where pupation usually occurs soon after cutting, the weevils, according to Davis, are forced to pupate on the ground. In those areas of the East, however, where the weevils pupate before the alfalfa is cut, pupae could easily survive on the alfalfa terminals.

Koehler and Gyrisco (1963) compared the feeding behavior of newly emerged eastern and western H. postica adults under laboratory conditions. The eastern weevils consumed a greater quantity of alfalfa initially than the western weevils, but fed for a shorter time before entering diapause.

Pienkowski et al. (1969) found that body proportions, without regard to sex, differed significantly among the eastern, western, and Egyptian alfalfa weevils. The proportions in the Egyptian weevil were intermediate between those of the eastern and western weevils.

In studies of the mating preference of eastern and western strains of H. postica, Armbrust et al. (1970b) found the male of the eastern strain to be more aggressive and to mate more often than the male of the western strain. This finding is in contrast to that of Blickenstaff (1969) who found that males of both strains did not show any mating preferences and were equally competitive in mating, when confined with eastern females only. The males of the western strain in Blickenstaff's (1969) studies seemed to reach sexual maturity earlier than the males of the eastern strain. In contrast, Armbrust et al. (1970b) found no difference in sexual maturity between strains.

Armbrust et al. (1970b) are of the opinion that the partial genetic incompatibility between the two strains (Blickenstaff, 1965) will probably have little effect when the two strains meet and mix. Based on their studies, Armbrust et al. (1970b) expect the male of the eastern strain of H. postica to contribute more to the genetic pool than the western male when the two strains meet under natural conditions. Blickenstaff (1969), however, thinks that when the two strains meet, the overall population might gradually decline at first and then become progressively more like the western strain.

Another difference between the two strains of H. postica is in their relative abilities to encapsulate eggs of the parasite Bathyplectes curculionis. Van den Bosch (1964a) found that the larvae of H. postica in California possessed only a feeble encapsulating ability against the eggs of B. curculionis. In contrast, Puttler (1967) found a high degree of encapsulating ability by

larvae of H. postica in the eastern United States against eggs of B. curculionis.

Davis (1967) made a comparative review of the eastern and western United States strains of H. postica. He concludes that only the crossbreeding experiments (Blickenstaff, 1965) clearly indicate true area differences. Most of the behavioral differences between the two populations, he suggests, are apparently environmentally controlled. He also believes that some of the differences may be genetic selections for adaptation to a particular area.

The western weevil is serious in areas with short summers and cold winters. In only a few cases has it adapted to warm winter areas. The eastern weevil does its worst damage in relatively warm areas, becoming less important over its northern range in the United States. The Egyptian alfalfa weevil apparently is even more adapted to hot climates (Davis, personal communication).

The Alfalfa Weevil Parasite, Bathyplectes

curculionis (Thomson)

Classification

According to Chamberlin (1926), Bathyplectes curculionis (Figure 3) was first described in 1887 by Thomson who assigned it to the genus Canidia which had been erected by Holmgren in 1858. Holmgren had confused the species with Campoplex subcinctus Grav. Ashmead in 1900 changed the name of the genus to Canidiella but Schmiedeknecht in 1909 reverted to use of the

genus Canidia. In 1914 Viereck found Canidia to be isogenotypic with Bathyplectes Forster and gave the latter name preference.

Colonization and establishment in the United States

Colonization in the western United States. Following the discovery of the alfalfa weevil in Utah, the search began in Europe for natural enemies of the weevil for possible attempts at biological control. The importation of natural enemies began in 1911. From 1911 to 1913, 12 species of parasites were released in Utah. Of these releases only B. curculionis became established (Chamberlin, 1924a, 1926; Clausen, 1956).

After its establishment in Utah, B. curculionis spread rapidly, the entire weevil-infested area in Utah being covered by 1920. Parasitism in the field often exceeded 90 percent (Chamberlin, 1926; Clausen, 1956). Chamberlin (1926) estimated that the parasite spread at least 196 miles in 6 years, from Ogden, Utah, in 1914 to Ashton, Idaho, in 1920. He thought the high rate of dispersal by B. curculionis suggested remarkable powers of flight and a high reproductive rate on the part of the parasite. Some workers have suggested individual farmers probably took the parasite from Utah into Idaho and Wyoming (Davis, personal communication). B. curculionis was successfully colonized in Colorado in 1918-19, Nevada in 1921-22, California in 1933-34 and Oregon in 1934 (Clausen, 1956).

B. curculionis was colonized on H. brunneipennis at Yuma, Arizona, in 1942. It was recovered at Bard, California, on the Arizona border, in 1953.

Earlier the parasite had been reared in 1952 from H. brunneipennis in San Diego County in California. The parasite apparently spread to Bard from the releases made at Yuma and probably reached San Diego County as cocoons in bales of alfalfa hay (van den Bosch, 1953; Dietrick and van den Bosch, 1953; Clausen, 1956; van den Bosch and Dietrick, 1959).

Colonization in the eastern United States. B. curculionis was introduced into the eastern United States in 1959 and 1960. Specimens were released in 1959 in Delaware, New Jersey and Virginia and recoveries of B. curculionis in 1960 indicated its establishment (Puttler et al., 1961; Brunson and Coles, 1968). Earlier, unsuccessful attempts were made from 1953 to 1955 to introduce the parasite into the eastern United States (Puttler et al., 1961). The westward spread was rapid, often without intentional releases in new areas (Davis, personal communication).

Life history of Bathyplectes curculionis

B. curculionis has one or two generations a year. The adult parasites emerge in the spring from overwintering cocoons and the females oviposit in larvae of the alfalfa weevil. The parasite larva feeds within the body of the host which usually does not die until it has spun its cocoon. The full grown parasite larva spins its own cocoon within that of the weevil. The cocoon of the parasite is a small brown capsule with a distinct white band around the middle. Two types of cocoon are produced by B. curculionis larvae (Figure 4). Larvae in light-textured, light brown cocoons give rise to new adults, resulting in a second generation in the same season. The



Figure 3. Adult *Bathyplectes curculionis*. Female (left), male (right).



Figure 4. Cocoons of *Bathyplectes curculionis*. Nondiapausing cocoon (left), Diapausing cocoon (right).

other is the overwintering cocoon which is darker and more heavily constructed. The larvae in these cocoons overwinter in a state of diapause, pupating and emerging as adults in the following spring (Chamberlin, 1926; Newton, 1933; Hamlin et al., 1949a; Brunson and Coles, 1968). Wilson and Armbrust (1970) found in the Vincennes area of Indiana that 39 percent of the first generation cocoons of B. curculionis were nondiapausing.

Hamlin et al. (1949a) reported that in the western United States the overwintered larvae of B. curculionis began pupating in the latter half of March with the pupal stage predominating by the middle of April. The emergence of adult parasites reached its peak in the second week of May.

In the eastern United States, the first brood of B. curculionis begins about 4 weeks before the peak abundance of the alfalfa weevil larvae whereas the second brood begins about 1 to 2 weeks after the peak abundance of the host larvae (Brunson and Coles, 1968).

Butler and Ritchie (1967) studied the development of B. curculionis at different temperatures, using the Egyptian alfalfa weevil, H. brunneipennis, as host. The duration of the combined egg and larval stage of B. curculionis varied from 20.8 days at 59 F (15 C) to 7.1 days at 86 F (30 C). The parasite developed approximately twice as fast as its host during the egg and larval stages.

Host defense reactions against B. curculionis

In 1959, van den Bosch and Dietrick reported that the larvae of the Egyptian alfalfa weevil, H. brunneipennis, in southern California possessed

a partial immunity to B. curculionis. The partial immunity was due to a defense reaction by the host in which its blood cells encapsulated the parasite egg, causing it to die. This phenomenon prevented parasitism by B. curculionis from reaching significantly higher proportions.

Puttler (1967) reported a similar immunity to B. curculionis by the larvae of the alfalfa weevil, H. postica, in Delaware and New Jersey and possibly throughout the weevil's distributional range in the eastern United States. The ability to encapsulate eggs of B. curculionis was thought to be characteristic of the eastern United States population of H. postica as parasites from different areas all evoked encapsulation in essentially the same degree.

Van den Bosch (1964a) found that H. brunneipennis possessed a much greater encapsulating capacity than Californian H. postica. In larvae of H. brunneipennis hemocyte reaction to eggs of B. curculionis was rapid, occurring within 5 hours of oviposition. Full encapsulation could occur within 9 hours and was invariably fatal to the eggs. Partially encapsulated eggs usually survived. Death was thought to result from the capsule's interference with respiration and nutrition of the parasite embryo.

Studies by Salt and van den Bosch (1967) showed that in California, B. curculionis existed in two strains, one in northern California parasitic on H. postica and the other parasitizing H. brunneipennis in southern California. About 94 percent of the eggs of the northern strain evoked a hemocytic reaction in the larvae of H. brunneipennis, 91 percent of this being so strong that the parasite failed to develop. On the other hand, about

50 percent of the eggs of the southern strain were encapsulated in H. brunneipennis. The reaction, however, was weak and less than 15 percent of the parasite eggs failed to develop. H. postica encapsulated less than 1 percent of the eggs of the northern B. curculionis but 15 percent of the eggs of the southern strain.

Eggs and larvae of B. curculionis implanted by the authors in larvae of the clover leaf weevil, Hypera punctata Fabricius, were thickly encapsulated.

The authors concluded from their studies that the population of B. curculionis in southern California had changed since the earlier studies by van den Bosch and Dietrick (1959) and by van den Bosch (1964a). These earlier studies showed a considerable proportion of the eggs of B. curculionis being destroyed in the larvae of H. brunneipennis. In contrast, the investigations by Salt and van den Bosch (1967) showed many southern B. curculionis did not evoke a reaction but successfully developed and destroyed their host. The required adaptation, it was thought, was one that would enable the parasite to avoid encapsulation in H. brunneipennis. Salt (1965) showed that the egg of another ichneumonid parasite, Nemeritis canescens, possessed a protective layer over its chorion which enabled the egg to escape encapsulation in the host. The protective layer was acquired in or near the calyx of the reproductive tract of the female parent.

Factors affecting incidence of encapsulation. Three factors have been shown to influence the incidence of encapsulation of B. curculionis eggs: (a) the degree of superparasitism, (b) the age of the host, and (c) the vigor of

the host (van den Bosch and Dietrick, 1959; van den Bosch, 1964a; Puttler, 1967).

Death of parasites occurs more frequently in lightly parasitized hosts than in heavily superparasitized hosts (van den Bosch and Dietrick, 1959; Puttler, 1967). The older the host, the greater is its encapsulating capacity. Thus fourth instar larvae possess the greatest capacity while first instars essentially lack the encapsulating capacity (van den Bosch, 1964a; Puttler, 1967). Lastly, van den Bosch (1964a) showed that starved hosts encapsulated fewer eggs of the parasite than hosts that were well fed.

Salt and van den Bosch (1967) point out that all three factors may operate through the availability of hemocytes, which can more effectively encapsulate one or a few parasite eggs than many; which are more abundant in older larvae; and which are likely to be less available in weak than in vigorous hosts.

Encapsulation of larvae of *B. curculionis*. In their investigations, Salt and van den Bosch (1967) observed three living larvae of *B. curculionis* that were encapsulated. However, the authors raised the possibility that the hemocytic reactions might not have been made to the surfaces of the larvae but to egg shells that had remained on the larvae. Salt (1965) mentioned other examples of hemocytic reactions to empty egg shells.

Hyperparasites of *B. curculionis*

Among the factors which tend to reduce the effectiveness of *B. curculionis* are hyperparasites. Chamberlin (1924b) recorded *Mesochorus*

nigripes Ratz and Gelis stevenii (Grav.) as the most important among the hyperparasites of B. curculionis in Europe. M. nigripes was also reported to be parasitizing Bathyplectes anurus (Thomson) (then referred to as B. corvina) and B. tristis (Grav.) in Europe. Dysart and Coles (1971) reared M. nigripes from cocoons of B. curculionis, B. stenostigma (Thomson) and B. anurus in Europe. M. nigripes and G. stevenii also issued from B. curculionis material obtained from Europe in the original shipments to Utah (Chamberlin, 1926), and M. nigripes has been reared from B. curculionis material obtained from Iran (Fisher, Schlinger, and van den Bosch, 1961). Perkes (1966) reported an unnamed new species of Mesochorus from cocoons of B. curculionis obtained from Cache Valley, Utah. Krasucki (1925) reared M. nigripes from the larvae of Hypera.

Sorenson (1934a) recorded eight hyperparasites of B. curculionis from the Uintah Basin of Utah. From one to six hyperparasites emerged from one cocoon of B. curculionis. On a few occasions, two different species of hyperparasites emerged from the same cocoon of B. curculionis. Since the total emergence from a single cocoon occurred on the same date, multiple parasitism rather than tertiary parasitism, was thought to be involved. In 1932, 7.79 percent of B. curculionis cocoons were reported to be hyperparasitized. Five of the hyperparasites (Eupteromalus n. sp., Dibrachys boucheanus, and three new unnamed species of Habrocytus) were also observed by the author to have fed as primary parasites on pupae of the alfalfa weevil.

Habrocytus sp. has also been reported as a parasite of the pupae of the Egyptian alfalfa weevil, H. brunneipennis (Fisher et al., 1961) and of the pupae of the alfalfa weevil, H. postica, in India (Rao et al., 1964). Yakhontov (1934) reported Habrocytus crassinervis as a hyperparasite of B. curculionis in Uzbekistan.

Michelbacher (1940b) reared Eupteromalus from cocoons of B. curculionis in California and Hamlin et al. (1949a) reported Eupteromalus viridescens Walsh as a hyperparasite of B. curculionis in the Salt Lake Valley, Utah.

Muesebeck et al. (1951) listed Catolaccus aeneoviridis (Gir.), Dibrachys cavus (Wlkr.), Eupelmella vesicularis (Retz.), Eupteromalus sp., Habrocytus spp., and Tetrastichus bruchophagi Gahan, as hyperparasites of B. curculionis in the United States.

Puttler (1966) reported four hyperparasites from cocoons of B. curculionis collected in New Jersey and Delaware. The species involved were the pteromalids Catolaccus aeneoviridis and Eupteromalus viridescens, the chalcid Spilochalcis albifrons (Walsh), and the ichneumonid Gelis sp. Day (1969) found C. aeneoviridis, Gelis sp., and S. albifrons to parasitize Bathyplectes anurus also.

Day (1969) also found D. cavus to parasitize both B. curculionis and B. anurus in the eastern United States. Earlier, Chamberlin (1924a) had mentioned D. cavus (then referred to as D. boucheanus (Ratzeburg)) as a hyperparasite of B. curculionis in Utah. Dysart and Coles (1971) reared D. cavus from cocoons of Bathyplectes stenostigma (Thomson) in

Europe. D. cavus has been recorded from a wide range of host species (Muesebeck et al., 1951).

Bathyplectes curculionis in Integrated Control of Hypera

Stern (1961) tested the effect of several insecticides on the Egyptian alfalfa weevil, H. brunneipennis, the parasite B. curculionis and other natural enemies of field crop pests, in California. Low dosages of heptachlor (2 to 2.4 ounces per acre) effectively controlled Hypera but had little effect on B. curculionis. Demeton had little or no effect on larvae of H. brunneipennis but had a moderate effect on B. curculionis. Bacillus thuringiensis Berliner, a biotic insecticide, had little effect on both H. brunneipennis and beneficial insects.

Of 12 insecticides evaluated in northern Utah for their possible inclusion in integrated control programs of the alfalfa weevil, Perkes (1966) found parathion (8 ounces per acre), methoxychlor (24 ounces per acre), Imidan (12 ounces per acre), Guthion (16 ounces per acre), and Bomyl (16 ounces per acre) to be suitable. These insecticides gave good weevil control but did not adversely affect B. curculionis.

Davis (1970) also conducted insecticidal experiments in northern Utah for the integrated control of H. postica. Carbofuran and phorate showed promise as early-season treatments in the spring. These insecticides had little or no effect on B. curculionis when used at the 3-inch growth stage. Numbers of the adult parasites were lowered by all treatments applied shortly before the alfalfa was cut; however, only a few longer-lasting

materials reduced the percentage of parasitized larvae. There was a quick return by Bathyplectes to plots treated with shorter residual insecticides. None of the treatments killed the parasitized larvae any more readily than the unparasitized. Postharvest treatments resulted in quick alfalfa growth and only slight damage to the parasites. Imidan, methoxychlor, and trichlorfon were less harmful to the parasites than other candidate insecticides. Trichlorfon was the least harmful to the parasites but was ineffective against H. postica.

In spite of intensive applications of methyl parathion against the alfalfa weevil in the Vincennes area of Indiana, B. curculionis increased in abundance in this area (Wilson and Armsrust, 1970). The authors found the reduction of the parasite to be least with a combination of malathion and methoxychlor applied at the 20 percent feeding stage; the reduction was greatest when methyl parathion was used as a stubble spray. A week's delay in applying methyl parathion to the stubble after the crop was harvested appeared to be less damaging to the parasite than spraying immediately after cutting. In the opinion of the authors, properly-timed chemical applications were compatible with the survival of B. curculionis.

Miscellaneous Literature on B. curculionis

Michelbacher (1940a, 1940b, 1943) found that in lowland middle California, B. curculionis was more effective against the alfalfa weevil in the San Francisco Bay area than in the San Joaquin Valley. The moderate climate of the former region was thought by the author to be better suited to

the parasite than the warmer more continental climate of the San Joaquin Valley.

In observations of the Egyptian alfalfa weevil, Hypera brunneipennis, and certain of its natural enemies in the Nile Valley and Delta, van den Bosch (1964b) found the weevil larvae to be parasitized by B. curculionis. The parasite had two broods, with the second brood going into aestival diapause. From limited samples, maximum parasitization rates of 26.7 percent and 44.0 percent were observed for the first and second broods, respectively. Immunity of the weevil to the parasite was not observed in Egypt but encapsulation occurred when the parasite was tested on H. brunneipennis in California.

The spread of B. curculionis in Illinois was reported by Dysart and Puttler (1965) and by Armbrust et al. (1967). The parasite was discovered in the state in 1964 even though it had not been released there. It was felt that B. curculionis arrived the same year as the alfalfa weevil because parasitization in one county (Pulaski) was substantial at 3.6 percent during the first season of recorded weevil activity. Both the parasite and the weevil had probably been present for at least a year prior to the parasite's discovery in the state (Dysart and Puttler, 1965).

Hagen and Manglitz (1967) studied parasitism of the alfalfa weevil by B. curculionis from 1963 to 1966 in a five-state area immediately east of the Rocky Mountains. The parasite occurred throughout the distributional range of the weevil with the highest rate of parasitism observed being 94 percent. Great fluctuations were observed in both the weevil and parasite populations.

The establishment and recovery of B. curculionis in New York was reported by Horn (1968). All but two of 356 cocoons of the parasite collected in the state in 1965 and 1966 entered diapause. In the opinion of the author this observation suggested that B. curculionis was single brooded in New York.

Wilson et al. (1969) reported on the buildup of B. curculionis in Indiana. In June, 1967, moderate parasitism of the alfalfa weevil by B. curculionis was observed near Vincennes, Knox County, and by May, 1968, a general buildup of the parasite was evident. The observation was particularly interesting because colonization attempts had not been made within 100 miles of Knox County, and the parasite buildup was in an area where alfalfa had been intensively treated in the previous season with methyl parathion.

Studies by Miller (1970a) of Hypera postica larval populations in Massachusetts for parasite activity showed increases in the duration and magnitude of parasitism by B. curculionis and decreases by Tetrastichus incertus (Ratzeburg), another larval parasite of H. postica. Neither parasite, either alone or in combination, was capable of preventing damage by H. postica.

Miller (1970b) also conducted instar preference and interspecific competition tests between B. curculionis and T. incertus for their host, the larval H. postica. B. curculionis preferred first to third instars of the host over fourth instars. On the other hand, T. incertus attacked second to fourth instars in preference to first instars. Parasitism by

B. curculionis increased under competition, while that of T. incertus decreased.

Studies of the feeding behavior of H. postica larvae parasitized by B. curculionis, were made by Armbrust, Roberts, and White (1970a). On a daily basis, an unparasitized larva consumed slightly more alfalfa (1.14 mg) than a parasitized larva. The difference, however, was non-significant. The alfalfa consumed per larva during the third and fourth instars was 16.85 mg more for an unparasitized than for a parasitized larva. Unparasitized larvae fed 1.3 days longer than parasitized larvae. The authors felt that the reduction in alfalfa consumed and the shorter feeding period of parasitized larvae could explain their field observations that under conditions of high parasitization the amount of damage observed was not proportional to the larval population.

In a study of the distribution and life history of B. curculionis in northern Idaho, Foster and Bishop (1970) found that the parasite was restricted to its host, H. postica, and showed no affinity for the closely-related species Hypera zoilus (Scopoli) and H. nigrirostris (Fabricius). In the field, B. curculionis effectively parasitized first, second, and third instars of the host larvae but was ineffective against the fourth instars. Under laboratory conditions, however, the parasite readily oviposited in all larval instars of the host.

Parasites of *Hypera*, other than *Bathyplectes curculionis*

In addition to *B. curculionis*, many parasites are recorded in the literature for *H. postica* and its closely-related species. Thus Chamberlin (1924b) mentioned 14 primary parasites of the alfalfa weevil in Europe. Several parasites were bred from the weevil in Uzbekistan (Yakhontov, 1934). Fisher et al. (1961) reported on five parasites of the Egyptian alfalfa weevil imported into the United States from Iran, and Brunson and Coles (1968) summarized the introduction of 10 parasites of the alfalfa weevil into the eastern United States. The latter authors also reported five native parasites of the alfalfa weevil from the eastern United States.

Bathyplectes spp., other than

B. curculionis

Bathyplectes anurus (Thomson). This parasite was formerly referred to as *Bathyplectes corvina* (Chamberlin, 1924a, 1924b; Day, 1970). *B. anurus* is a univoltine species which parasitizes first and second instar larvae of *H. postica*. The parasite overwinters as a diapausing adult inside its cocoon. The parasite larva is capable of causing its cocoon to jump (Brunson and Coles, 1968). Day (1970) found that the jumping ability of its cocoon increased the survival of diapausing *B. anurus* larvae by enabling many to escape hyperparasites and adverse microclimates. Puttler (1967) found no evidence of encapsulation of eggs of *B. anurus* in the eastern United States form of *H. postica*.

Bathyplectes stenostigma (Thomson). B. stenostigma is a univoltine parasite of the alfalfa weevil larvae which was discovered in Europe in 1961 (Dysart and Coles, 1971). According to these authors B. stenostigma is the parasite which was referred to as Bathyplectes n. sp. by Puttler (1967) and as Bathyplectes sp. "bagged" and Bathyplectes n. sp. by Brunson and Coles (1968, pages 5 and 8, respectively) when describing the release of this parasite in the eastern United States. Dysart and Coles (1971) also state that B. stenostigma is again the parasite which Day (1969) and Miller (1970a) mentioned as B. contracta.

B. stenostigma females parasitize all instars of H. postica but smaller larvae are preferred (Dysart and Coles, 1971).

Observations in Europe showed that H. postica larvae are attacked in sequence by B. anurus, B. curculionis, and B. stenostigma with minimal competition between the three parasite species (Dysart and Coles, 1971). Puttler (1967) did not observe any hemocytic reaction to the eggs of B. stenostigma in the larvae of H. postica in the eastern United States.

Other species of Bathyplectes. Chamberlin (1924b) mentioned B. tristis (Grav.) as a parasite of the larvae of Hypera postica and H. punctata in Europe. The same author (Chamberlin, 1933) also found B. exigua (Grav.) to occur sparingly on Hypera rumicis in Oregon. The usual host of B. exigua was H. nigrirostris. Rao et al. (1964) recorded an unnamed species of Bathyplectes from the larvae of H. postica in India.

Tetrastichus incertus (Ratzeburg)

(Hymenoptera: Eulophidae)

T. incertus parasitizes mostly third and fourth instar larvae of H. postica which, after spinning their cocoons and succumbing to the parasite, assume a mummified appearance. The parasite produces a variable number of progeny per host, but the usual number is about five. There are several generations per year. The parasite diapauses and overwinters in the host mummies. T. incertus was introduced into the eastern United States, beginning 1960 (Brunson and Coles, 1968). Schroder et al. (1969) reported on the distribution and establishment of the parasite in the eastern United States.

T. incertus was among the parasites of the alfalfa weevil studied by Chamberlin (1924b) in Europe. In 1925 Chamberlin also published features of the life history of the parasite together with its previous history and distribution.

Miller (1966) studied the emergence and mating of T. incertus, and Streams and Fuester (1967) reported on the biology and the distribution of the parasite around a 1961 release site in Pennsylvania. The female parasite was usually observed to feed on the host fluid after parasitization was completed. Parasitism in southeastern Pennsylvania averaged 71 and 73 percent during the summer months of 1964 and 1965, respectively.

The oviposition behavior of T. incertus was studied by Horn (1970). Studies by Miller (1970a, 1970b) on Bathyplectes curculionis and T. incertus as biological control agents of H. postica in Massachusetts, and on interspecific competition between the two parasites have already been referred to.

Microctonus spp. (Hymenoptera: Braconidae)

Two species of Microctonus, M. aethiops (Nees) and M. colesi Drea (Drea, 1968a), occur on the alfalfa weevil in the eastern United States (Coles and Puttler, 1963; Brunson and Coles, 1968).

M. aethiops, a double brooded parasite, was released on the alfalfa weevil at different localities in the eastern United States, beginning in 1957. It parasitizes the adult weevil (Brunson and Coles, 1968). According to Coles and Puttler (1963), M. aethiops has been recorded on adult weevils of the genera Hypera and Sitona in Europe and was introduced into the United States from France in 1948 against the sweet clover weevil, Sitona cylindricollis (Fabricius).

The second parasite, M. colesi, was first found in Pennsylvania parasitizing H. postica (Coles and Puttler, 1963), and it possibly was present in the weevils originally introduced into the eastern United States (Brunson and Coles, 1968). According to Fuester (1970), M. colesi was the species referred to as Microctonus sp. "Domestic Black" by Brunson and Coles (1968). Drea (1968a) described it as a new species.

M. colesi is unisexual and univoltine (Drea, 1968b) and parasitizes large weevil larvae. The parasite completes its development in, and emerges from, the adult weevil to form a gray cocoon (Brunson and Coles, 1968).

Drea (1968b) reported on a third Microctonus parasite, Microctonus n. sp., said to be known only from H. postica in France. This species is bisexual and like M. colesi, parasitizes the larval stage of the host.

Partial to complete castration may result when males of H. postica are parasitized by Microctonus spp. (Drea, 1968b). Brunson and Coles (1968) reported that sexually mature H. postica females cease oviposition almost immediately after parasitization by M. aethiops. The reproductive organs of parasitized first-brood weevils fail to develop normally and the parasitized weevils do not reproduce.

Parasites of the prepupae and pupae
of Hypera

Dibrachoides druso (Walker) (Hymenoptera: Pteromalidae). Formerly referred to as Dibrachoides dynastes (Foerster), D. druso is an external parasite of the prepupae and pupae of the alfalfa weevil (Chamberlin, 1924b; Smith, 1930; Clausen, 1956; Brunson and Coles, 1968). Fisher et al. (1961) reported D. druso as a gregarious ectoparasite of mature larvae, prepupae and pupae of the Egyptian alfalfa weevil, Hypera brunneipennis. Laboratory investigations indicated, however, that the parasite prefers mature larvae. The parasite has also been reared from Hypera nigrirostris (Fab.) and bred in the laboratory from Hypera punctata (Fab.) (Smith, 1930; Chamberlin, 1933).

D. druso was released in Utah against the alfalfa weevil in the period 1911-13 and has since been collected in that and other states (Clausen, 1956). The parasite was also colonized on H. brunneipennis in southern California in 1961-62 (Gonzalez, van den Bosch, and Dawson, 1969).

Hemiteles graculus (Gravenhorst) (Hymenoptera: Ichneumonidae). H. graculus is a Palearctic ectoparasite of the pupae and prepupae of the alfalfa weevil, H. postica (Chamberlin, 1924a; Puttler, 1963). Oviposition by the parasite is preceded by paralysis of the host caused by repeated insertion of the parasite's ovipositor into the host's abdomen. The female parasite feeds on the host during the process of paralyzing the latter (Puttler, 1963). The author also observed that the insertion of the ovipositor of the female H. graculus into H. postica cocoons not only paralyzed the hosts but also larvae of Bathyplectes curculionis which were present in the hosts.

Other prepupal and pupal parasites. Poinar and Gyrisco (1963) recovered two hymenopterous parasites, Spilochalcis albifrons (Walsh) and Gelis sp., from the pupae of H. postica in New York. Later, S. albifrons and Gelis sp. were reported as hyperparasites of Bathyplectes curculionis and B. anurus (Puttler, 1966; Day, 1969).

Rao et al. (1964) recorded the eulophid Necremnus sp. as a pupal parasite of H. postica in India. The parasite was identified as very closely related to the species N. leucarthros (Nees). Chamberlin (1924b) reported Necremnus leucarthros as a parasite of the prepupae of H. postica in Europe. He (Chamberlin, 1933) also mentioned an unnamed species of Necremnus as an external parasite of the prepupae and pupae of Hypera rumicis (L) in Oregon.

The pteromalid genus Habrocytus has also been reported as a prepupal and pupal parasite of Hypera. Fisher et al. (1961) reported that although Habrocytus sp. could develop as a gregarious ectoparasite of

mature larvae, prepupae, or young pupae of Hypera brunneipennis, the parasite preferred young pupae of the host. Rao et al. (1964) reared Habrocytus sp. from field-collected pupae of H. postica in India. Habrocytus spp. have also been mentioned as hyperparasites of Bathyplectes curculionis (Sorenson, 1934a; Muesebeck et al., 1951).

Chamberlin (1924b) reported Itopectis maculator (Fab.) as parasitizing the prepupae and pupae of H. postica in Europe while Shaw and Ziener (1964) recovered Itopectis conquisitor (Say) from H. postica pupae in Massachusetts. A wide host range has been recorded for I. conquisitor (Muesebeck et al., 1951).

Egg parasites of Hypera

Several parasitic species are recorded as attacking the eggs of Hypera postica (Chamberlin, 1924b; Brunson and Coles, 1968). The pteromalid Peridesmia phytonomi Gahan was considered by Chamberlin (1924b) as probably the most important of all the egg parasites of H. postica in Europe. P. phytonomi also attacked the eggs of Hypera punctata. Two other pteromalid egg parasites, Peridesmia discus (Walker) and Trichomalus inops (Walker) were imported from southern France into the United States against H. postica (Brunson and Coles, 1968). The mymarid Patasson luna (Girault), has been recorded as a parasite of the eggs of H. postica (Chamberlin, 1924b; Shaw and Ziener, 1964; Brunson and Coles, 1968). Chamberlin (1924b) also mentioned P. luna (then referred to as Anaphoidea luna) as an egg parasite of H. punctata. Fisher et al. (1961) and van den Bosch (1964b) reported

unidentified species of Patasson as attacking the eggs of H. brunneipennis.

Hamlin et al. (1949a) recorded the mymarid species Anaphes pratensis Foerst. as an internal egg parasite of H. postica.

Miscellaneous parasites of H. postica

Krasucki (1925) reared from the larvae of Hypera the ichneumonid parasites, Stenocryptus nigriventris Thoms., Adelognathus sp. and Mesochorus nigripes Ratz. The latter has also been reported as a hyperparasite of Bathyplectes spp. (Chamberlin, 1924b, 1926; Fisher et al., 1961; Dysart and Coles, 1971).

In addition to Bathyplectes curculionis and B. anurus, another ichneumonid Cryptus sp. and an eulophid Tetrastichus sp. were reared from the larvae of the alfalfa weevil in Uzbekistan (Yakhontov, 1934). The braconids Microctonus aethiops (then referred to as Perilitus aethiops), M. secalis, Dinocampus coccinellae and an unidentified species were recovered from adult weevils.

Two tachinid species, Campogaster exigua (Meigen) and Hyaolmyodes triangulifera (Loew) were mentioned by Brunson and Coles (1968) as parasitic on adult H. postica.

Non-insect parasites of H. postica. Yakhontov (1934) recorded the mite Erythraeus nemorum Koch as a parasite of the alfalfa weevil. It was bred from the adults.

A mermithid nematode Hexameris arvalis Poinar and Gyrisco, parasitic on the alfalfa weevil, was reported and described from New York

state (Poinar and Gyrisco, 1960, 1962a, 1962b). The nematode was found parasitizing the larvae, and, on several occasions, the pupae and adults of H. postica. From one to three nematodes were found in a single larva. Parasitized larvae were wrinkled and slightly larger than normal larvae. They were bulky in appearance, sluggish and responded less to probing than normal larvae. Parasitism reached 33 percent in some fields, but H. arvalis was not considered economically important because of its sparse and irregular distribution and low numbers in most fields.

MATERIALS AND METHODS

General Rearing Techniques

Rearing of parasite-free *Hypera postica* larvae

Adult alfalfa weevils were collected in the spring and summer by sweeping infested alfalfa fields in Cache Valley, northern Utah. In the winter months, the adult weevils were obtained by putting debris and soil collected from weevil overwintering sites in Berlese funnels in the laboratory.

Collection of eggs. The weevils were placed in 1-gallon glass jars (Figure 5) each provided with a bouquet of alfalfa held in a water-filled plastic vial measuring 8.5 cm high and 4 cm in diameter. The glass jars were covered with nylon cloth held in place by rubber bands. The alfalfa bouquets served as food and oviposition sites for the weevils. The bouquets were replaced every other day and the old stems were examined for eggs. The leaves were stripped off the stems which were then split with a razor blade. Two methods were employed in removing the eggs. The usual method was to remove the eggs with a moist camel hair brush and place them on moist filter papers in 9 cm diameter petri dishes. There were two filter papers per dish. When many stems and eggs were involved, the split stems were cut into smaller pieces and placed in a tray filled with water. The eggs were then washed off from the stem pieces, sieved and placed on moist filter papers



Figure 5. An ovipositional cage used in rearing field-collected adult alfalfa weevils.

in petri dishes as before. When not immediately needed, the eggs were stored at 7-10 C.

Rearing of larvae. The eggs in closed petri dishes were incubated at temperatures fluctuating between 26 C and 30 C. The eggs hatched in 5-6 days, with the majority hatching on the fifth day.

The newly-hatched larvae were transferred with a moist camel hair brush into glass jars each measuring 6 cm high and 6 cm in diameter and filled with alfalfa leaves. After 3-4 days, the larvae were usually transferred to alfalfa bouquets in glass jars. Weevil-free alfalfa raised in the greenhouse was used in rearing the larvae. The rearing of the larvae was maintained at a temperature of 25-26 C and a photophase of 8 hours. The relative humidity was about 40 percent. Under these conditions, the larvae molted about every 3-4 days. About 3-4 days were also required from the fourth instar stage to the spinning of the cocoon. A further 2-3 days were required from the cocoon stage to the pupal stage which lasted about 5 days. On the average the weevils developed from egg deposition to adults in about 27 days.

Rearing of adult *Bathyplectes curculionis*

Alfalfa weevil larvae were also collected in the spring and summer by sweeping infested alfalfa fields in Cache Valley, Utah. The larvae were reared in the laboratory in 1-gallon ice cream cartons provided with alfalfa leaves as food. More food was added as necessary until the adult weevil stage was reached or, in the case of parasitized larvae, the cocoons of *Bathyplectes* were formed.

Diapausing Bathyplectes cocoons were maintained at a temperature of about 26 C and 16 hours photophase for about a month and then stored in a cold room at about 2 C for at least 3 months. The cocoons were then removed as required and held at 26 C for emergence of adult B. curculionis.

The emergence chamber (Figure 6) consisted of a plastic vial (8.5 cm high and 4 cm in diameter) the bottom of which had been removed and replaced with a piece of nylon cloth. The cocoons were put in the vial placed on a piece of wire gauze resting on a water-filled plastic cup in a 1-gallon glass jar. The evaporation of water from the cup provided the necessary humidity for the cocoons.

On an average, the adult Bathyplectes emerged in 12-21 days. The ratio of female parasites to males, determined from a sample of 393 individuals, was 1.3:1.0. Upon emergence, the parasites were left in the emergence chamber for about 24 hours. Miller (1970b) considered this period sufficient for mating to occur. When not immediately needed the parasites were placed in cages and stored at 7-10 C. The cages had holes in the sides with plugs of cotton moistened with a mixture of honey and water which served as food for the parasites.

Determination and Calculation of Percentage Parasitism

Determination of parasitism

Unless otherwise stated, the determination of parasitism was done by rearing the weevil larvae and counting the numbers of mature Bathyplectes larvae (either in cocoons or not) and the numbers of host pupae

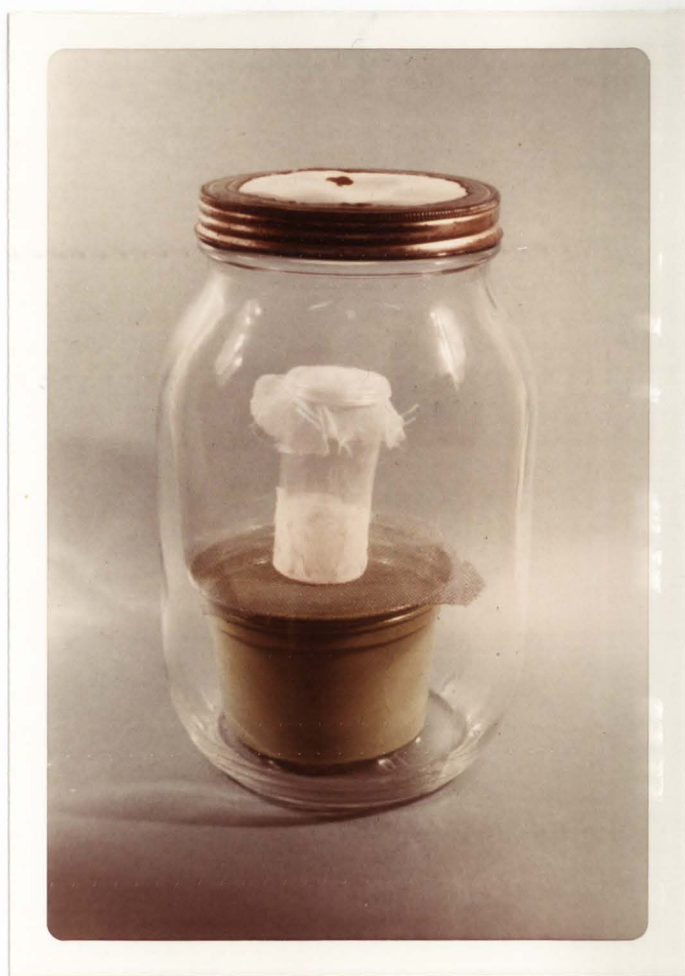


Figure 6. Equipment used for the emergence of adult Bathyplectes curculionis.

formed. The rearing was done in 1-pint ice cream cartons provided with bouquets of alfalfa and covered with petri dish halves. The dissection of alfalfa weevil larvae to determine parasitism by Bathyplectes has also been used by some investigators (Hamlin et al., 1949a; van den Bosch and Dietrick, 1959).

Several workers found no difference between the rearing and dissection methods in determining percentage parasitism of alfalfa weevil larvae by B. curculionis (Puttler, 1967; Wilson et al., 1969; Wilson and Armbrust, 1970). Hagen and Manglitz (1967), however, obtained largely negative results by dissection and so used rearing to determine parasitism. Michelbacher (1940a), Perkes (1966) and Miller (1970a) also used the rearing method to determine parasitism. The rearing method is less tedious and provides live material for other studies (Davis, 1970). Unifested alfalfa from the greenhouse was used in rearing the larvae.

Calculation of percentage parasitism

Since some larvae died during rearing and it was difficult to determine whether these were parasitized or not, the calculation of percentage parasitism was based on the numbers of parasites and weevils recovered respectively as mature larvae (either in cocoons or not) and as pupae. Dead weevil larvae were disregarded. Michelbacher (1940a) and Oatman, Platner, and Greany (1969) respectively used this method to calculate percentage parasitism of the larval alfalfa weevil by B. curculionis and of the potato tuber-worm by the braconid parasite Orgilus lepidus Muesebeck. The method is

similar to that advocated by Chamberlin (1926) for the determination of parasitism of H. postica larvae by B. curculionis and which he thought represented more closely parasitism in the field. Chamberlin suggested a comparison of the number of parasite cocoons formed with the number of adult weevils emerging.

Studies Aimed at Identifying Parasitized Larvae

Color segregation of field-collected larvae

Some reports in the literature suggest that alfalfa weevil larvae parasitized by B. curculionis are lighter green than normal larvae (Newton, 1933; Sorenson, 1934b). Fourth instar larvae were, therefore, collected from the field and segregated according to color. The two color forms present were green and light green or yellow. The larvae in each color group were reared in smaller groups of 100 each to determine parasitism. Survival of the two groups of larvae at the end of the experiment was also determined by counting the numbers of weevil pupae and mature parasite larvae (either in cocoons or not). There were six replicates in each color group.

Transmission of light through larvae

An attempt was made to identify parasitized larvae by transmitting light through them. The aim was to detect the parasite larva within the host. Larvae collected from the field and those reared in the laboratory and exposed to female parasites, were examined individually under a dissecting microscope

with the larvae being illuminated by a light source underneath the stage of the microscope.

Separation of larvae with lesion-like areas

Early in the study, some members of a group of larvae raised and exposed to female parasites in the laboratory were observed to have a yellowish or pale area on the body. In some cases the affected area was also swollen. I suspected that the larvae with such marks might be parasitized and the mark to be characteristic of parasitized larvae. These larvae were, therefore, separated from the normal-looking larvae and both groups were reared.

Host Instar Parasitization and Survival Studies

Experiments were conducted to determine the preference of B. curculionis females for the four instars of the alfalfa weevil larvae and to test the survival of these instars following parasitization.

Separate parasitization of different instars

In these experiments, each instar was parasitized separately and percentage parasitism and instar survival following parasitization were determined. Fifty larvae of each instar were exposed to two female parasites for 12 hours under continuous light. Parasites were discarded after each test. A parasitization cage (Figure 7) consisted of a 1-pint glass jar (9 cm high and 9 cm in diameter) holding a bouquet of alfalfa in a plastic vial. The bracts and buds were removed from the bases and axils respectively of the alfalfa leaves to eliminate hiding places for the smaller larvae. The larvae

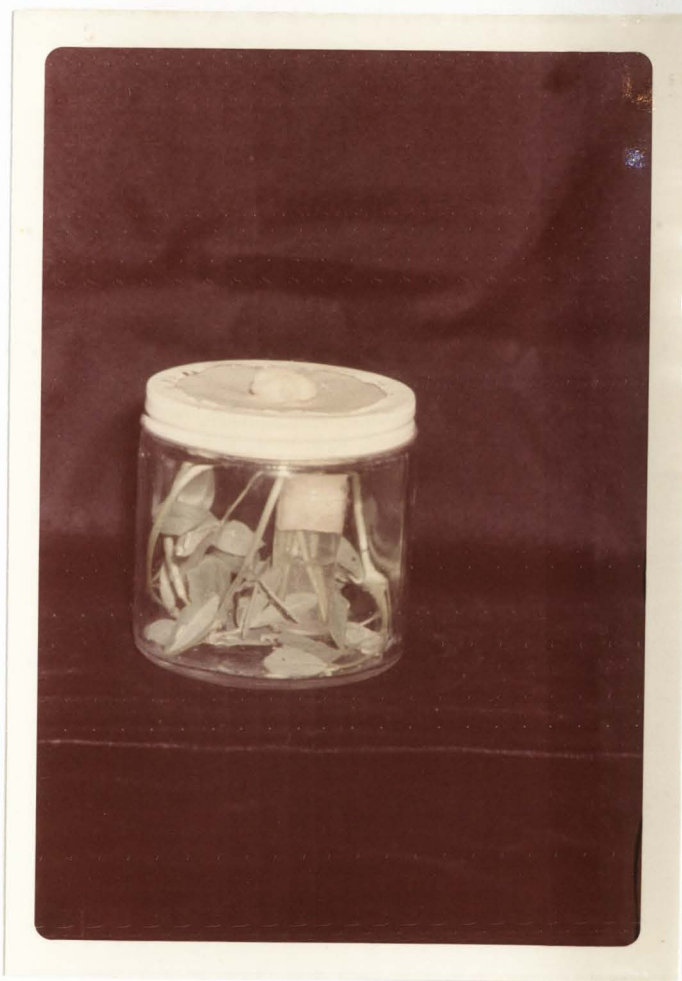


Figure 7. Cage used in parasitization of alfalfa weevil larvae by Bathyplectes curculionis.

were placed on the alfalfa bouquet. The cage was stoppered with a metal lid from which most of the surface had been removed and replaced with organdy. A hole in the center of the lid held a piece of cotton moistened with a mixture of water and honey which served as food for the parasites.

The number of live individuals were determined at 12 hours and 5 days after the start of the experiment and at the end of the experiment--the pupal stage of the weevils or the mature larval stage of the parasites (either in cocoons or not). The percentage parasitism was determined as described previously.

A control test was run to compare the survival of parasite-free larvae with those exposed to the parasites. There were eight replications of each series.

Simultaneous exposure of host instars to parasites

The preference of B. curculionis for the different instars of the alfalfa weevil larvae and the survival of the parasitized host instars were again studied by exposing larvae of all instars simultaneously to female parasites. Twenty-five larvae of each instar (a total of 100 larvae) were exposed to two female B. curculionis in a parasitization cage under the same conditions as described above for the "separate parasitization of different instars." A control test was also run and survivors were determined at the same periods as before. Each series was replicated six times.

Individual host "stinging" and survival studies

The survival of first and second instar alfalfa weevil larvae was further studied after the larvae had been punctured by B. curculionis ovipositors. The larvae were placed in small groups in a petri dish with a female parasite and observed continuously. Larvae were removed after being "stung." Twenty larvae of each instar were individually "stung" once by a female parasite. Twenty larvae from each instar were also individually "stung" three times each by a female parasite. The numbers of survivors of the "stung" larvae were compared daily with those of a control group until the larvae spun their cocoon.

Some observations were made on the ovipositional behavior of B. curculionis during these studies.

Larval Development and Activity Studies

The development and activity of parasitized and unparasitized larvae were studied at 25-26 C and under 8 hours photoperiod. The relative humidity was about 40 percent.

Development of parasitized and unparasitized larvae

Twenty larvae of each instar were parasitized and the number of days they required to develop to the cocoon stage was compared with that of unparasitized larvae of the same instar. For tests involving the second, third and fourth instars, newly-molted larvae were used. Larvae in the

pre-molt stage were selected and held overnight. Those which molted within 12 hours were used in the experiments. The procedure provided experimental insects which were similar in age, size and physiological state (Waldbauer, 1962, 1964). A portion of the newly-molted larvae was exposed to female parasites; the other portion was left unparasitized and used as a control.

For experiments involving first instar larvae, 1-day old larvae were used. I realized that the use of newly-hatched larvae would carry the same advantages as did newly-molted larvae of older instars. In fact the first tests using first instars were with newly-hatched larvae but because parasitism by B. curculionis of these larvae was erratic, they were abandoned in favor of 1-day old larvae.

Activity of parasitized and unparasitized larvae

The activity of parasitized and unparasitized second and fourth instar larvae in the larval development studies was measured by placing a larva on a grid divided into 1 cm squares and counting the number of squares entered by the larva in 5 minutes. The measurements were begun a day after the larvae had molted (and the group to be parasitized had been exposed to parasites) and repeated daily until 50 percent or more of either the parasitized or the control larvae spun the cocoon.

Growth and the Consumption and Utilization of Food Studies

Measurements of food consumption and utilization and of growth by parasitized and unparasitized alfalfa weevil larvae were made during the third

and fourth instars at temperatures of 22.2 C and 30 C. The larvae were tested individually, each larva being held in a 5.5 cm diameter petri dish lined with two moistened filter papers. The photoperiod regime was 12 hours light and 12 hours darkness; the relative humidity varied between 20 and 30 percent at 22.2 C and was about 40 percent at 30 C. Food consumption and utilization were measured on a dry weight basis. (See, however, the calculation of dry weight-fresh weight consumption index, below.) Specimens were dried in a vacuum oven at 103 C for at least 48 hours. Growth was measured by recording the daily fresh weights of each larva. Records were also taken of the gain in larval fresh weight from the beginning of the third instar to the day preceding the cocoon formation and the gains in fresh and dry weights at the cocoon stage. Weighings were done on a Cahn microbalance (Model GRAM).

The experiments began with starved, newly-molted third instar larvae and terminated when the larvae spun their cocoon. Second instar larvae in the premolt stage were held overnight without food. Larvae which molted into the third instar within 12 hours were selected for the experiments. Waldbauer (1962, 1964) pointed out the advantages of using starved, newly-molted insects in feeding and growth studies. The experiments are started with animals similar in age, size and physiological condition and the guts are almost empty of residual fecal material.

A portion of the newly-molted larvae was exposed to female parasites and the other portion was used as control larvae.

Food consumption and utilization

According to Waldbauer (1968) "utilization" of food is "a general term which includes digestion, metabolism and conversion to body substance." In these studies the consumption and digestibility of food as well as the conversion of ingested and digested food to body matter were measured for parasitized and unparasitized larvae.

A modification of the method employed by Koehler and Gyrisco (1963) to study the feeding behavior of the adult alfalfa weevil, was used in the present work to measure food consumption. These workers found no significant difference between weights of 70 pairs of opposite leaflets of alfalfa trifoliolates, selected for similarity. Thus if one of the leaflets was offered to a weevil for consumption and the opposite leaflet was held as a control, the difference in weight between the control leaflet and the partly eaten leaflet represented the quantity consumed.

In the present study, I compared the fresh and dry weights of leaf discs (6.5 mm in diameter) punched from equivalent positions of opposite leaflets of alfalfa trifoliolates. As in Koehler and Gyrisco's (1963) study, the leaflets were chosen for similarity in surface area and thickness. The fresh and dry weights of 100 pairs of leaf discs were compared statistically and no significant differences were found (Table 1).

It was also observed that many middle leaflets of alfalfa trifoliolates were symmetrically divided by the midrib and that the opposite halves were similar in thickness and surface area. The fresh and dry weights of 100 pairs of leaf discs punched from equivalent positions of opposite halves of such

Table 1. Fresh and dry weights of 6.5 mm leaf discs from equivalent positions of opposite leaflets of alfalfa trifoliolates

State of leaf disc	Mean weight (mg) of 100 leaf discs	
	A	B
Fresh	3.58	3.59 ^{NS}
Dry	0.749	0.750 ^{NS}

NS = Not significantly different at the 5% level.

Table 2. Fresh and dry weights of 6.5 mm leaf discs from equivalent positions of opposite halves of middle leaflets of alfalfa trifoliolates

State of leaf disc	Mean weight (mg) of 100 leaf discs	
	A	B
Fresh	4.39	4.41 ^{NS}
Dry	0.837	0.841 ^{NS}

NS = Not significantly different at the 5% level.

middle leaflets were, therefore, compared statistically. Again no significant differences were evident (Table 2).

Thus in the present investigation, if a leaf disc from either one of the opposite leaflets or one half of a middle leaflet was offered to a larva, a disc from the equivalent position of the opposite leaflet or the opposite half of the middle leaflet was held as a control. It was usually necessary to feed more than one leaf disc to a larva. The control leaf discs were kept under the same conditions of temperature and humidity as those supplied to the larvae. Uneaten portions of leaf discs were collected daily and replaced with fresh discs. The uneaten portions of leaf discs and the control discs were then dried and weighed. The difference between the dry weight of control leaf discs and the dry weight of the uneaten portions of leaf discs supplied to a larva, represented the dry weight of alfalfa consumed by the larva.

The feces of each larva were also removed daily, dried and weighed.

Consumption index. The consumption index proposed by Hopkins (1912) as the rate of food intake by an animal relative to the mean weight of the animal during the feeding period, was calculated for parasitized and unparasitized larvae. Waldbauer (1962, 1964, 1968) suggested the calculation of the consumption index (C.I.) as:

$$C.I. = \frac{F}{TA}$$

where: F = weight of food consumed.

T = duration of feeding period in days.

A = mean weight of animal during feeding period.

Waldbauer (1968) pointed out that consumption indices may be calculated from: (a) the fresh weight of the food eaten and the mean fresh weight of the animal (fresh weight C.I.); (b) the dry weight of food and the mean fresh weight of the animal (dry weight-fresh weight C.I.); and (c) the dry weight of food and the mean dry weight of the animal (dry weight C.I.).

The dry weight-fresh weight C.I. was used in the present study. The method of Soo Hoo and Fraenkel (1966) was used in calculating the mean fresh weight (A) of a larva. The mean weight was obtained by dividing the sum of the initial, final and intermediate weights by the number of weighings. Waldbauer (1962) estimated the mean fresh weight of the tobacco hornworm (Manduca sexta) by averaging the initial and final weights. However, in a later publication (Waldbauer, 1964), he calculated the mean weight from weighted averages of daily weights.

Approximate digestibility. The approximate digestibility (A.D.) (Waldbauer, 1968) of food by a larva was calculated as:

$$\text{A.D.} = \frac{\text{Dry weight of food ingested} - \text{Dry weight of feces}}{\text{Dry weight of food ingested}} \times 100$$

A number of authors, including Trager (1953) and Waldbauer (1964), referred to the approximate digestibility as the "coefficient of digestibility." Waldbauer (1968), however, thought that this was misleading because in insects "the difference between the weight of food ingested and the weight of the feces actually represents the food which is stored or metabolized less metabolic wastes discharged in the urine or as fecal metabolic products." The approximate digestibility has also been referred to as the "coefficient of

utilization" or the "percentage utilization" (Evans, 1939; Evans and Goodliffe, 1939; Crowell, 1941; Smith, 1959; Dadd, 1960; Hirano and Ishii, 1962) but Waldbauer (1968) again considers this term inappropriate.

Conversion of ingested food to body matter. The efficiency with which a larva converted ingested food to body matter (E.C.I.) (Waldbauer, 1964, 1968) was calculated as:

$$\text{E.C.I.} = \frac{\text{Dry weight gained by larva}}{\text{Dry weight of food ingested}} \times 100$$

Conversion of digested food. The conversion by a larva of digested food into body tissue (E.C.D.) (Waldbauer, 1964, 1968) was calculated as:

$$\text{E.C.D.} = \frac{\text{Dry weight gained by larva}}{\text{Dry weight of food ingested} - \text{Dry weight of feces}} \times 100$$

The dry weight gained by a larva was calculated as the difference between the dry weight of the larva at the end and the beginning of the experiment. Parasitized larvae, at the end of the experiment, were first dissected and the parasite larvae removed before the host larvae were dried and weighed. The fresh and dry weights of parasite larvae were also determined. The final dry weight of a parasitized larva was taken as the sum of the dry weights of the host and the parasite larva at the end of the experiment.

A direct measurement of the dry weight at the beginning of the experiment was, of course, impossible. An estimate of the initial dry weight of each larva was, therefore, calculated from the mean percentage dry matter

of 50 newly-molted, starved third instar larvae which had been killed by freezing and dried.

The period of the experiment included one molt by the larvae (from the third to the fourth instar) and the spinning of the cocoon. Since these physiological processes resulted in weight loss to the larvae, the weight gain obtained in the experiment was actually a "net weight gain," lower than the "gross" or "total weight gain." Thus the E.C.I. and E.C.D. which were calculated using the "net weight gain" were actually net E.C.I. and net E.C.D. (Waldbauer, 1968).

Analysis of Data

Statistical analysis of the data on the host instar parasitization and survival studies was by the analysis of variance and the F test of significance. In addition, Duncan's multiple range test was used to determine possible significant differences among means in experiments with more than two treatments.

The data on the larval development and activity studies and on the growth, food consumption and food utilization experiments, were statistically analyzed by the "t" test.

RESULTS

Studies Aimed at Identifying Parasitized Larvae

Color segregation of field-collected larvae

The rearing of field-collected, green and yellow fourth instar Hypera postica larvae showed that 11.3 and 32.7 percent of the green and yellow larvae respectively were parasitized by Bathyplectes curculionis. The difference in the rates of parasitism was significant at the 1 percent level. Only 45.7 percent of the mature parasite larvae from the two types of hosts constructed cocoons. The rest died without constructing cocoons.

Survival of the H. postica larvae at the end of the experiment was obtained by counting the numbers of H. postica pupae and mature B. curculionis larvae (either in cocoons or not). The survival rate for the green larvae was 88.3 percent and that for the yellow larvae, 76.8 percent. The difference was significant at the 5 percent level.

Transmission of light through larvae

Efforts to identify parasitized H. postica larvae by transmitting light through them to detect B. curculionis larvae were unsuccessful. The weevil larvae were so opaque that their contents were impossible to see.

Separation of larvae with lesion-like areas

The presence of lesion-like areas on some H. postica larvae which had been exposed to B. curculionis proved to be unrelated to parasitism.

Both adult weevils and parasite cocoons were recovered from this group of larvae. On the other hand, both adult weevils and parasites also developed from another group of larvae which had been exposed to B. curculionis but which were without lesions. Later in the study, lesion-like areas were observed on some laboratory-reared H. postica larvae which had not been exposed to parasites.

Host Instar Parasitization and Survival Studies

Separate parasitization of different instars

Parasitism rates. The rates of parasitism by B. curculionis of the four instars of H. postica larvae after the separate exposure of each instar to female parasites, are given in Table 3. In each test, 50 host larvae were exposed to two female parasites for 12 hours. There were eight replications of each series.

Each of the means for the first, second and third instars differed significantly at the 1 percent level from the mean for the fourth instar, as determined by Duncan's multiple range test. There was, however, no significant difference at the 5 percent level among the means for the first three instars.

Instar survival. Table 4 summarizes the survival of the four instars of H. postica larvae after the separate exposure of the instars to B. curculionis females. There was no significant difference in each instar between the survival of unexposed and exposed larvae within 12 hours from the start of

Table 3. Rates of parasitism of the instars of H. postica larvae after being separately exposed to B. curculionis females.

Instar	Original no. of larvae per replicate	Mean no. of survivors (hosts + parasites) per replicate at weevil pupation/mature larval parasite stage	Mean ^{a, b, c} % parasitism ^d
1st	50	16.0	75.6 a
2nd	50	25.4	71.4 a
3rd	50	34.3	71.0 a
4th	50	43.4	13.5

^aMean of 8 replicates.

^bMeans followed by the same letter are not significantly different at the 5% level as determined by Duncan's multiple range test.

^cMeans for the 1st, 2nd and 3rd instars are each significantly different at the 1% level from the mean for the 4th instar.

^dBased on no. of survivors (hosts + parasites).

the experiment. However, survival of the unexposed larvae of each of the first three instars was generally significantly higher after 5 days and at the end of the experiment, than that of the exposed larvae.

Simultaneous exposure of host instars to parasites

Parasitism rates. The mean rates of parasitism by B. curculionis of the instars of H. postica larvae following the simultaneous exposure of all four instars to female parasites are presented in Table 5. A hundred host

Table 4. Survival of the instars of *H. postica* larvae after being separately exposed to *B. curculionis* females^a

Period after start of experiment	Mean ^b % survival at different periods							
	1st instar		2nd instar		3rd instar		4th instar	
	Control	Exposed larvae	Control	Exposed larvae	Control	Exposed larvae	Control	Exposed larvae
12 hr	85.8 ^{NS}	83.3	96.5 ^{NS}	94.8	98.0 ^{NS}	97.8	100	100
5 days	64.3**	48.3	86.8*	71.8	93.1*	84.9	94.8 ^{NS}	93.5
At weevil pupation/ mature larval para- site stage	42.3*	32.0	66.8 ^{NS}	50.8	82.3*	68.5	86.3	86.8 ^{NS}

^a Analysis compares the controls and exposed larvae at a given interval of each instar.

^b Mean of 8 replicates, with 50 larvae initially per replicate.

NS = Not significantly different from other mean at the 5% level.

* = Significantly different from other mean at the 5% level.

** = Significantly different from other mean at the 1% level.

Table 5. Rates of parasitism of the instars of *H. postica* larvae after being simultaneously exposed to *B. curculionis* females

Instar	Original no. of larvae per instar per replicate	Mean no. of survivors (hosts + parasites) per replicate at weevil pupation/mature larval parasite stage	Mean ^{a, b, c} % parasitism ^d
1st	25	11.0	46.7 ab
2nd	25	15.2	56.4 a
3rd	25	16.0	56.5 a
4th	25	23.5	23.7 b

^a Mean of 6 replicates.

^b Means followed by the same letter are not significantly different at the 5% level as determined by Duncan's multiple range test.

^c Means for the 2nd and 3rd instars differ significantly at the 5% level from the mean for the 4th instar.

^d Based on no. of survivors (hosts + parasites).

larvae, made up of 25 larvae of each of the four instars, were exposed to two *B. curculionis* females for 12 hours. Each test was replicated six times. There was no significant difference at the 5 percent level among the means for the first, second and third instars. Each of the means for the second and third instars differed significantly at the 5 percent level from the mean for the fourth instar but no significant difference at the 5 percent level was observed between the means for the first and fourth instars.

Instar survival following simultaneous exposure to parasites. The survival of the different instars of H. postica larvae following their simultaneous exposure to B. curculionis females was generally similar to the survival of unexposed larvae (Table 6). The exceptions were with the third instars in which the survival of the unexposed larvae on the fifth day after the start of the experiment and at the end of the experiment, was significantly higher at the 1 percent level than that of the exposed larvae.

Individual host "stinging" and survival studies

Tables 7 and 8, and Figure 8 give the survival of first and second instar H. postica larvae after they have been individually punctured by B. curculionis ovipositors. With each instar, the survival of the control larvae was higher than that of the punctured larvae. Of the latter larvae, survival was poorer with those which were "stung" three times than those which were "stung" once.

Ovipositional behavior of B. curculionis. The approach of B. curculionis females to H. postica larvae was usually rather slow and deliberate with the antennae often curled downwards. On reaching the host, the parasite usually touched the host with its antennae before mounting it and ovipositing. Larvae in motion were seldom attacked.

Host puncturing or ovipositional action--the insertion and withdrawal of the ovipositor--was fast. The process was timed with a stopwatch on 123 occasions and the average duration was 3.9 seconds. On five occasions, however, parasites seemed to have difficulty withdrawing their ovipositors

Table 6. Survival of the instars of *H. postica* larvae after being simultaneously exposed to *B. curculionis* females^a

Period after start of experiment	Mean ^b % survival at different periods							
	1st instar		2nd instar		3rd instar		4th instar	
	Control	Exposed larvae	Control	Exposed larvae	Control	Exposed larvae	Control	Exposed larvae
12 hr	70.7	74.7 ^{NS}	86.7 ^{NS}	83.3	98.0 ^{NS}	96.0	100	100
5 days	56.0 ^{NS}	50.7	72.7 ^{NS}	69.3	90.0 ^{**}	69.3	96.0	96.0
At weevil pupation/ mature larval para- site stage	50.7 ^{NS}	44.0	63.3 ^{NS}	60.7	84.0 ^{**}	64.0	93.3	94.0 ^{NS}

^aAnalysis compares the controls and exposed larvae at a given interval of each instar.

^bMean of 6 replicates, with 25 larvae initially per instar per replicate.

NS = Not significantly different from other mean at the 5% level.

** = Significantly different from other mean at the 1% level.

Table 7. Survival of first instar H. postica larvae after being "stung" by B. curculionis females

Days after start of experiment	% survival of 20 larvae		
	Control	Larvae "stung" once	Larvae "stung" three times
0	100	100	100
1	90	90	50
2	90	85	45
3	90	75	45
4	80	65	35
5	75	60	25
6	75	60	25
7	75	60	25
8	75	60	25
9	75	55	20
10	70	50	20
11	70	50	20
12	70	50	20
13	70	50	20
14	65	45	20
15	65	40	20
16	65	40	20
17	65	40	20
18	65	40	20

Table 8. Survival of second instar *H. postica* larvae after being "stung" by *B. curculionis* females

Days after start of experiment	% survival of 20 larvae		
	Control	Larvae "stung" once	Larvae "stung" three times
0	100	100	100
1	100	75	65
2	100	75	50
3	95	75	50
4	95	75	35
5	95	75	30
6	95	75	30
7	95	75	30
8	95	70	25
9	95	70	25
10	95	70	25
11	95	70	25
12	95	70	25
13	90	70	25
14	90	70	25

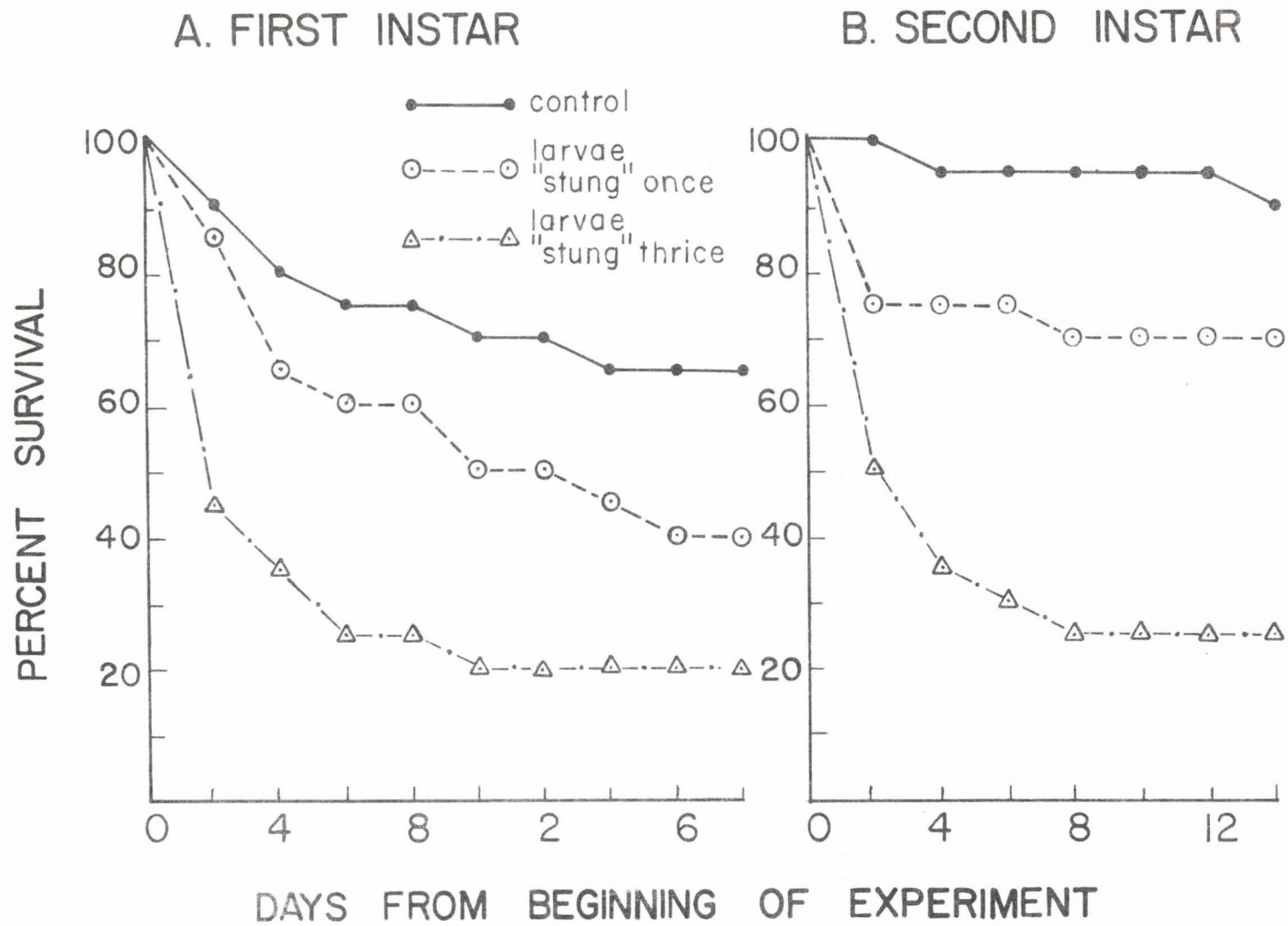


Figure 8. Survival of first and second instar *Hypera postica* larvae after being "stung" by *Bathypsectes curculionis* females.

as both parasites and hosts thrashed in attempts to free themselves. In these five instances, much longer periods elapsed between the insertion and the withdrawal of the ovipositor, the average period being 26.5 seconds. If these five exceptional cases are excluded, the average ovipositional period becomes 3 seconds. The larvae often writhed from the insertion of the parasite's ovipositor.

Repeated "stinging" of a larva by a parasite was observed on several occasions. Also when "stung" larvae were introduced to different parasites, they were again attacked.

Several female parasites were observed to make ovipositional movements even in the absence of larvae. Two females repeatedly inserted their ovipositors into a piece of alfalfa leaf and a piece of alfalfa stem respectively.

Larval Development and Activity Studies

Development of parasitized and unparasitized larvae

The developmental periods at 25-26 C of parasitized and unparasitized H. postica larvae from the beginning of each instar to the cocoon stage are summarized in Table 9. Both parasitized and unparasitized first instar larvae required 13.6 days on the average to reach the cocoon stage. There was also no significant difference between the mean developmental periods of unparasitized and parasitized second instar larvae. On the other hand, the mean developmental periods of parasitized third and fourth instar

Table 9. Developmental periods at 25-26 C of parasitized and unparasitized H. postica larvae from the beginning of each instar to the cocoon stage

Mean ^a no. of days (\pm SE) from beginning of instar to cocoon stage							
1st instar		2nd instar		3rd instar		4th instar	
Control	Parasitized	Control	Parasitized	Control	Parasitized	Control	Parasitized
13.6 \pm 0.23	13.6 \pm 0.23	10.4 \pm 0.36	10.6 \pm 0.30 ^{NS}	6.8 \pm 0.19	7.9** \pm 0.16	4.2 \pm 0.17	7.0** \pm 0.22

^aMean for 20 larvae.

NS = Not significantly different from other mean at the 5% level.

** = Significantly different from other mean at the 1% level.

larvae were significantly greater at the 1 percent level than those of unparasitized third and fourth instar larvae respectively.

Activity of parasitized and unparasitized larvae

Neither the unparasitized nor the parasitized larvae were found to be more active than the other. There were no significant differences at the 5 percent level between the daily activity scores--the number of 1 cm squares entered by a larva in 5 minutes--of unparasitized and parasitized larvae (Tables 10 and 11).

Growth and the Consumption and Utilization of Food Studies

Growth

The mean growth patterns of parasitized and unparasitized H. postica larvae during the third and fourth instars at 22.2 C and 30 C are shown in Figure 9. (Each growth curve is the mean for 20 larvae, except that for parasitized larvae at 22.2 C which is the mean for 18 larvae.) The growth curves were S-shaped. At either temperature, growth measured by the daily fresh weights was poorer with the parasitized larvae. The lower growth of parasitized larvae at both temperatures are again illustrated by: (a) the mean gain in fresh weight from the beginning of the third instar to the day preceding the cocoon formation (Table 12); (b) the mean gain in fresh weight from the beginning of the third instar to the cocoon stage (Table 13); and (c) the gain in dry weight from the beginning of the third instar to the cocoon stage (Table 14).

Table 10. Activity scores of parasitized and unparasitized *H. postica* larvae from the beginning of the second instar to the cocoon stage. (The parasitized larvae were exposed to female parasites at the beginning of the second instar)

Days from beginning of second instar	Mean no. (\pm SE) of 1 cm squares entered by larva in 5 minutes ^{a, b}	
	Unparasitized	Parasitized
1	4.4 \pm 0.97	4.6 \pm 0.96
2	3.2 \pm 0.58	3.1 \pm 0.66
3	2.6 \pm 0.83	3.5 ^c \pm 0.65
4	3.1 \pm 0.75	1.7 \pm 0.44
5	2.5 \pm 0.57	4.1 \pm 1.05
6	3.3 \pm 0.92	3.0 \pm 0.98
7	1.7 \pm 0.47	1.6 \pm 0.39
8	1.8 \pm 0.39	2.2 \pm 0.88
9	2.1 ^d \pm 1.15	2.2 ^e \pm 0.66

^aDifferences not significant at the 5% level.

^bMean for 20 larvae, unless otherwise indicated.

^cMean for 19 larvae.

^dMean for 15 larvae.

^eMean for 18 larvae.

Table 11. Activity scores of parasitized and unparasitized fourth instar *H. postica* larvae. (The parasitized larvae were exposed to female parasites at the beginning of the fourth instar)

Days from beginning of fourth instar	Mean no. (\pm SE) of 1 cm squares entered by larva in 5 minutes ^{a, b}	
	Unparasitized	Parasitized
1	1.7 \pm 0.54	3.4 \pm 0.90
2	1.0 \pm 0.31	1.7 \pm 0.50
3	1.5 ^c \pm 0.53	1.7 \pm 0.52

^aDifferences not significant at the 5% level.

^bMean for 20 larvae, unless otherwise indicated.

^cMean for 17 larvae.

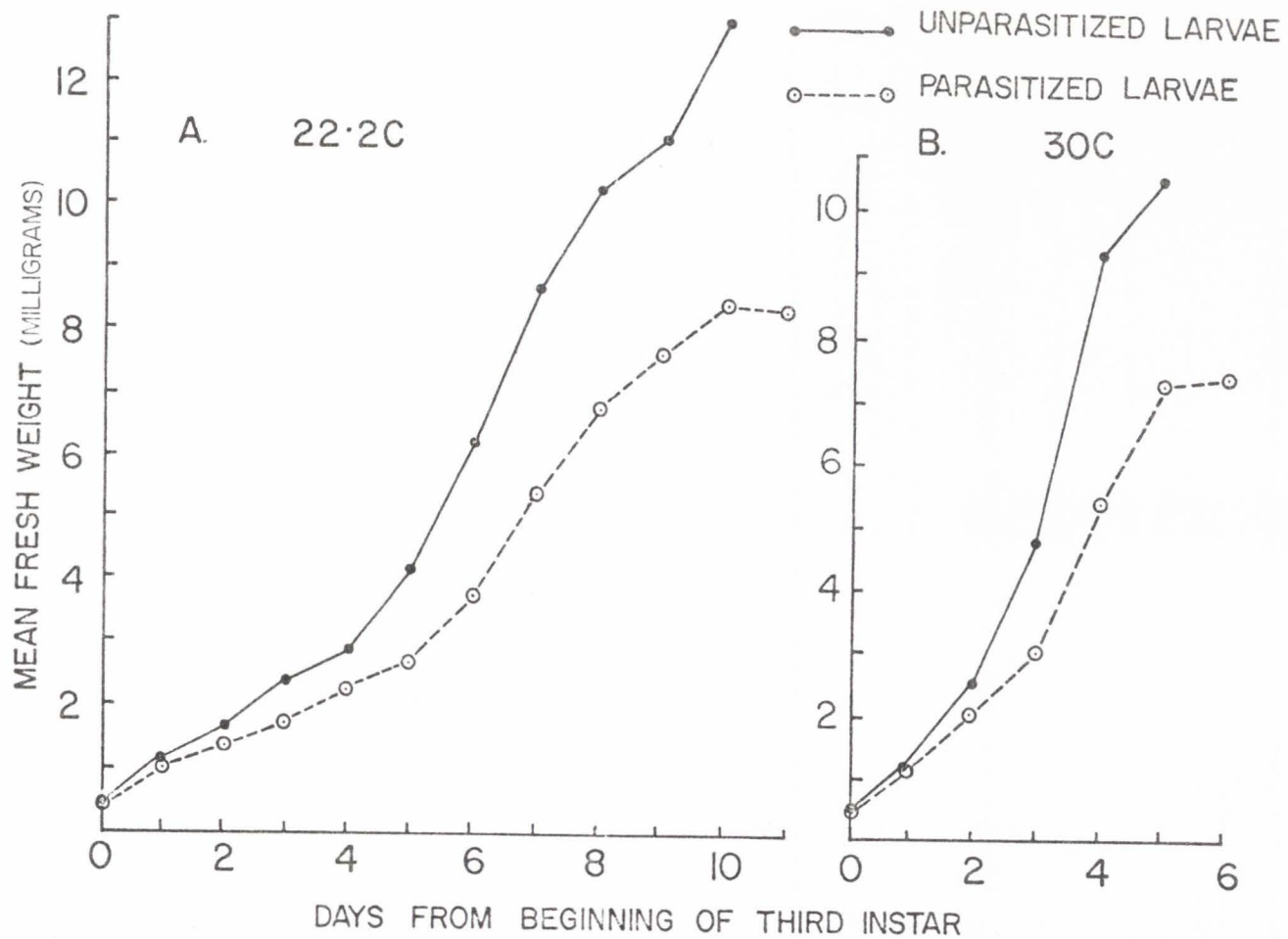


Figure 9. Mean growth of parasitized and unparasitized *Hypera postica* larvae at 22.2 C (A) and 30 C (B).

Table 12. Comparison of mean^a fresh weight gains by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the day preceding the cocoon formation

Temperature	Weight in milligrams (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	12.41** \pm 0.27	8.28 ^b \pm 0.30
30 C	10.94** \pm 0.29	7.93 ^b \pm 0.35

^a Mean for 20 larvae.

^b Includes weight of parasite larvae.

**Significantly different at the 1% level.

Table 13. Comparison of mean^a fresh weight gains by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage

Temperature	Weight in milligrams (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	10.97** \pm 0.27	7.13 ^{b,c} \pm 0.30
30 C	10.27** \pm 0.24	6.90 ^c \pm 0.33

^a Mean for 19 larvae, unless otherwise indicated.

^b Mean for 20 larvae.

^c Includes weight of parasite larvae.

**Significantly different at the 1% level.

Table 14. Comparison of mean^a dry weight gains by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage

Temperature	Weight in milligrams (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	1.68* \pm 0.04	1.49 ^{b,c} \pm 0.06
30 C	1.74** \pm 0.04	1.50 ^c \pm 0.07

^a Mean for 19 larvae, unless otherwise indicated.

^b Mean for 20 larvae.

^c Includes weight of parasite larvae.

*Significantly different at the 5% level.

**Significantly different at the 1% level.

Table 15. Comparison of fresh and dry weight gains by unparasitized *Hypera postica* larvae reared at 22.2 C and 30 C

Measurement	Weight in milligrams (\pm SE)	
	22.2 C	30 C
Mean gain in fresh weight from beginning of third instar to day preceding cocoon formation	12.41 ^a ** \pm 0.27	10.94 ^a \pm 0.29
Mean gain in fresh weight from beginning of third instar to cocoon stage	10.97 ^{NS,b} \pm 0.27	10.27 ^b \pm 0.24
Mean gain in dry weight from beginning of third instar to cocoon stage	1.68 ^{NS,b} \pm 0.04	1.74 ^b \pm 0.04

^a Mean for 20 larvae.

^b Mean for 19 larvae.

**Significantly different at the 1% level.

NS = Not significantly different at the 5% level.

Each of these measurements was significantly lower for the parasitized larvae than for the unparasitized.

The mean larval fresh weight at the beginning of the experiment (i.e. the mean fresh weight of starved, freshly-molted third instar larvae) was about 0.50 mg. Thus the mean fresh weight gains from the beginning of the third instar to the day preceding the cocoon formation (Table 12), indicate that at 22.2 C the fresh weight of unparasitized larvae increased on the average about 26 times during the period and that of parasitized larvae about 18 times. At 30 C, unparasitized larvae increased an average of about 23 times in fresh weight from the beginning of the third instar to the day preceding the cocoon stage. Parasitized larvae increased in fresh weight about 17 times at this temperature.

The mean fresh weight gains at the cocoon stage (Table 13) were lower than those on the day preceding the cocoon formation (Table 12). The decrease in weight gains at the cocoon stage was due to a decrease in food consumption and to weight loss represented by the energy and material used in spinning the cocoon.

Miscellaneous comparisons. Table 15 summarizes the data on fresh and dry weight gains by unparasitized larvae at 22.2 C and 30 C. Table 16 gives a similar summary for parasitized larvae.

The mean gain in fresh weight by unparasitized larvae from the beginning of the third instar to the day preceding the cocoon stage was significantly greater at the 1 percent level at 22.2 C than at 30 C. No significant difference,

Table 16. Comparison of fresh and dry weight gains by parasitized *Hypera postica* larvae reared at 22.2 C and 30 C

Measurement	Weight in milligrams ^{a,b} (\pm SE)	
	22.2 C	30 C
Mean gain in fresh weight from beginning of 3rd instar to day preceding cocoon formation	8.28 ^c \pm 0.30	7.93 ^c \pm 0.35
Mean gain in fresh weight from beginning of 3rd instar to cocoon stage	7.13 ^c \pm 0.30	6.90 ^d \pm 0.33
Mean gain in dry weight from beginning of 3rd instar to cocoon stage	1.49 ^c \pm 0.06	1.50 ^d \pm 0.07

^a Including weight of parasite larvae.

^b Differences not significant at the 5% level.

^c Mean for 20 larvae.

^d Mean for 19 larvae.

Table 17. Weight comparisons of *Bathyplectes curculionis* larvae reared at 22.2 C and 30 C and removed from weevil larvae after cocoons were spun

Type of measurement	Mean weight in milligrams (\pm SE)	
	22.2 C	30 C
Fresh larvae	1.51 ^{NS,a} \pm 0.11	1.29 ^b \pm 0.12
Dried larvae	0.37 ^{*,c} \pm 0.02	0.28 ^d \pm 0.03

NS = Not significantly different at the 5% level.

*Significantly different at the 5% level.

^a Mean of 18 larvae.

^b Mean of 21 larvae.

^c Mean of 17 larvae.

^d Mean of 19 larvae.

on the other hand, was observed between the gain in fresh weight for the same period by parasitized larvae at 22.2 C and 30 C.

The gain in fresh weight by unparasitized larvae from the beginning of the third instar to the cocoon stage was not significantly different at either 22.2 C or 30 C. The gain in fresh weight by parasitized larvae at the cocoon stage was similarly not significantly different at either 22.2 C or 30 C.

No significant difference existed between the mean dry weight gained by unparasitized larvae at 22.2 C and at 30 C. Similarly, the mean dry weight gained by parasitized larvae at 22.2 C did not differ significantly from that gained by similar larvae at 30 C.

Fresh and dry weights of B. curculionis larvae. Table 17 gives the mean fresh and dry weights of B. curculionis larvae at the cocoon stage of the host when the hosts were reared at 22.2 C and 30 C respectively.

The mean fresh weight of B. curculionis larvae recovered from hosts reared at 22.2 C was greater than that of parasite larvae which developed in hosts reared at 30 C. The difference, however, was not significant at the 5 percent level. On the other hand, the mean dry weight of B. curculionis larvae from hosts reared at 22.2 C was significantly greater at the 5 percent level than that of parasites developing in hosts which were reared at 30 C.

Food consumption and utilization

Daily food consumption. Figure 10 depicts the mean daily food consumption at 22.2 C and 30 C by parasitized and unparasitized H. postica larvae during the third and fourth instars. At both temperatures, the mean daily food

intake by parasitized larvae was generally lower than that by unparasitized larvae.

The mean daily food consumption and the mean daily increments in larval weights are shown graphically in Figures 11 and 12. For either parasitized or unparasitized larvae, the curves for larval weight gains and food consumption were similar. With unparasitized larvae at either 22.2 C or 30 C, food consumption and larval weight gains reached peaks on the same day (Figures 11A and 12A). Following the peaks, larval weight gains declined faster than did food consumption. With parasitized larvae, food consumption at either temperature reached a maximum later than did larval weight increments (Figures 11B and 12B).

Cumulative food consumption. The mean cumulative food consumption by parasitized and unparasitized larvae is given in Figure 13. At both 22.2 C and 30 C, the cumulative food consumption by parasitized larvae was below that by unparasitized larvae.

Total food consumption. The total amounts (dry weights) of alfalfa consumed by parasitized and unparasitized alfalfa weevil larvae during the third and fourth instars at 22.2 C and 30 C are shown in Table 18. The total food consumed by unparasitized larvae at 22.2 C was significantly greater at the 1 percent level than that by parasitized larvae at the same temperature. This was in spite of the fact that at this temperature parasitized larvae fed for an average of 10.3 ± 0.36 days and unparasitized larvae for an average of 9.5 ± 0.34 days. At 30 C, no significant difference existed at the 5 percent level between the mean total food consumption (6.57 mg) by unparasitized larvae and that (6.01 mg)

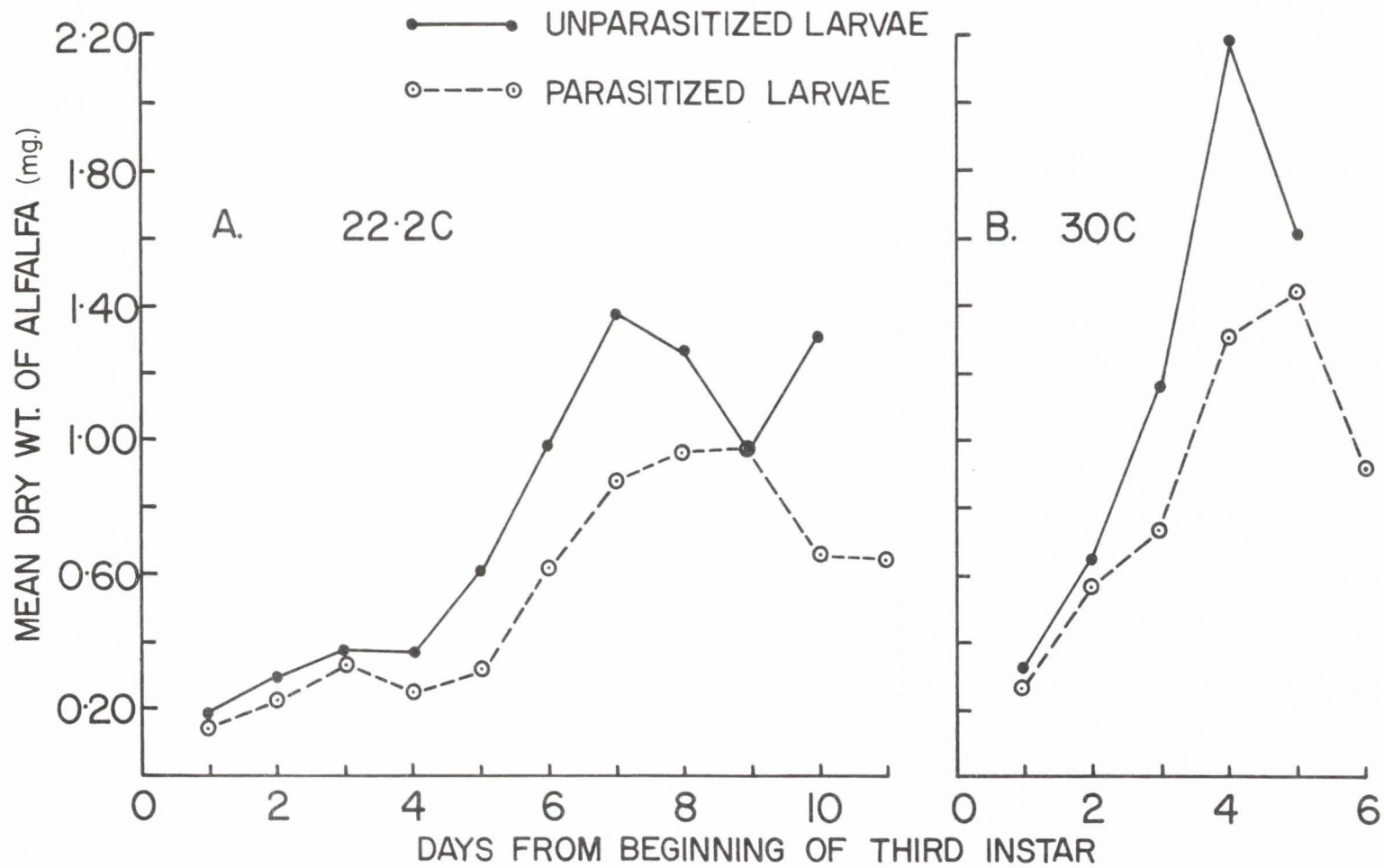


Figure 10. Mean daily food consumption by parasitized and unparasitized *Hypera postica* larvae at 22.2 C (A) and 30 C (B).

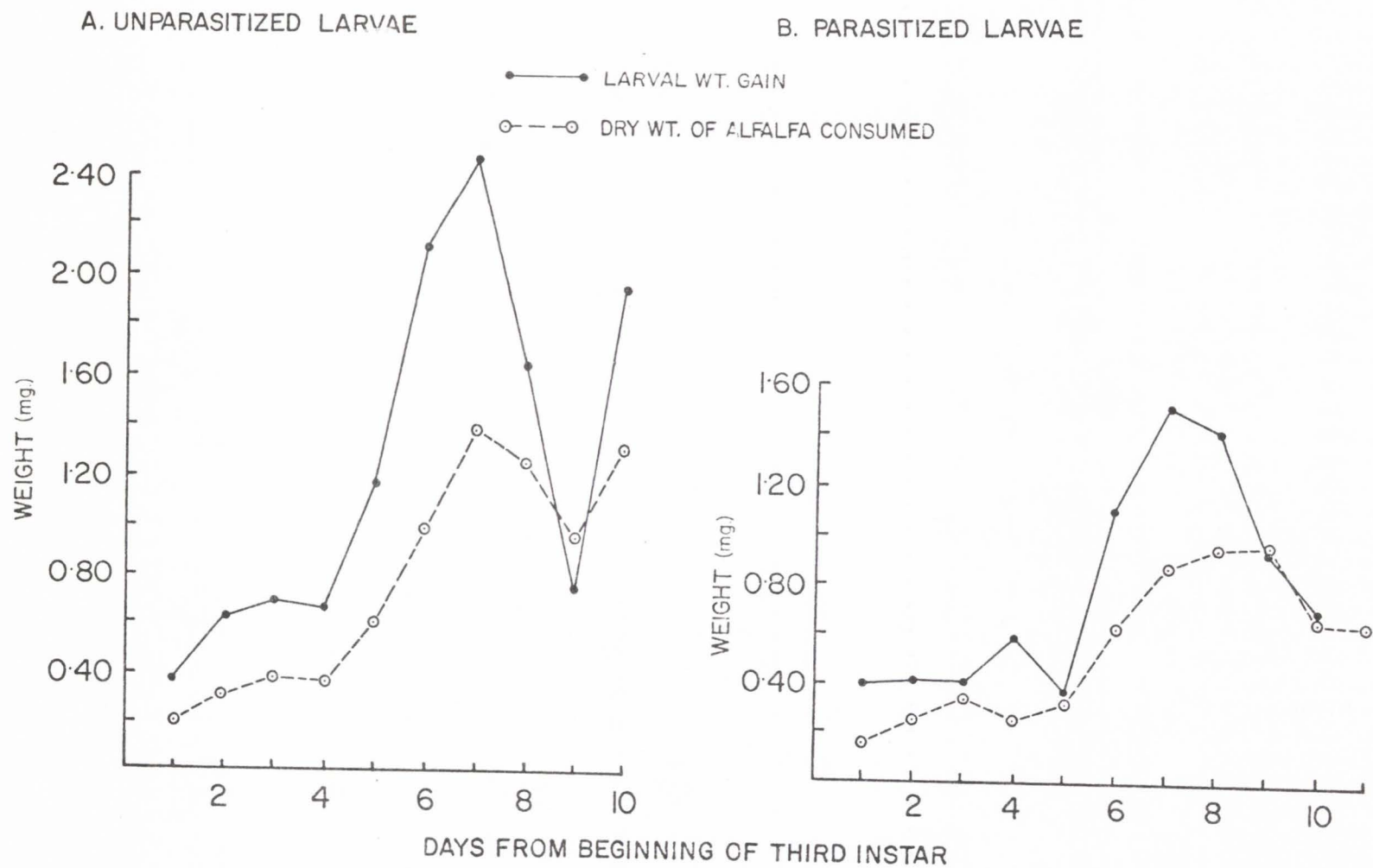


Figure 11. Mean daily weight gains and mean daily food consumption by parasitized and unparasitized *Hypera postica* larvae reared at 22.2 C.

A. UNPARASITIZED LARVAE

B. PARASITIZED LARVAE

● — ● LARVAL WT. GAIN

○ - - ○ DRY WT. OF ALFALFA CONSUMED

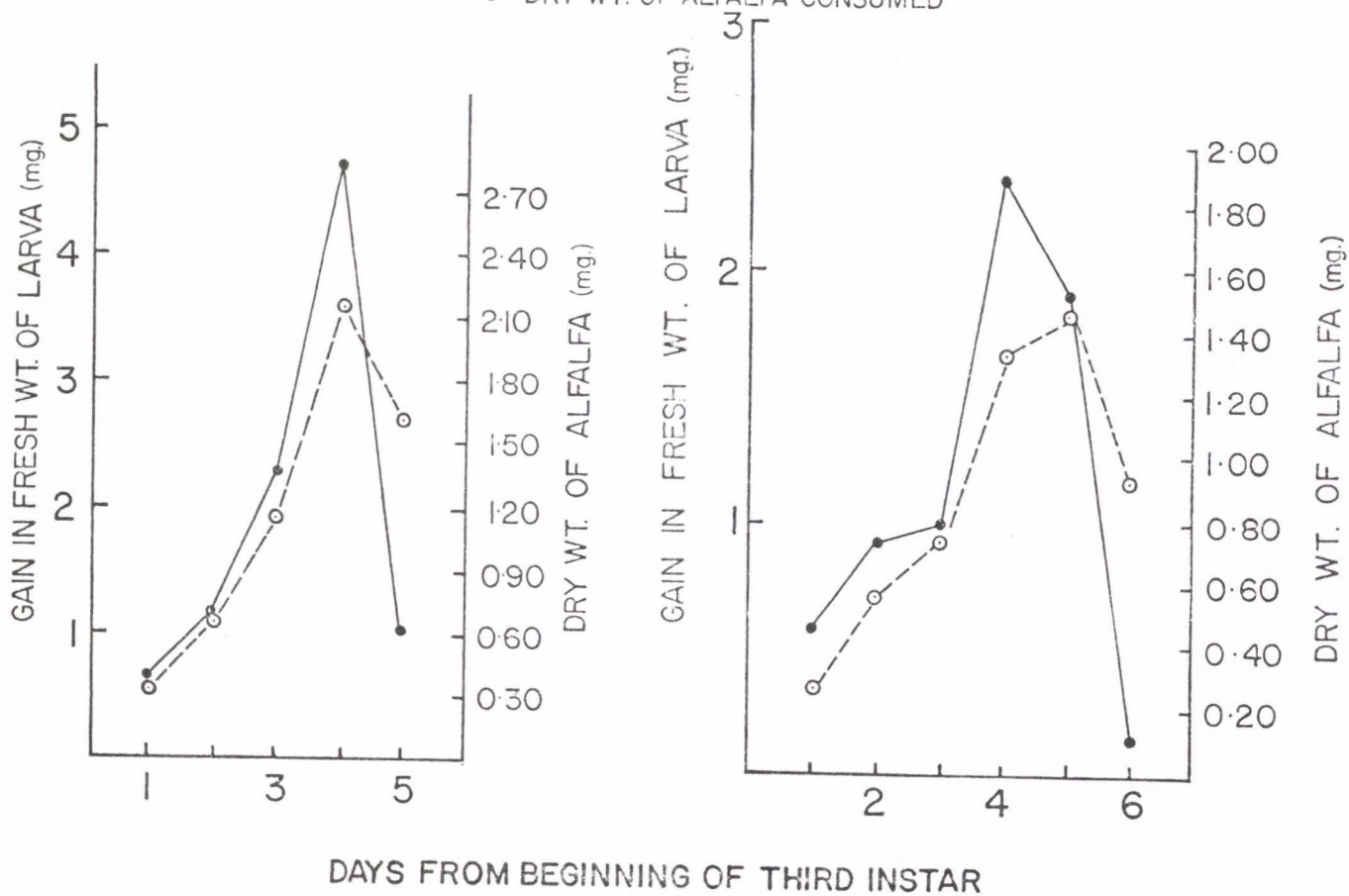


Figure 12. Mean daily weight gains and mean daily food consumption by parasitized and unparasitized *Hypera postica* larvae reared at 30 C.

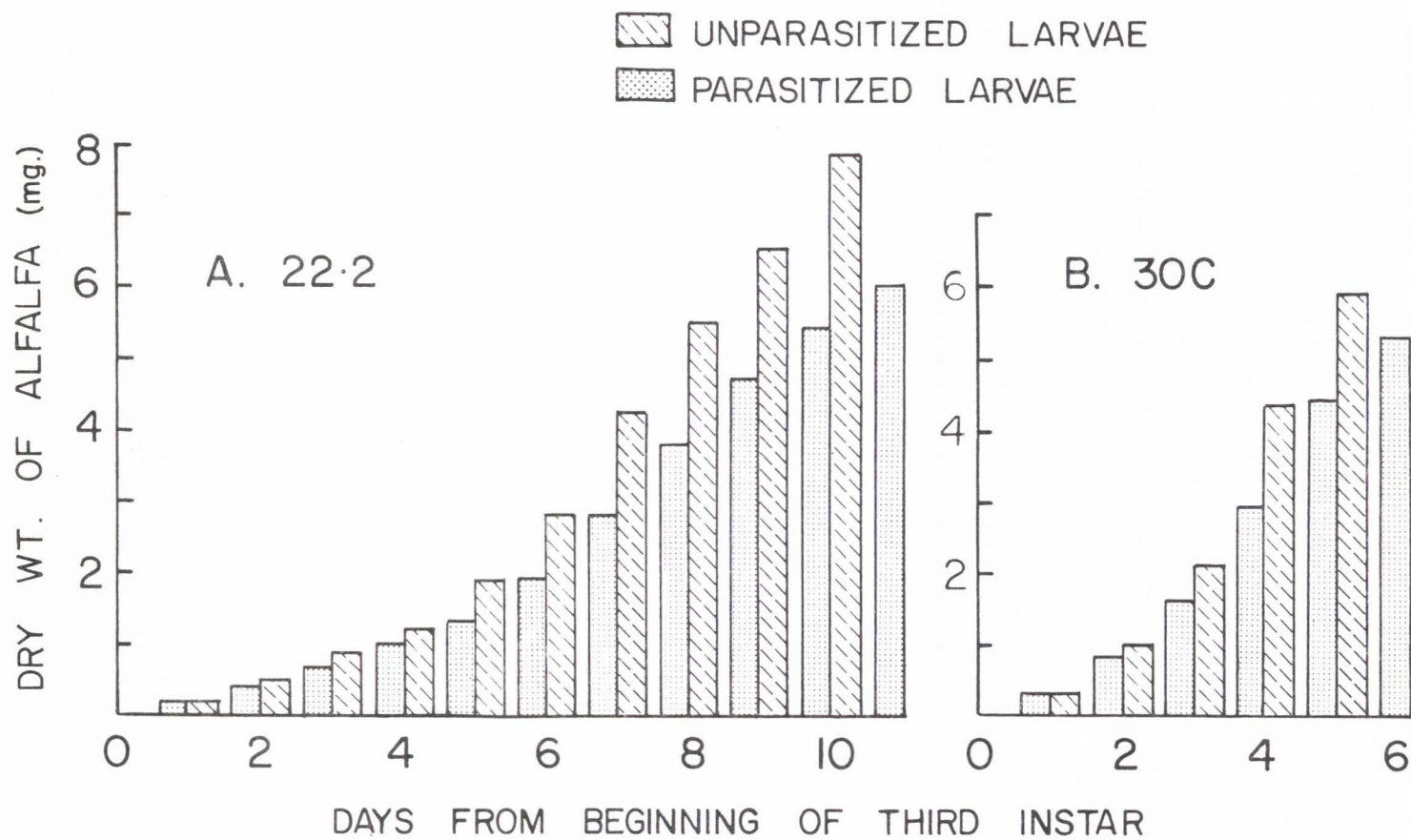


Figure 13. Mean cumulative food consumption by parasitized and unparasitized *Hypera postica* larvae at 22.2 C (A) and 30 C (B).

Table 18. Comparison of total food consumption by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean ^a dry weight (mg \pm SE) of alfalfa consumed	
	Unparasitized larvae	Parasitized larvae
22.2 C	7.25** \pm 0.25	5.98 ^b \pm 0.24
30 C	6.57 ^{NS} \pm 0.18	6.01 \pm 0.25

^a Mean for 20 larvae, unless otherwise indicated.

^b Mean for 15 larvae.

** = Significantly different at the 1% level.

NS = Not significantly different at the 5% level.

by parasitized larvae. The feeding periods of parasitized and unparasitized larvae averaged 6.4 ± 0.28 and 5.4 ± 0.17 days respectively at 30 C.

Food consumption per larva per day. The dry weight of food consumed per larva per day (the total dry weight of alfalfa consumed by a larva divided by the number of days required by that larva to develop from the beginning of the third instar to the cocoon stage) is summarized for parasitized and unparasitized larvae in Table 19. At both 22.2 C and 30 C, the mean food consumption per larva per day was significantly higher, at the 1 percent level, for unparasitized than for parasitized larvae.

Dry weight-fresh weight consumption index. No difference was observed between the dry weight-fresh weight consumption index (dry weight of food consumed per unit of larval fresh weight per day) for parasitized and unparasitized larvae at both 22.2 C and 30 C (Table 20).

Approximate digestibility. The approximate digestibility (A.D.) of alfalfa by parasitized and unparasitized alfalfa weevil larvae did not differ

Table 19. Comparison of food consumption per larva per day^a by parasitized and unparasitized Hypera postica larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean ^b dry weight (mg ± SE) of alfalfa consumed per larva per day	
	Unparasitized larvae	Parasitized larvae
22.2 C	0.71** ± 0.02	0.53 ^c ± 0.02
30 C	1.20** ± 0.05	0.90 ± 0.04

^a Total dry weight of food consumed divided by no. of days from beginning of third instar to cocoon stage.

^b Mean for 20 larvae, unless otherwise indicated.

^c Mean for 15 larvae.

**Significantly different at the 1% level.

Table 20. Comparison of consumption indices (C.I.) by parasitized and unparasitized Hypera postica larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean dry weight-fresh weight C.I. ^{a,b} (± SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	0.14 ± 0.004	0.14 ^c ± 0.003
30 C	0.24 ± 0.009	0.24 ^d ± 0.009

^a Dry weight of food consumed per unit of larval fresh weight per day.

^b Mean for 20 larvae, unless otherwise indicated.

^c Mean for 15 larvae.

^d Mean for 19 larvae.

Table 21. Comparison of approximate digestibility by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean ^a % approximate digestibility (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	77.3 \pm 0.57	77.9 ^{b, NS} \pm 0.72
30 C	78.9 \pm 0.73	80.3 ^{NS} \pm 0.65

^aMean for 20 larvae, unless otherwise indicated.

^bMean for 15 larvae.

NS = Not significantly different at the 5% level.

Table 22. Comparison of the net efficiency of conversion of ingested food to body matter (E.C.I.) by parasitized and unparasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean ^a % net E.C.I. (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	23.5 \pm 0.77	26.4 ^{*,b} \pm 1.05
30 C	26.8 \pm 1.06	25.5 ^{NS} \pm 1.17

^aMean for 19 larvae, unless otherwise indicated.

^bMean for 15 larvae.

*Significant (but only barely) at the 5% level.

NS = Not significantly different at the 5% level.

significantly at the 5 percent level at either 22.2 C or 30 C (Table 21).

Figure 14 depicts the relationship with age of the A.D.'s for parasitized and unparasitized larvae. At both temperatures, the A.D.'s declined with age, the decline being more pronounced at 30 C than at 22.2 C.

Net efficiency of conversion of ingested food. Table 22 summarizes the net efficiency of conversion of ingested food to body matter (E.C.I.) by parasitized and unparasitized H. postica larvae at 22.2 C and 30 C.

At 22.2 C, the net E.C.I. by parasitized larvae was greater than that by unparasitized larvae. The difference was marginally significant at the 5 percent level. At 30 C, the net E.C.I. by unparasitized larvae was slightly higher than that by parasitized larvae but the difference was not significant at the 5 percent level.

Net efficiency of conversion of digested food. At either 22.2 C or 30 C, there was no significant difference, at the 5 percent level, in the net efficiencies of conversion of digested food to body matter (E.C.D.'s) by parasitized and unparasitized alfalfa weevil larvae (Table 23).

Miscellaneous comparisons. Data on food consumption and utilization by unparasitized larvae at 22.2 C and 30 C are given in Table 24 and those by parasitized larvae in Table 25. The total food consumption by unparasitized larvae at 22.2 C was significantly greater, at the 5 percent level, than that by similar larvae at 30 C. The mean food consumption per larva per day by unparasitized larvae was, on the other hand, significantly greater, at the 1 percent level, at 30 C than at 22.2 C.

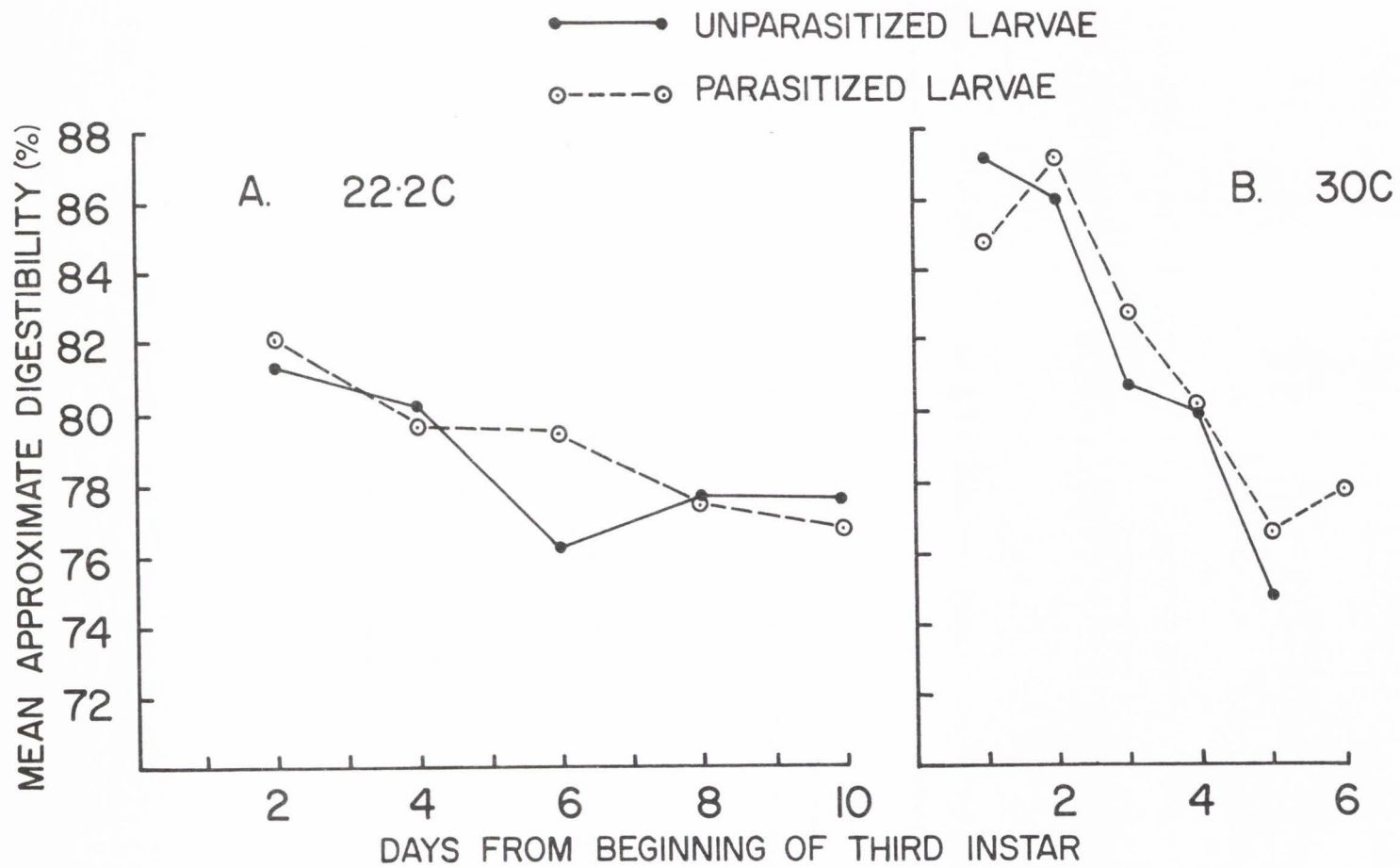


Figure 14. The relationship with age of the approximate digestibility by parasitized and unparasitized *Hypera postica* larvae at 22.2 C (A) and 30 C (B).

Table 23. Comparison of the net efficiency of conversion of digested food to body matter (E.C.D.) by parasitized and unparasitized Hypera postica larvae from the beginning of the third instar to the cocoon stage

Temperature	Mean ^a % net E.C.D. (\pm SE)	
	Unparasitized larvae	Parasitized larvae
22.2 C	30.6 \pm 1.18	33.9 ^{b, NS} \pm 1.51
30 C	34.0 \pm 1.57	32.0 ^{NS} \pm 1.70

^a Mean for 19 larvae, unless otherwise indicated.

^b Mean for 15 larvae.

NS = Not significantly different at the 5% level.

Table 24. Comparison of food consumption and utilization by unparasitized Hypera postica larvae from the beginning of the third instar to the cocoon stage in larvae reared at 22.2 C and 30 C

Measurement	Observations ^a (\pm SE)	
	22.2 C	30 C
Mean total dry wt. (mg) of alfalfa consumed	7.25* \pm 0.25	6.57 \pm 0.18
Mean dry wt. (mg) of alfalfa consumed per larva per day	0.71 \pm 0.02	1.20** \pm 0.05
Mean dry wt. -fresh wt. C.I.	0.14 \pm 0.004	0.24** \pm 0.009
Mean approx. digestibility (%)	77.3 \pm 0.57	78.9 ^{NS} \pm 0.73
Mean net E.C.I. (%)	23.5 ^b \pm 0.77	26.8 ^{*, b} \pm 1.06
Mean net E.C.D. (%)	30.6 ^b \pm 1.18	34.0 ^{NS, b} \pm 1.57

*Significantly different at the 5% level.

**Significantly different at the 1% level.

NS = Not significantly different at the 5% level.

^a Mean for 20 larvae, unless otherwise indicated.

^b Mean for 19 larvae.

Table 25. Comparison of food consumption and utilization by parasitized *Hypera postica* larvae from the beginning of the third instar to the cocoon stage in larvae reared at 22.2 C and 30 C

Measurement	Observation ^a (\pm SE)	
	22.2 C	30 C
Mean total dry wt. (mg) of alfalfa consumed	5.98 \pm 0.24	6.01 ^{b, NS} \pm 0.25
Mean dry wt. (mg) of alfalfa consumed per larva per day	0.53 \pm 0.02	0.90 ^{**b} \pm 0.04
Mean dry wt. -fresh wt. C.I.	0.14 \pm 0.003	0.24 ^{**c} \pm 0.009
Mean approx. digestibility (%)	77.9 \pm 0.72	80.3 ^{*b} \pm 0.65
Mean net E.C.I. (%)	26.4 \pm 1.05	25.5 ^{c, NS} \pm 1.17
Mean net E.C.D. (%)	33.9 \pm 1.51	32.0 ^{c, NS} \pm 1.70

^a Mean for 15 larvae, unless otherwise indicated.

^b Mean for 20 larvae.

^c Mean for 19 larvae.

*Significantly different at the 5% level.

**Significantly different at the 1% level.

NS = Not significantly different at the 5% level.

No significant difference, at the 5 percent level, existed between the total food consumption by parasitized larvae at 22.2 C and 30 C. However, the mean food consumption per parasitized larva per day was significantly greater, at the 1 percent level, at 30 C than at 22.2 C.

The dry weight-fresh weight consumption index was significantly greater, at the 1 percent level, for both types of larvae at 30 C than at 22.2 C.

The approximate digestibility (A.D.) of food by unparasitized larvae did not differ significantly, at the 5 percent level, at either 22.2 C or 30 C. However, the A.D. by parasitized larvae at 30 C was significantly greater, at the 5 percent level, than that by similar larvae reared at 22.2 C.

The net efficiency of conversion of ingested food to body matter (E.C.I.) by unparasitized larvae was significantly greater, at the 5 percent level, at 30 C than at 22.2 C. No significant difference, at the 5 percent level, was, however, evident between the net E.C.I.'s by parasitized larvae at both temperatures.

There was no significant difference, at the 5 percent level, in the net efficiencies of conversion of digested food to body tissue (E.C.D.'s) by unparasitized larvae at 22.2 C and 30 C nor was there any significant difference in the net E.C.D.'s by parasitized larvae at the two temperatures.

DISCUSSION

Studies Aimed at Identifying Parasitized Larvae

The results from rearing field-collected, green and yellow fourth instar Hypera postica larvae showed that yellow or light-green larvae were more heavily parasitized on a percentage basis than green larvae. In spite of this, as many as 67.3 percent of the yellow larvae were unparasitized.

Many carton-reared larvae in the laboratory often assumed a light color, irrespective of their exposure to parasites. In addition, younger larvae often showed no color differentiation.

Thus, observations that alfalfa weevil larvae parasitized by B. curculionis are light-green or yellow (Newton, 1933; Sorenson, 1934b) are only partially correct. Color difference is, therefore, not a reliable method for distinguishing parasitized H. postica larvae from the unparasitized.

On the whole, no practical method was found to identify alfalfa weevil larvae parasitized by B. curculionis. However, very late in the fourth instar, just prior to or after the spinning of its cocoon, a parasitized larva may be distinguished by its light color, its often rather smooth appearance and sometimes by the presence of a pinkish tinge. These characteristics come too late to be of any practical importance as the construction of the parasite cocoon usually follows almost immediately.

The lack of a method to identify parasitized larvae prolonged the present study and made it more difficult. A weevil larva usually was determined to be parasitized only after the parasite larva constructed its cocoon or issued from the host following the spinning of the latter's cocoon. In the growth and food utilization experiments, the weevil larvae were dissected at the cocoon stage to determine if they were parasitized. On many occasions, records were taken on supposedly parasitized larvae only to discover at the end of the experiment that they were free of parasites. These experiences were particularly frustrating with the studies on larval development and activity and on growth, food consumption and food utilization.

Host Instar Parasitization and Survival Studies

Levels of parasitism

The results of the studies on the rates of parasitism (Tables 3 and 5), especially those of the "separate parasitization of instars" (Table 3) show that the first three instars of H. postica larvae are either about equally preferred by B. curculionis or are about equally susceptible to it. The results also show that the fourth instar larvae are either least preferred by the parasite or are least susceptible to it. Miller (1970b) obtained similar results with the eastern United States form of H. postica larvae in Massachusetts, although the levels of parasitism obtained in his study were much lower than those found in the present study. In laboratory studies of parasitism by B. curculionis of the four instars of H. postica, he found a

significant difference in parasitism at the 1 percent level between the means of each of the first three instars and the mean for the fourth instar. There was, however, no significant difference at the 5 percent level among the means of the first three instars. These findings exactly parallel my own in the "separate parasitization of different instars" experiment (Table 3).

Foster and Bishop (1970) in Idaho also found that "B. curculionis effectively parasitized first, second, and third instar larvae of the alfalfa weevil, but was ineffective in parasitizing larvae of the fourth instar in the field." Brunson and Coles (1968), however, reported that B. curculionis mostly parasitizes first and second instar H. postica larvae. Studies by van den Bosch and Dietrick (1959) indicated that the smaller larvae of the Egyptian alfalfa weevil, Hypera brunneipennis, were either preferred by B. curculionis or were more susceptible to attack by the parasite.

Thus the first three instars of H. postica larvae either seem to be more susceptible to attacks by B. curculionis or are preferred by the parasite over the fourth instar larvae.

A number of factors may explain the poor rate of parasitism of the fourth instar alfalfa weevil larvae by B. curculionis. Hemocytic encapsulation of the parasite eggs in the host as does occur in the larvae of the eastern United States form of H. postica (Puttler, 1967) and of H. brunneipennis (van den Bosch and Dietrick, 1959; van den Bosch, 1964a) may be suspected. Van den Bosch and Puttler in their respective studies observed that the encapsulating ability of the host increased with age. However, van den Bosch (1964a) and Salt and van den Bosch (1967) noted that the encapsulating

ability of the western United States form of H. postica (specifically H. postica in California) was very slight. Thus encapsulation of B. curculionis eggs was probably not the cause of the poor parasitism observed in the fourth instar alfalfa weevil larvae. Foster and Bishop (1970) speculate that a time factor may be involved, that is B. curculionis eggs oviposited in old larvae do not have enough time to hatch and mature before the larvae pupate.

The cause of the poor parasitism in fourth instar H. postica larvae and the degree of hemocytic reaction to B. curculionis eggs in non-Californian western United States form of H. postica larvae would form an interesting study, but were not investigated in the current work.

Host instar survival following parasitization

The pattern of survival of H. postica larvae following their exposure to B. curculionis females (Tables 4, 6, 7 and 8, and Figure 8) shows that some of the younger larvae died either from the ovipositional action of the parasites or from the development of the parasite larvae within the hosts. The younger the larvae, the poorer seemed to be their survival after parasitization. Also survival was poorer in larvae which were "stung" more than once (Tables 7 and 8, and Figure 8).

The incubation period of Bathyplectes eggs at approximately 23 C was determined by van den Bosch (1964a) as about 72 hours. Thus it can be assumed that host puncturing by B. curculionis ovipositors was the principal cause of death in those punctured larvae which died within the first two days

after oviposition by B. curculionis. Later host mortality may be attributed mainly to the feeding and other activities of parasite larvae.

Host mortality due to ovipositional action, similar to that described in the present study, has been reported by Rahman (1970b). He found that small larvae of the imported cabbageworm, Pieris rapae (L.), were "evidently killed by being mutilated" during the act of oviposition by the braconid parasite Apanteles rubecula Marsh. Mutilation with the ovipositor was also one of the means by which adult females of the parasite Metaphycus helvolus (Comp.) killed the black scale, Saissetia oleae (Bern.) (DeBach, 1943). Burnett (1962) reported premature death of the whitefly Trialeurodes vaporariorum (Westw.) as a result of attacks by the chalcid parasite Encarsia formosa Gahan.

Premature death of host insects due to attacks by a parasite, contributes to the immediate effectiveness of the parasite in controlling the host. In the long term, however, the process may be detrimental to the parasite as the eggs laid in such hosts are wasted and do not contribute to the parasite's population.

The accessibility in the field of first and early second instar alfalfa weevil larvae to parasites may be questioned, as these larvae tend to be secluded in alfalfa stems, and in leaf and flower buds (Foster and Bishop, 1970). If, however, premature death of young weevil larvae due to B. curculionis attack occurs in the field, then the parasite causes a greater host mortality than is measurable by most current techniques.

Ovipositional behavior of *B. curculionis*

Most of my observations on the ovipositional behavior of *B. curculionis* agree with those of Foster and Bishop (1970). However, there is a disagreement on the duration of oviposition. The average duration observed in the present study was about 3-4 seconds. Foster and Bishop, on the other hand, reported that "ovipositional contact averaged about 30 seconds in duration." Possibly the two workers were measuring the duration of oviposition when female parasites apparently had difficulty withdrawing their ovipositors from the hosts. It will be recalled that in the five cases when this occurred the average duration was 26.5 seconds.

Oatman et al. (1969) found oviposition by the braconid parasite *Orgilus lepidus* Muesebeck into the potato tuberworm *Phthorimaea operculella* (Zeller), to be quick, usually occurring in 2-3 seconds.

Larval Development and Activity Studies

Development of parasitized and unparasitized larvae

The developmental periods to the cocoon stage of *H. postica* larvae parasitized at the beginning of the third and fourth instars respectively were significantly longer (at the 1 percent level) than those of unparasitized larvae of the same ages. On the other hand, no significant differences were observed in the developmental periods of parasitized and unparasitized first and second instars to the cocoon stage (Table 9).

The prolonged developmental periods of H. postica larvae parasitized during the later instars presumably represent a physiological conditioning of the hosts by the parasite to allow completion of its own larval development. Parasite larvae developing in younger hosts apparently have enough time to complete their development without a similar conditioning of the host.

Lewis (1970) mentioned an example of a parasite controlling the physiology of its host, although in a different manner from that reported here for B. curculionis and H. postica. He reported that when larvae of Heliothis zea (Boddie) were parasitized during the late instars by the braconid, Macroplitis croceipes (Cresson), the host development was stopped soon enough to prevent them from reaching a stage unsuitable for parasite development. When parasitized in the early instars, however, development proceeded so the host could provide the parasite with food and a pupal cell which the mature parasite larva utilized for its own pupal stage.

Activity of parasitized and unparasitized larvae

No significant difference was found between the activity of parasitized and unparasitized H. postica larvae (Tables 10 and 11). This finding contrasts with those of other workers. For example, alfalfa weevil larvae parasitized by the mermithid nematode Hexamermis arvalis Poinar and Gyrisco were sluggish and responded less to probing than unparasitized larvae (Poinar and Gyrisco, 1960, 1962a).

Taylor (1964) reported the sarcophagid parasite Blaesoxipha filipjevi Rohd. caused some sluggishness in the grasshopper Zonocerus variegatus (L.).

Filmed as received

without page(s) 93.

UNIVERSITY MICROFILMS.

parasitized alfalfa weevil larvae in the present study, however, food consumption at either 22.2 C or 30 C reached a peak later than larval weight increments (Figures 11B and 12B). Presumably, the phenomenon of the weight increments and food consumption reaching peaks together, is the normal case in insects and that the deviation observed with the parasitized H. postica larvae was the result of parasitism.

The observation made in the present study that the food consumption by H. postica larvae continued at a relatively high rate when larval weight gains were declining, is similar to those made by Edwards (1964) for the swift moth, Hepialus humuli, and Carne (1966) for Paropsis atomaria, respectively.

Food consumption and utilization

The finding in the present research that the total food consumption per H. postica larva during the third and fourth instars was higher for an unparasitized larva (especially at 22.2 C) than for a larva parasitized by Bathyplectes curculionis (Table 18), is similar to that made by Armbrust et al. (1970a) with the eastern United States form of H. postica larvae in Illinois. Also, my finding that the food consumption per larva per day was higher for unparasitized larvae (Table 19) agrees with that observed by Armbrust et al. (1970a). However, while the difference in the daily food consumption per larva between unparasitized and parasitized larvae was statistically significant in the present study, the difference found by Armbrust et al. was statistically nonsignificant.

Another difference in the findings of the two studies relates to the lengths of feeding days for parasitized and unparasitized larvae. Armbrust et al. (1970a) noted that unparasitized larvae fed 1.3 days longer than parasitized larvae. By contrast, it was found in the present study that at 22.2 C, the feeding period of unparasitized larvae averaged 9.5 days and that of parasitized larvae 10.3 days. At 30 C, unparasitized larvae fed for a mean of 5.4 days and parasitized larvae for 6.4 days.

I agree with Armbrust et al. (1970a) that parasitism by B. curculionis of H. postica larvae has a dual benefit: the reduced feeding by parasitized larvae has an immediate economic gain to the farmer in addition to the benefit of a reduction in the next adult generation.

Other workers have also reported reduced larval feeding as a result of parasitism. Tower (1916) found that larvae of the armyworm, Cirphis unipuncta Haworth, parasitized by Apanteles militaris Say ate about half as much food as unparasitized larvae during the same period. Tower also concluded that parasitism by A. militaris has a direct benefit.

Rahman (1970a) observed that unparasitized larvae of the imported cabbageworm, Pieris rapae (L.), consumed more food than larvae parasitized by the solitary braconid Apanteles rubecula Marsh. However, P. rapae larvae parasitized by the gregarious parasite A. glomeratus (L.) consumed more food than the normal larvae. Rahman thus concluded that parasitism by A. rubecula not only reduces the next generation of P. rapae but also has an immediate benefit in reducing damage by the pest. On the other hand,

parasitism by A. glomeratus increases the damage caused by P. rapae in the current generation.

Rahman (1970a) also found in his study that unparasitized P. rapae larvae fed significantly more at 22.5 C than at 24.3 C. This finding is similar to that in the present study where the total food consumption by unparasitized H. postica larvae was significantly higher at 22.2 C than at 30 C (Table 24). Fewkes (1960), however, observed no effect with temperature on the amount of food eaten by the nabid Stalia major Costa.

Dry weight-fresh weight consumption index. Waldbauer (1968) thinks the dry weight-fresh weight C.I. (dry weight of food ingested per unit of fresh weight of insect, per day) is of nutritional interest since it measures the rate of intake of nutrients into the digestive system. Table 26 compares the dry weight-fresh weight C.I.'s obtained in the present work for H. postica larvae, with those reported for other insects. The lower C.I.'s for parasitized and unparasitized H. postica larvae reared at 22.2 C was apparently due to the longer feeding periods at this temperature than at 30 C.

Comparisons of the efficiencies of utilization by different insects.

Tables 27, 28 and 29 compare the efficiencies of food utilization observed in the present study for parasitized and unparasitized alfalfa weevil larvae, with those recorded elsewhere for other insects.

Waldbauer (1968) advised that data on food utilization from different sources should be compared with discretion because of various reasons. For instance, if utilization data are presented for different stages of an insect, it

Table 26. Comparisons of dry weight-fresh weight consumption indices (C.I.)^a for different insects

Insect	Food	Temperature	Dry weight-fresh weight C.I.	Authority
<u>Manduca sexta</u> (?) (Lepidop.: Sphingidae)	<u>Lycopersicon esculentum</u> (tomato)	-	0.34	Waldbauer (1968)
As above	<u>Solanum tuberosum</u> (potato)	-	0.26	As above
<u>Celerio euphoribiae</u> (Lepidop.: Sphingidae)	Artificial ^b diet	-	0.20	House (1965) Calculated by Waldbauer (1968)
As above	As above ^b	-	0.18	As above
As above	As above ^b	-	0.16	As above
<u>Hypera postica</u> (Coleop.: Curculionidae) (Normal or parasitized)	<u>Medicago sativa</u> (alfalfa)	22.2 C	0.14	Present study
As above	As above	30 C	0.24	As above

^a Dry weight of food consumed per unit of fresh weight of insect, per day.

^b Different levels of nutrients.

Table 27. Comparisons of the approximate digestibilities (A. D.) of food by different insects^a

Insect	Food	Temperature	Stage	A. D. (%)	Authority
<u>Melanoplus bilituratus</u> (Orthop. Acrididae)	<u>Triticum aestivum</u> (Wheat)	30 C	Whole nymphal stage	32	Smith (1959)
<u>Prodenia eridania</u> (Lepidop. : Noctuidae)	<u>Lycopersicon esculentum</u> (Solanaceae)	-	5th instar	63.7	Soo Hoo and Fraenkel (1966)
As above	<u>Phaseolus lunatus</u> (Leguminosae)	-	As above	72.6	As above
As above	As above	-	5th and 6th instars	48.5	Crowell (1941)
<u>Blatta orientalis</u> (Dictyop. : Blattidae)	Powdered milk, yeast and cholesterol	20 C	Last two instars	95	Lafon (1951) Cited by Waldbauer (1968)
<u>Tenebrio molitor</u> (Coleop. : Tenebrionidae)	Bran	27 C	Larvae (4 days)	46.3	Evans and Goodliffe (1939)
<u>Hypera postica</u> (Coleop. : Curculionidae) (Unparasitized)	<u>Medicago sativa</u> (alfalfa)	22 C	3rd and 4th instars	77.3	Present study
As above	As above	30 C	As above	78.9	As above
<u>H. postica</u> (Parasitized)	As above	22.2 C	As above	77.9	As above
As above	As above	30 C	As above	80.3	As above

^aMeasurements on dry weight basis.

should be remembered that the efficiency of utilization is likely to differ with the different stages of that insect. Some efficiencies of conversion are based on gross weight gain while others are based on net weight gain. Such measurements are not comparable. Similarly, measurements based on dry weights on one hand and fresh weights on the other, are also not comparable.

The efficiency of utilization varies with temperature and other physical factors. With leaf-feeding insects, digestibility and efficiency of conversion vary widely with the species of food plant. Leaves of the same plant species may also vary in nutritional value. Waldbauer (1968) also mentioned the question of accuracy between different workers.

Approximate digestibility (A.D.). The high A.D.'s observed in the present work for H. postica larvae (Tables 21 and 27) indicate a high adaptation of the insect to its host plant.

Among the possible factors which may explain the high digestibility of alfalfa by H. postica larvae may be mentioned the rate of passage of food through the alimentary canal (Soo Hoo and Fraenkel, 1966). The high digestibility observed suggests a slow passage of food through the gut. Secondly, with chewing insects, small individuals are likely to chew off smaller pieces of food which would present a larger surface area for digestion (Soo Hoo and Fraenkel, 1966; Waldbauer, 1968). With the small size of H. postica larvae, it is likely that their food is ingested in small pieces. Thirdly, digestibility might have been enhanced by the fact that fresh and succulent alfalfa leaves were fed to the larvae during the experiment.

The decline of the A.D. with time which was observed for parasitized and unparasitized alfalfa weevil larvae (Figure 14) agrees with findings made with other insects. Smith (1959) observed that the dry weight A.D.'s of Triticum aestivum (wheat), Avena sativa (oats) and Agropyron smithii (western wheat grass) for nymphs of the grasshopper Melanoplus bilituratus (Walker) declined over a 40-day period. The digestibility of grass by nymphs of Schistocerca gregaria (Forsk.) decreased steadily from 78.2 percent in the first instar to 35 percent in the fifth (Davey, 1954).

The A.D. also varies within instars. The dry weight A.D. for the fifth instar silkworm, Bombyx mori, varied from 40 percent during the first two days to 27 percent during the sixth and seventh days (Hiratsuka, 1920). Other examples of the decline of digestibility with age are given by Waldbauer (1963).

The more pronounced decrease in the A.D. with age for H. postica larvae at 30 C than at 22.2 C (Figure 14), may be explained on the basis of the more rapid development of the larvae at the former temperature. As the larvae matured faster at 30 C, their digestibility of alfalfa also declined faster than at 22.2 C.

Net efficiency of food conversion. The net efficiencies of conversion of ingested food to body substance (E.C.I.) by H. postica larvae are generally higher than those reported for other insects, except Prodenia eridania (Table 28). However, the net efficiencies of conversion of digested food to body substance (E.C.D.) by H. postica larvae are generally somewhat similar to those recorded for other insects except again for P. eridania (Table 29).

Table 28. Comparisons of the net efficiency of conversion of ingested food to body substance (E.C.I.) by different insects^a

Insect	Food	Temperature	Stage	Net E.C.I. ^b (%)	Authority
<u>Melanoplus</u> <u>bilituratus</u> (Orthop.: Acrididae)	<u>Triticum</u> <u>aestivum</u> (Wheat)	30 C	Whole nymphal stage	10	Smith (1959) Calculated by Waldbauer (1968)
As above	<u>Avena</u> <u>sativa</u> (Oats)	As above	As above	8	As above
<u>Bombyx</u> <u>mori</u> (Lepidop.: Bombycidae)	<u>Morus</u> <u>alba</u> (Mulberry)	-	4th and 5th instars	19	Shyamala et al. (1960) Calculated by Waldbauer (1968)
<u>Mamestra</u> <u>brassicae</u> (Lepidop.: Noctuidae)	<u>Beta</u> sp. (Beet)	25 C	5th instar to pupa	14	Hirano and Noguchi (1963) Calculated by Waldbauer (1968)
<u>Prodenia</u> <u>eridania</u> (Lepidop.: Noctuidae)	<u>Phaseolus</u> <u>vulgaris</u> (Leguminosae)	-	5th and 6th instars	33.5	Crowell (1941)
<u>Hypera</u> <u>postica</u> (Coleop.: Curculionidae)	<u>Medicago</u> <u>sativa</u> (alfalfa)	22.2 C	3rd and 4th instars	23.5	Present study
As above	As above	30 C	As above	26.8	As above
<u>H. postica</u> (Parasitized)	As above	22.2 C	As above	26.4	As above
As above	As above	30 C	As above	25.5	As above

^aMeasurements on dry weight basis.^bBased on net weight gain.

Table 29. Comparisons of the net efficiency of conversion of digested food to body substance (E.C.D.) by different insects^a

Insect	Food	Temperature	Stage	Net E.C.D. ^b (%)	Authority
<u>Melanoplus</u> <u>bilituratus</u> (Orthop.: Acrididae)	<u>Triticum</u> <u>aestivum</u> (Wheat)	30 C	Whole nymphal stage	32	Smith (1959)
<u>Carausius</u> <u>morosus</u> (Phasmida)	<u>Hedera</u> <u>helix</u> (Araliaceae)	20 C	Whole nymphal stage	39	Lafon (1951) Cited by Waldbauer (1968)
<u>Bombyx</u> <u>mori</u> (Lepidop.: Bombycidae)	<u>Morus</u> <u>alba</u> (Mulberry)	-	4th and 5th instars	48	Shyamala et al. (1960) Cited by Waldbauer (1968)
<u>Mamestra</u> <u>brassicae</u> (Lepidop.: Noctuidae)	<u>Beta</u> sp. (Beet)	25 C	5th instar to pupa	29	Hirano and Noguchi (1963). Cited by Waldbauer (1968)
<u>Prodenia</u> <u>eridania</u> (Lepidop.: Noctuidae)	<u>Phaseolus</u> <u>vulgaris</u> (Leguminosae)	-	5th and 6th instars	69	Calculated from Crowell (1941) by present author
<u>Hypera</u> <u>postica</u> (Coleop.: Curculionidae) (Unparasitized)	<u>Medicago</u> <u>sativa</u> (alfalfa)	22.2 C	3rd and 4th instars	30.6	Present study
As above	As above	30 C	As above	34.0	As above
<u>H. postica</u> (Parasitized)	As above	22.2 C	As above	33.9	As above
As above	As above	30 C	As above	32.0	As above

^aMeasurements on dry weight basis.^bBased on net weight gain.

The relatively high net E.C.I. 's and net E.C.D. 's of alfalfa by H. postica larvae again reflect a high adaptation of the insect to the plant.

The E.C.I. measures the overall ability of an insect to utilize for growth the food which it consumes. The E.C.I. varies with both the digestibility of the food and the proportional amounts of the digestible portion of that food which are either converted to body tissue or metabolized for energy (Waldbauer, 1968).

The E.C.D. decreases as the proportion of digested food which is converted to energy increases. The E.C.D. is, therefore, affected by factors which influence the energy requirements for life processes or for the support of activity (Waldbauer, 1968). Thus, the fact that no difference in activity was observed between parasitized and unparasitized H. postica larvae (Tables 10 and 11) is apparently reflected in the finding that no significant difference also existed between the net E.C.D. 's by the two types of larvae at either 22.2 C or 30 C (Table 23).

A difference in food consumption apparently explains the differential growth achieved by unparasitized and parasitized larvae at 22.2 C. With the exception of the net E.C.I. which was significantly higher for parasitized than for unparasitized larvae (Table 22), no significant differences existed between the dry weight-fresh weight C.I. 's, the A.D. 's and the net E.C.D. 's for unparasitized and parasitized larvae at 22.2 C. Thus the higher total growth achieved by unparasitized than by parasitized larvae at this temperature was due to the significantly higher total food consumption by the unparasitized larvae (Table 18).

The higher total growth (Table 15) by unparasitized larvae at 22.2 C than at 30 C (illustrated by the significantly higher total gain in fresh weight on the day preceding the cocoon stage) is also apparently explained by the difference in food consumption. The total food consumption by unparasitized larvae was significantly higher at 22.2 C than at 30 C (Table 24). On the other hand, the lack of a significant difference between the total food consumption by parasitized larvae at 22.2 C and 30 C (Table 25) apparently also explains the absence of a significant difference in growth between these larvae at the two temperatures (Table 16).

Other workers have found poor growth to be the result of a low food intake. Waldbauer (1962) observed that poor growth by maxillectomized larvae of the tobacco hornworm, Manduca sexta (Johansson), on non-solanaceous plants was related to a low food consumption. Rahman (1970a) noted that as unparasitized larvae of the imported cabbageworm, Pieris rapae, consumed more food at 22.5 C than at 24.3 C, they became heavier.

The higher total growth achieved by unparasitized larvae at 30 C over parasitized larvae at the same temperature seems to be the result of a combination of factors. Although at this temperature no significant differences existed in the total food consumption, the C.I.'s, the A.D.'s, the net E.C.I.'s and the net E.C.D.'s between unparasitized and parasitized larvae, nevertheless the total food consumption (Table 18), the net E.C.I. (Table 22) and the net E.C.D. (Table 23) were each slightly higher for unparasitized larvae. Thus the higher total growth by unparasitized larvae at 30 C, is apparently due to the combined effect of the higher total food consumption,

the higher net E.C.I. and the higher net E.C.D. by the unparasitized larvae. Soo Hoo and Fraenkel (1966) found that some plants did not support optimal larval growth of the armyworm, Prodenia eridania, because of any one or a combination of the following factors: a low A.D., a low efficiency of food conversion, and a low rate of food consumption.

SUMMARY AND CONCLUSIONS

The effects of parasitism by the ichneumonid parasite Bathyplectes curculionis (Thomson) on the larvae of the western United States form of the alfalfa weevil, Hypera postica (Gyllenhal), were studied. The relationship of larval age to parasitism, the effect of parasitism on host development and activity, and the effect of parasitism on larval growth, food consumption and food utilization were measured. Efforts were made to find a practical method to identify parasitized larvae.

The rates of parasitism of the four instars of H. postica and the survival of the larvae following parasitization were studied by exposing larvae to B. curculionis females in three experiments. The survival of the exposed larvae was compared with that of unexposed larvae. In the first experiment, the four host instars were exposed separately to female parasites and the levels of parasitism and survival of the exposed larvae were recorded. Parasitism rates of each of the first three instars was significantly higher at the 1 percent level than that of the fourth instar but no significant difference at the 5 percent level existed among the levels of parasitism of the first three instars. In the second experiment, the host instars were simultaneously exposed to female parasites and parasitism rates and survival were determined as before. No significant difference, at the 5 percent level, was observed among the parasitism rates of the first three instars. Parasitism of either the second or third instar was significantly

higher at the 5 percent level than that of the fourth instar but there was no significant difference at the 5 percent level between the parasitism rates of the first and fourth instar larvae.

The survival of parasitized first and second instar larvae was further studied in the third experiment. Survival of larvae which had been individually "stung" once or thrice by female B. curculionis was compared with that of "unstung" larvae. Oviposition was quick, occurring usually in about 3-4 seconds.

The results indicate that the first three instars of H. postica larvae are either preferred by B. curculionis females over the fourth instar larvae or are more susceptible to attack by the parasite. It is recommended that the reasons for poor parasitism of the fourth instar larvae be investigated as well as the extent of encapsulation of B. curculionis eggs by the Utah populations of western H. postica larvae.

Many younger weevil larvae died following oviposition by Bathyplectes. Death was probably from both the puncturing by the parasite's ovipositor and the feeding and other activities of parasite larvae within host larvae. The severity of these effects on host larvae decreased with age and increased with multiple "stinging." If these phenomena also occur in the field, then the parasite causes more host mortality than is measurable by most existing techniques.

The effects of parasitism on the development and activity of H. postica larvae were investigated at 25-26 C. Larvae of each instar were parasitized at the beginning of that instar (except the first instar which was

parasitized when larvae were one day old) and the number of days needed to develop to the cocoon stage was compared with that of unparasitized larvae. There was no significant difference between the length of developmental time for larvae parasitized during either the first or second instar and that for unparasitized larvae of the same age. The development time for larvae parasitized during the third or fourth instar was significantly longer, at the 1 percent level, than that of unparasitized larvae. It is postulated that the prolonged development of larvae parasitized during the last two instars was the result of a physiological conditioning of the hosts by the parasite to enable it to complete its own larval development.

Activity of parasitized and unparasitized H. postica larvae was measured by placing a larva on a grid divided into 1 cm squares and counting the number of squares entered by the larva in 5 minutes. No significant difference in activity was observed between parasitized and unparasitized larvae.

Growth, food consumption, and food utilization were measured for parasitized and unparasitized H. postica larvae during the third and fourth instars at 22.2 C and 30 C. Growth was measured by the daily larval fresh weights and also by the gain in fresh weight from the beginning of the third instar to the day preceding the cocoon stage, and by the gain in both fresh and dry weights at the cocoon stage. Food consumption and utilization were measured on a dry weight basis.

The growth curves of the larvae at either temperature were S-shaped. Growth was significantly slower with parasitized larvae at each of the

temperatures. Significantly higher total growth was achieved by unparasitized larvae at 22.2 C than at 30 C. There was, however, no significant difference in the total growth of parasitized larvae between temperatures. The mean dry weight of B. curculionis larvae at the cocoon stage of the host was significantly greater for parasite larvae which developed from hosts raised at 22.2 C than for parasites from hosts reared at 30 C. The fresh weights of parasite larvae were, however, not significantly different. It is concluded that the lower temperature was more conducive to growth of both H. postica and B. curculionis larvae.

At either 22.2 C or 30 C, the total food consumption by unparasitized larvae was higher than that by parasitized larvae. However, while the difference at 22.2 C was significant at the 1 percent level, that at 30 C was nonsignificant at the 5 percent level. The food consumption per larva per day was significantly higher for unparasitized larvae at both temperatures but there was no difference in the dry weight-fresh weight consumption index (C.I.) at either temperature between unparasitized and parasitized larvae. The conclusion is drawn that parasitism of H. postica larvae by B. curculionis is doubly beneficial to the alfalfa grower. There is a reduction in crop damage due to the reduced feeding by parasitized larvae and there is a lowering of the population of the next weevil generation.

No significant difference existed, at the 5 percent level, between the approximate digestibility (A.D.) of alfalfa by parasitized larvae and that by unparasitized larvae at either 22.2 C or 30 C. The A.D.'s by both types of larvae declined with age at both temperatures, the decline being more

pronounced at 30 C. The net efficiency of conversion of ingested food to body matter (E.C.I.) by parasitized larvae was higher at 22.2 C than that by unparasitized larvae at the same temperature. The difference was marginally significant at the 5 percent level. At 30 C, however, no significant difference at the 5 percent level was observed between the net E.C.I.'s by the two types of larvae. The net efficiencies of conversion of digested food to body matter (E.C.D.'s) were not significantly different, at the 5 percent level, at either temperature between parasitized and unparasitized larvae.

It is concluded that at 22.2 C, total growth by unparasitized larvae was significantly greater than that by parasitized larvae primarily because of the significantly higher total food consumption by the unparasitized larvae. At 30 C, on the other hand, the higher total growth by unparasitized larvae over parasitized larvae was thought to be due to a combination of the higher total food consumption, the higher net E.C.I. and the higher net E.C.D. by unparasitized larvae.

The high efficiency of food utilization observed in the study for H. postica larvae indicates an excellent adaptation of the insect to its food plant.

No practical method was discovered to distinguish parasitized from unparasitized larvae. The lack of such a method prolonged the study.

LITERATURE CITED

- Armbrust, E. J., A. C. Banerjee, H. B. Petty, and C. E. White. 1967. Distribution of the alfalfa weevil in Illinois and the spread of Bathyplectes curculionis. J. Econ. Entomol. 60(2):604-605.
- Armbrust, E. J., S. J. Roberts, and C. E. White. 1970a. Feeding behavior of alfalfa weevil larvae parasitized by Bathyplectes curculionis. J. Econ. Entomol. 63(5):1689-1690.
- Armbrust, E. J., C. E. White, and S. J. Roberts. 1970b. Mating preference of eastern and western United States strains of the alfalfa weevil. J. Econ. Entomol. 63(2):674-675.
- Armitage, H. M. 1949. (First report of the Egyptian alfalfa weevil, Hypera brunneipennis, in the Imperial Valley of California.) Calif. Dep. Agr. Bull. 38(4):165.
- Blickenstaff, C. C. 1965. Partial intersterility of eastern and western U.S. strains of the alfalfa weevil. Am. Entomol. Soc. Amer. 58(4):523-526.
- Blickenstaff, C. C. 1969. Mating competition between eastern and western strains of the alfalfa weevil, Hypera postica. Am. Entomol. Soc. Amer. 62(5):956-958.
- Brunson, M. H., and L. W. Coles. 1968. The introduction, release, and recovery of parasites of the alfalfa weevil in eastern United States. USDA Prod. Res. Rep. 101. 12 p.
- Burnett, T. 1962. An effect of parasite attack on host mortality, as exemplified by Encarsia formosa and Trialeurodes vaporariorum. Can. Entomol. 94(7):673-679.
- Butler, G. D., Jr., and P. L. Ritchie, Jr. 1967. The life cycle of Hypera brunneipennis and a parasite, Bathyplectes curculionis, in relation to temperature. J. Econ. Entomol. 60(5):1239-1241.
- Campbell, W. V., T. G. Bowery, and K. G. Jester. 1961. Seasonal history and control of the alfalfa weevil in North Carolina. J. Econ. Entomol. 54(4):743-747.

- Carne, P. B. 1966. Growth and food consumption during the larval stages of Paropsis atomaria (Coleoptera: Chrysomelidae) Entomol. Exp. Appl. 9:105-112.
- Chamberlin, T. R. 1924a. Introduction of parasites of the alfalfa weevil into the United States. USDA Dep. Circ. 301. 9 p.
- Chamberlin, T. R. 1924b. Studies of the parasites of the alfalfa weevil in Europe. J. Econ. Entomol. 17(6):623-632.
- Chamberlin, T. R. 1925. A new parasite of the alfalfa weevil. J. Econ. Entomol. 18:597-602.
- Chamberlin, T. R. 1926. The introduction and establishment of the alfalfa weevil parasite, Bathyplectes curculionis (Thoms.), in the United States. J. Econ. Entomol. 19:302-310.
- Chamberlin, T. R. 1933. Some observations on the life history and parasites of Hypera rumicis (L.) (Coleoptera: Curculionidae). Proc. Entomol. Soc. Wash. 35:101-109.
- Clausen, C. P. 1956. Biological control of insect pests in the continental United States. USDA Tech. Bull. 1139. 151 p.
- Coles, L. W., and B. Puttler. 1963. Status of the alfalfa weevil biological control program in the eastern United States. J. Econ. Entomol. 56(5):609-611.
- Cothran, W. R. 1966. A bibliography of the alfalfa weevil, Hypera postica (Gyllenhal). Bull. Entomol. Soc. Amer. 12(2):151-160.
- Cothran, W. R. 1968. A bibliography of the alfalfa weevil, Hypera postica (Gyllenhal) Supplement I. Bull. Entomol. Soc. Amer. 14(4):285-288.
- Crowell, H. H. 1941. The utilization of certain nitrogenous and carbohydrate substances by the southern armyworm, Prodenia eridania Cram. Ann. Entomol. Soc. Amer. 34:503-512.
- Dadd, R. H. 1960. Observations on the palatability and utilisation of food by locusts, with particular reference to the interpretation of performances in growth trials using synthetic diets. Entomol. Exp. Appl. 3:283-304.
- Davey, P. M. 1954. Quantities of food eaten by the desert locust, Schistocerca gregaria (Forsk.), in relation to growth. Bull. Entomol. Res. 45:539-551.

- Davis, D. W. 1967. How different are the eastern and western forms of the alfalfa weevil? *Utah Acad. Sci., Arts and Letters.* 44:353-357.
- Davis, D. W. 1970. Insecticidal control of the alfalfa weevil in northern Utah and some resulting effects on the weevil parasite Bathyplectes curculionis. *J. Econ. Entomol.* 63(1):119-125.
- Day, W. H. 1969. Biological notes on Dibrachys cavus, a secondary parasite attacking parasites (Bathyplectes spp.) of the alfalfa weevil in the eastern United States. *J. Econ. Entomol.* 62(5):1225-1226.
- Day, W. H. 1970. The survival value of its jumping cocoons to Bathyplectes anurus, a parasite of the alfalfa weevil. *J. Econ. Entomol.* 63(2):586-589.
- DeBach, P. 1943. The importance of host-feeding by adult parasites in the reduction of host populations. *J. Econ. Entomol.* 36(5):647-658.
- Dietrick, E. J., and R. van den Bosch. 1953. Further notes on Hypera brunneipennis and its parasite, Bathyplectes curculionis. *J. Econ. Entomol.* 46(6):1114.
- Drea, J. J. 1968a. A new species of Microctonus (Hymenoptera: Braconidae) parasitizing the alfalfa weevil. *Entomol. News.* 79:97-102.
- Drea, J. J. 1968b. Castration of male alfalfa weevils by Microctonus spp. *J. Econ. Entomol.* 61(5):1291-1295.
- Dysart, R. J., and L. W. Coles. 1971. Bathyplectes stenostigma, a parasite of the alfalfa weevil in Europe. *Ann. Entomol. Soc. Amer.* 64(6):1361-1367.
- Dysart, R. J., and B. Puttler. 1965. The alfalfa weevil parasite Bathyplectes curculionis in Illinois and notes on its dispersal. *J. Econ. Entomol.* 58(6):1154-1155.
- Edwards, C. A. 1964. The bionomics of swift moths. I. The ghost swift moth, Hepialus humuli (L.). *Bull. Entomol. Res.* 55:147-160.
- Evans, A. C. 1939. The utilisation of food by certain lepidopterous larvae. *Trans. Roy. Entomol. Soc. Lond.* 89:13-22.
- Evans, A. C., and E. R. Goodliffe. 1939. The utilisation of food by the larva of the mealworm Tenebrio molitor L. (Coleop.). *Proc. Roy. Entomol. Soc. Lond.* A 14:57-62.

- Evans, W. G. 1959. The biology and control of the alfalfa weevil in Virginia. Virginia Agr. Exp. Sta. Bull. 502. 28 p.
- Fewkes, D. W. 1960. The food requirements by weight of some British Nabidae (Heteroptera). Entomol. Exp. Appl. 3:231-237.
- Fisher, T. W., E. I. Schlinger, and R. van den Bosch. 1961. Biological notes on five recently imported parasites of the Egyptian alfalfa weevil, Hypera brunneipennis. J. Econ. Entomol. 54(1):196-197.
- Foster, D. E., and G. W. Bishop. 1970. Distribution and life history of Bathyplectes curculionis (Thomson) (Ichneumonidae: Hymenoptera) in northern Idaho. Idaho Agr. Exp. Sta. Res. Bull. 78. 20 p.
- Fuester, R. W. 1970. Separation of first-stage larvae of two species of Microctonus (Hymenoptera: Braconidae) which attack the alfalfa weevil. Ann. Entomol. Soc. Amer. 63(6):1777-1778.
- Gonzalez, D., R. van den Bosch, and L. H. Dawson. 1969. Establishment of Dibrachoides druso on the Egyptian alfalfa weevil in southern California. J. Econ. Entomol. 62(6):1320-1322.
- Hagen, A. F., and G. R. Manglitz. 1967. Parasitism of the alfalfa weevil in the western plains states from 1963 to 1966. J. Econ. Entomol. 60(6):1663-1666.
- Hamid, A., K. Samad, and M.A.H. Qadri. 1969. Biology of Brachycoryphus nursei (Hymenoptera: Ichneumonidae) in Karachi, Pakistan. Ann. Entomol. Soc. Amer. 62(6):1382-1385.
- Hamlin, J. C., F. V. Lieberman, R. W. Bunn, W. C. McDuffie, R. C. Newton, and L. J. Jones. 1949a. Field studies of the alfalfa weevil and its environment. USDA Tech. Bull. 975. 84 p.
- Hamlin, J. C., W. C. McDuffie, and F. V. Lieberman. 1949b. Alfalfa weevil distribution and crop damage in the United States. USDA Circ. 815. 21 p.
- Hirano, C., and S. Ishii. 1962. Utilization of dietary carbohydrates and nitrogen by rice stem borer larvae, under axenic conditions. Entomol. Exp. Appl. 5:53-59.
- Hirano, C., and H. Noguchi. 1963. Food utilization by the last instar larvae of the cabbage armyworm, Mamestra brassicae L., fed on plant leaves of different food values. Jap. J. Appl. Entomol. Zool. 7: 311-315. (Original not seen; cited by G. P. Waldbauer. 1968. The consumption and utilization of food by insects. Advan. Insect Physiol. 5:229-288.)

- Hiratsuka, E. 1920. Researches on the nutrition of the silk worm. Bull. Ser. Exp. Sta. Jap. 1:257-315. (Original not seen; cited by G. P. Waldbauer. 1968. The consumption and utilization of food by insects. Advan. Insect Physiol. 5:229-288.)
- Hobbs, G. A., W. O. Nummi, and J. F. Virostek. 1959. History of the alfalfa weevil, Hypera postica (Gyll.) (Coleoptera: Curculionidae), in Alberta. Can. Entomol. 91:562-565.
- Hopkins, F. G. 1912. Feeding experiments illustrating the importance of accessory factors in normal dietaries. J. Physiol. Lond. 44:425-460.
- Horn, D. J. 1968. Bathyplectes curculionis, a parasite of the alfalfa weevil, in New York. J. Econ. Entomol. 61(5):1469-1470.
- Horn, D. J. 1970. Oviposition behavior of Tetrastichus incertus, a parasite of the alfalfa weevil. J. Econ. Entomol. 63(1):303-304.
- House, H. L. 1965. Effects of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and the nutrition of a phytophagous larva, Celerio euphorbiae (Linnaeus) (Lepidoptera: Sphingidae). Can. Entomol. 97:62-68.
- Jackson, C. G., D. E. Bryan, G. D. Butler, Jr., and R. Patana. 1970. Development, fecundity, and longevity of Leschenaultia adusta, a tachinid parasite of the salt-marsh caterpillar. J. Econ. Entomol. 63(5):1396-1397.
- Koehler, C. S., and G. G. Gyrisco. 1963. Studies on the feeding behavior of alfalfa weevil adults from the eastern and western United States. J. Econ. Entomol. 56(4):489-492.
- Krasucki, A. 1925. Spostrzezenia nad pojawem Ziolomirkow (Phytonomus Schonh.) w Dublanach ob. Lwowa w roku 1923. (Observations on the occurrence of Phytonomus spp. in Dublany near Lemberg in 1923.) Polskie Pismo Entomol. 4:62-67. (English summary in: Rev. Appl. Entomol. A 13:214-215.)
- Lafon, M. 1951. Quelques documents sur l'appétit et la consommation alimentaire chez les insectes. Ann. Natr. Paris. 5:485-504. (Original not seen; cited by G. P. Waldbauer. 1968. The consumption and utilization of food by insects. Advan. Insect Physiol. 5:229-288.)
- Lewis, W. J. 1970. Study of species and instars of larval Heliothis parasitized by Microplitis croceipes. J. Econ. Entomol. 63(2):363-365.

- MacLachlan, D. S. 1967. (First report of the alfalfa weevil, Hypera postica, in eastern Canada). USDA Coop. Econ. Insect Rep. 17:524.
- Manglitz, G. R., and B. A. App. 1957. Biology and seasonal development of the alfalfa weevil in Maryland. J. Econ. Entomol. 50(6):810-813.
- Michelbacher, A. E. 1940a. Effect of Bathyplectes curculionis on the alfalfa weevil population in lowland middle California. Hilgardia: 13:81-99.
- Michelbacher, A. E. 1940b. Further notes on Bathyplectes curculionis and the alfalfa weevil in lowland middle California. J. Econ. Entomol. 33(6):892-895.
- Michelbacher, A. E. 1943. The present status of the alfalfa weevil in California. Calif. Agr. Exp. Sta. Bull. 677. 24 p.
- Miller, M. C. 1966. Emergence and mating of Tetrastichus incertus, a parasite of the alfalfa weevil. J. Econ. Entomol. 59:1532-1533.
- Miller, M. C. 1970a. Biological control of the alfalfa weevil in Massachusetts. J. Econ. Entomol. 63(2):440-443.
- Miller, M. C. 1970b. Studies of interspecific competition between Tetrastichus incertus and Bathyplectes curculionis, larval endoparasites of the alfalfa weevil. J. Econ. Entomol. 63(3):719-721.
- Muesebeck, C. F. W., K. V. Krombein, H. K. Townes, and others. 1951. Hymenoptera of America North of Mexico. USDA Agr. Monogr. 2. 1420 p.
- Newton, J. H. 1933. The alfalfa weevil in Colorado. Colorado Agr. Exp. Sta. Bull. 399. 19 p.
- Oatman, E. R., G. R. Platner, and P. D. Greany. 1969. The biology of Orgilus lepidus (Hymenoptera: Braconidae), a primary parasite of the potato tuberworm. Ann. Entomol. Soc. Amer. 62(6):1407-1414.
- Perkes, R. R. 1966. Biological studies of the parasites and predators of the alfalfa weevil with particular reference to the effects of selected insecticides. Unpublished M.S. thesis. Utah State University, Logan, Utah. 57 p.
- Pienkowski, R. L., F. K. Hsieh, and G. L. LeCato, III. 1969. Sexual dimorphism and morphometric differences in the eastern, western, and Egyptian alfalfa weevils. Ann. Entomol. Soc. Amer. 62(6): 1268-1269.

- Poinar, G. O., Jr., and G. G. Gyrisco. 1960. A nematode parasite of the alfalfa weevil (Hypera postica (Gyll.)). *J. Econ. Entomol.* 53:178-179.
- Poinar, G. O., Jr., and G. G. Gyrisco. 1962a. A new mermithid parasite of the alfalfa weevil, Hypera postica (Gyllenhal). *J. Insect Pathol.* 4:201-206.
- Poinar, G. O., Jr., and G. G. Gyrisco. 1962b. Studies on the bionomics of Hexameris arvalis Poinar and Gyrisco, a mermithid parasite of the alfalfa weevil, Hypera postica (Gyllenhal). *J. Insect Pathol.* 4:469-483.
- Poinar, G. O., Jr., and G. G. Gyrisco. 1963. Hymenopterous parasites of the alfalfa weevil, Hypera postica, in New York. *J. Econ. Entomol.* 56(4):533-534.
- Poos, F. W., and T. L. Bissell. 1953. The alfalfa weevil in Maryland. *J. Econ. Entomol.* 46(1):178-179.
- Prokopy, R. J., and G. G. Gyrisco. 1965. Summer migration of the alfalfa weevil, Hypera postica (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Amer.* 58(5):630-641.
- Puttler, B. 1963. Notes on the biology of Hemiteles graculus (Hymenoptera: Ichneumonidae) parasitizing the alfalfa weevil, Hypera postica. *Ann. Entomol. Soc. Amer.* 56:857-859.
- Puttler, B. 1966. Biological notes on some hyperparasites of Bathyplectes curculionis (Thomson). *J. Econ. Entomol.* 59(2):483-484.
- Puttler, B. 1967. Interrelationship of Hypera postica (Coleoptera: Curculionidae) and Bathyplectes curculionis (Hymenoptera: Ichneumonidae) in the eastern United States with particular reference to encapsulation of the parasite eggs by the weevil larvae. *Ann. Entomol. Soc. Amer.* 60(5):1031-1038.
- Puttler, B., D. W. Jones, and L. W. Coles. 1961. Introduction, colonization, and establishment of Bathyplectes curculionis, a parasite of the alfalfa weevil in the eastern United States. *J. Econ. Entomol.* 54(5):878-880.
- Rahman, M. 1970a. Effect of parasitism on food consumption of Pieris rapae larvae. *J. Econ. Entomol.* 63(3):820-821.
- Rahman, M. 1970b. Mutilation of the imported cabbageworm by the parasite Apanteles rubecula. *J. Econ. Entomol.* 63(4):1114-1116.

- Rao, B. R. S., B. Parshad, A. Ram, R. P. Singh, and M. L. Srivastava. 1964. On some new records of parasites of Hypera postica (Gyllenhal) (Coleoptera: Curculionidae). *Current Sci.* 33:658-659.
- Salt, G. 1965. Experimental studies in insect parasitism. XIII. The haemocytic reaction of a caterpillar to eggs of its habitual parasite. *Proc. Roy. Soc. Lond. B* 162:303-318.
- Salt, G., and R. van den Bosch. 1967. The defense reactions of three species of Hypera (Coleoptera, Curculionidae) to an ichneumon wasp. *J. Invert. Pathol.* 9:164-177.
- Schroder, R. F. W., J. L. Huggans, D. J. Horn, and G. T. York. 1969. Distribution and establishment of Tetrastichus incertus in the eastern United States. *Ann. Entomol. Soc. Amer.* 62(4):812-815.
- Shaw, F. R., and W. H. Ziener. 1964. Survey of parasites of the alfalfa weevil in western Massachusetts. *USDA Coop. Econ. Insect Rep.* 14:138.
- Shyamala, M. B., K. Sharada, M. G. Bhat, and J. V. Bhat. 1960. Chloromycetin in the nutrition of the silkworm Bombyx mori L. II. Influence on digestion and utilization of protein, fat, and minerals. *J. Insect Physiol.* 4:229-234.
- Smith, D. S. 1959. Utilization of food plants by the migratory grasshopper, Melanoplus bilituratus (Walker) (Orthoptera: Acrididae), with some observations on the nutritional value of the plants. *Ann. Entomol. Soc. Amer.* 52:674-680.
- Smith, H. D. 1930. The bionomics of Dibrachoides dynastes (Foerster), a parasite of the alfalfa weevil. *Ann. Entomol. Soc. Amer.* 23:577-593.
- Soo Hoo, C. F., and G. Fraenkel. 1966. The consumption, digestion, and utilization of food plants by a polyphagous insect, Prodenia eridania (Cramer). *J. Insect Physiol.* 12:711-730.
- Sorenson, C. J. 1934a. Some hyperparasites of the alfalfa weevil parasite, Bathyplectes curculionis (Thoms.) occurring in the Uintah Basin of Utah. *Proc. Utah Acad. Sci., Arts and Letters.* 11:249-251.
- Sorenson, C. J. 1934b. The alfalfa weevil. *Utah Agr. Exp. Sta. Leaflet.* 53. 4 p.

- Stern, V. M. 1961. Further studies of integrated control methods against the Egyptian alfalfa weevil in California. *J. Econ. Entomol.* 54(1): 50-55.
- Streams, F. A., and R. W. Fuester. 1967. Biology and distribution of Tetrastichus incertus, a parasite of the alfalfa weevil. *J. Econ. Entomol.* 60(6):1574-1579.
- Taylor, T. A. 1964. Blaesoxipha filipjevi Rohd. (Diptera, Sarcophagidae) parasitising Zonocerus variegatus (L.) (Orthoptera, Acridoidea) in Nigeria. *Bull. Entomol. Res.* 55:83-86.
- Titus, E. G. 1909. The alfalfa leaf-weevil. *J. Econ. Entomol.* 2:148-153.
- Titus, E. G. 1910. The alfalfa leaf-weevil. *Utah Agr. Exp. Stat. Bull.* 110. 72 p.
- Titus, E. G. 1911. The genera Hypera and Phytonomus (Coleoptera, Family Curculionidae) in America, north of Mexico. *Ann. Entomol. Soc. Amer.* 4:383-494.
- Titus, E. G. 1913. The control of the alfalfa weevil. *Utah Agr. Exp. Sta. Circ.* 10:105-120.
- Tower, D. G. 1916. Comparative study of the amount of food eaten by parasitized and nonparasitized larvae of Cirphis unipuncta. *J. Agr. Res.* 6(12):455-458.
- Trager, W. 1953. Nutrition, pp. 350-386. In K. D. Roeder (Ed.). *Insect physiology*. John Wiley and Sons, Inc., New York. 1100 p.
- USDA. 1967. Alfalfa weevil situation in the U.S. - 1966. *Coop. Econ. Insect Rep.* 17:19-25.
- USDA. 1969. Summary of insect conditions in the United States - 1968. *Coop. Econ. Insect Rep.* 19:153.
- USDA. 1971. The alfalfa weevil--How to control it. *Entomol. Res. Div. Leaflet* 368. 8 p.
- van den Bosch, R. 1953. Bathyplectes curculionis as a parasite of Hypera brunneipennis. *J. Econ. Entomol.* 46:161-162.
- van den Bosch, R. 1964a. Encapsulation of the eggs of Bathyplectes curculionis (Thomson) (Hymenoptera: Ichneumonidae) in larvae of Hypera brunneipennis (Boheman) and Hypera postica (Gyllenhal) (Coleoptera: Curculionidae). *J. Insect Pathol.* 6:343-367.

- van den Bosch, R. 1964b. Observations on Hypera brunneipennis (Coleoptera: Curculionidae) and certain of its natural enemies in the Near East. *J. Econ. Entomol.* 57(2):194-197.
- van den Bosch, R., and E. J. Dietrick. 1959. The interrelationships of Hypera brunneipennis (Coleoptera: Curculionidae) and Bathyplectes curculionis (Hymenoptera: Ichneumonidae) in southern California. *Ann. Entomol. Soc. Amer.* 52:609-616.
- Waldbauer, G. P. 1962. The growth and reproduction of maxillectomized tobacco hornworms feeding on normally rejected non-solanaceous plants. *Entomol. Exp. Appl.* 5:147-158.
- Waldbauer, G. P. 1964. The consumption, digestion and utilization of solanaceous and non-solanaceous plants by larvae of the tobacco hornworm, Protoparce sexta (Johan.) (Lepidoptera: Sphingidae). *Entomol. Exp. Appl.* 7:253-269.
- Waldbauer, G. P. 1968. The consumption and utilization of food by insects. *Advan. Insect Physiol.* 5:229-288.
- Wehrle, L. P. 1940. The discovery of an alfalfa weevil (Hypera brunneipennis Boheman) in Arizona. *J. Econ. Entomol.* 33(1):119-121.
- White, C. E., E. J. Armbrust, J. R. DeWitt, and S. J. Roberts. 1969. Evidence of a second generation of the alfalfa weevil in southern Illinois. *J. Econ. Entomol.* 62(2):509-510.
- Wilson, M. C., and E. J. Armbrust. 1970. Approach to integrated control of the alfalfa weevil. *J. Econ. Entomol.* 63(2):554-557.
- Wilson, M. C., R. T. Huber, J. F. Gerhold, and T. R. Hintz. 1969. Buildup of the alfalfa weevil parasite Bathyplectes curculionis in Indiana. *J. Econ. Entomol.* 62(6):1517-1518.
- Yakhontov, V. V. 1934. The alfalfa weevil or Phytonomus (Phytonomus variabilis Hbst.). (In Russian)--Demy 8vo, 240 p. Moscow, Obe'd. gosud. Izd. Sredneaz. Otd. (English summary in: *Rev. Appl. Entomol.* A 22:334-336.)

VITA

Yeboā A. Duodu

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Host-Parasite Relationship Studies of the Larval Alfalfa Weevil and the Ichneumonid Parasite Bathyplectes curculionis (Thomson).

Major Field: Entomology

Biographical Information:

Personal Data: Born at Agona Nsaba, Ghana.

Education: Attended Presbyterian Elementary School at Agona Nsaba, Ghana; attended Presbyterian Secondary School at Odumase-Krobo, Ghana, receiving the West African School Certificate (First Division) in 1955; obtained the Cambridge Higher School Certificate at St. Augustine's College, Cape Coast, Ghana, in 1957; attended University of Ghana and received the Bachelor of Science degree in Agriculture in 1962; obtained the Master of Science degree in Entomology from Utah State University, Logan, Utah, in 1968; completed requirements for the Doctor of Philosophy degree in Entomology at Utah State University in 1972.