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LABORATORY COMPARISON OF THE POTENTIAL OF APANTELES
RUFICRUS HALIDAY AND APANTELES MILITARIS WALSH (HYMENOPTERA:
BRACONIDAE) FOR CONTROL OF THE ARMYWORM, PSEUDALETIA
UNIPUNCTA (HAWORTH) (LEPIDOPTERA: NOCTUIDAE) IN MICHIGAN

Michigan State University

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IN MICHIGAN

By

Antonio Edilton Rolim

A DISSERTATION

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ABSTRACT

LABORATORY COMPARISON OF THE POTENTIAL OF
APANTELES RUFICRUS HALIDAY AND APANTELES MILITARIS WALSH
(HYMENOPTERA: BRACONIDAE) FOR CONTROL OF THE ARMYWORM,
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Following its introduction from Pakistan in 1977-79, A. ruficrus Haliday was successfully reared on the armyworm, Pseudaletia unipuncta (Haworth), in the laboratory and released in the field but, to date, there is no evidence of establishment.

In alternative host tests A. ruficrus showed a low acceptability for the noctuids Peridroma saucia (Hübner), Agrotis ipsilon (Hufnagel), and Amathes c-nigrum (L.).

Its potential for armyworm control was assessed through comparisons with a common native parasitoid, A. militaris Walsh. In host size preference tests militaris attacked all armyworm instars, but preferred 2nd to 4th instars. A. ruficrus oviposited successfully only in 1st to 4th instars.

Parasitoid functional responses in terms of hosts parasitized at controlled host and parasitoid densities in a cage system (1.95 m² surface area) simulating field conditions confirmed the superior searching characteristics of militaris over ruficrus. Mean numbers of hosts killed increased for rising host and parasitoid densities for both species, but only under very high densities of both parasitoid and host was ruficrus able to parasitize armyworm larvae.

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Data on reproductive parameters were contrasted under confined, cage or field conditions. Production of F_1 progeny was always greater for militaris than for ruficrus. Both field and cage F_1 progeny means were significantly lower than those produced under a strictly confined situation (vials). Both species made repeated attacks when confined in vials which often resulted in superparasitism.

Both species have similar developmental cycles, but ruficrus has a slightly shorter life cycle (19.6 days at 23°C against 22.1 days for militaris). While an inverse relationship exists between host instar and number of days spent by each parasitoid in the host larva, the average length of pupal stage was not influenced by the host instar in which larvae originated. This averaged about 7.1 days for militaris and 5.5 days for ruficrus.

DEDICATION

For my parents,
Euclides and Hilda Rolim,
as a symbol of filial gratitude.

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Deo gratias.

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INTRODUCTION

The armyworm, Pseudaletia unipuncta (Haworth), occurs from southern Canada to northwestern South America (Godfrey 1972). It has periodically been a major problem in the North Central region of the U.S. and, in Michigan, outbreaks have caused substantial losses recently to crops such as small grains and corn (Untung 1978; Ruppel 1979b).

Repeated outbreaks point to ineffective regulation below economic levels by its endemic natural enemies, requiring widespread insecticide treatment. The armyworm is particularly annoying because its outbreaks are unpredictable, both as to time and place. Because of its spotty distribution during outbreaks and the resultant difficulty to develop or implement a management program for endemic natural enemies, it seemed to be a likely candidate for improved control by the introduction of a new natural enemy.

At the outset of this project, available biological control records suggested the feasibility of this venture since previous introduction of Apanteles ruficrus Haliday into New Zealand against the "northern army caterpillar", Pseudaletia (Mythimna) separata (Walker), had met with great success (Anon. 1975; Cumber et al. 1977). Prior to the introduction, several parasitoids of P. separata, including a strain of A. ruficrus, had been established fortuitously in New Zealand, but were affording little control. Since 1971 the

introduction of new strains from Pakistan was very effective in controlling the species, resulting in enormous savings in grain crops and pastures (Mohyuddin and Shah 1977). Comparison of the frequency of outbreaks in some areas in 1976 with the average of the previous 10 years showed that between 2 to 4 million dollars were saved annually due to the absence of serious outbreaks in pastures alone (Hill 1977). The impact was mostly in the North Island where, apart from the enormous benefits to grazing, increased maize production caused New Zealand to go from importer to exporter status. The selection of A. ruficrus as a potential candidate for control of P. unipuncta was also considered, based on the fact that P. separata is in the same genus as our local armyworm.

In 1977, a strain of this promising parasitoid was introduced from Pakistan into Mid-Michigan. It has been cultured in an insectary and released several times in what might be called a "classical" attempt at improving the biological control of a native pest. Unfortunately, it has not been recovered in the field to date.

At the same time preliminary testing of alternative hosts were conducted with A. ruficrus, comparative laboratory studies were undertaken with a common native parasitoid, Apanteles militaris. These studies were aimed at qualitatively evaluating and, if feasible, quantifying some of the intrinsic characteristics and capacities which might prevent establishment of A. ruficrus or which could otherwise interfere with its effectiveness should it become established.

The guidelines for assessing the value of an introduced biological control organism are often not discrete. However,

characteristics such as high searching ability, high reproductive capacity, and adaptation to its host have long been recognized as fundamental to insect pest regulation and critical to establishment. Thus, they are desirable in any effective natural enemy. The number of hosts found and parasitized is the most practical means to evaluate the searching ability of a parasitoid. It can also be used as a measure of parasitoid reproduction, assuming that each host encountered is oviposited upon, which also implies leaving some progeny (Hassell 1978). The experiments described here were devised, in part, to provide information on such parameters and to assess which species might be superior in nature. Even though both species were investigated independently, the evaluation of various basic properties of each in relation to a common host provides some information on their competitive superiority.

A. militaris was selected among several native parasitoids for these comparative studies because its frequency of occurrence and abundance in the armyworm population were consistently high in field samples taken from 1977 to 1980 in outbreak and non-outbreak areas (see also Untung 1978). This species is very well adapted to the whole geographic range of P. unipuncta, showing intrinsic characteristics of selectivity and synchronization with its host (Breeland 1958). Also, biological similarities exist between them with respect to their morphology and behavior (Clausen 1962; Mason 1981), which makes A. militaris one of the most likely endemic natural enemies with which A. ruficrus would compete in the field. It was assumed that, if these species attacked the same host and if they overlapped in their distribution, then competitive interference among

them could exist. This assumption has led to the examination of their functional responses, reproductive capacities and other characteristics, including their relative rates of oviposition and tendencies to superparasitize. Competitive interference, however, would only be likely to occur if environmental conditions favored the adaptation of A. ruficrus to the new habitat and if its intrinsic characteristics allowed it to naturally exploit the target host.

In general, little data is available comparing laboratory results on the assessment of such biological parameters or on the competitive interactions of parasitoid species following field release of a new parasitoid. This is primarily because pre- and post-introduction studies are usually abandoned as soon as the exotic natural enemy is found unsuitable or, more commonly, if its establishment cannot be confirmed after several colonization releases. Few workers have actually delved into the reasons why promising bio-control agents failed to adapt to their target host (even when the host was found suitable in the laboratory) and to the new environment. If some of these studies had been continued, they would perhaps have added to our insight of host-parasitoid relationships and might have provided the answer to some of the problems in attaining successful biological control.

LITERATURE REVIEW

The Armyworm Problem

For more than a century, the armyworm, Pseudaletia unipuncta (Haworth), has been a potentially destructive pest of cereal crops and forage grasses in the eastern half of North America (Breeland 1958; Guppy 1961). In the North Central U.S., this species is a major problem, frequently occurring in widespread outbreaks (Rings and Musick 1976). Populations are typically low and occur in scattered locations, but occasionally increase quickly, resulting in local outbreaks of serious proportions. There are numerous reports in the literature of the nineteenth and early twentieth centuries on the ravages caused by P. unipuncta over extensive areas (e.g., Riley 1883; Panton 1897; Slingerland 1897; Fernald 1914; Baker 1915, 1939; Britton 1915; Gibson 1915a; Davis and Satterthwait 1916; Knight 1916; Walton 1916).

There is, in general, a considerable amount of basic biology published on the armyworm. However, the descriptive approach has been used in most studies before 1950 (Breeland 1958). Relatively little experimental research on basic physiology, genetics or population ecology (including parasitoid-host dynamics) has been published. Moreover, experimental work has been usually restricted to time periods during or following major outbreak years (Guppy 1961). This

lack of continuity makes armyworm data somewhat unreliable, or, at best, incomplete. The most comprehensive reviews on armyworm biology, including past history, geographical distribution, descriptive characters, life history, natural enemies, behavior, seasonality and early control measures are found in Riley (1883), Slingerland (1897), Davis and Satterthwait (1916) and, more recently, in Breeland (1958) and Guppy (1961), from whom the following notes on its life cycle are taken.

Briefly summarized, the life history and habits have been described as follows: upon the arrival of extended warm weather, in early spring, the overwintering larvae complete their development, pupate in the soil and begin emerging as adults. The moths lay their eggs in tightly compact masses on the grasses or the small grains that are available early in the season. The eggs take about a week to hatch, depending on prevailing temperatures. The newly hatched larvae begin feeding immediately on young blades of grass, giving them a general skeletonized appearance. This kind of feeding is characteristic of the first two larval instars. These smaller caterpillars feed at night and hide in the soil or near the crowns of the plants during the day. Therefore, their presence in the field is rarely, if ever, noticed. The remaining instars (3rd through 6th) straddle the outer margin of the grass blade and cut holes from the margin to the midrib until the blade is stripped clean. Armyworms eat the above-ground portion of plants and their feeding increases considerably as they grow larger. When full grown, the armyworm is ca. 4 to 5 cm long. When their numbers are high, large armyworms will also feed during the day and may move from field to field. Pupation is preceded

by a short prepupal period of a day or two during which the larvae do not feed. The pupal stage is spent in the soil at a depth of about 2 to 3 cm and lasts approximately two weeks.

In Michigan, it is thought that three armyworm generations occur, the 1st generation being the most destructive. There has been increasing concern since 1975 due to unusual consecutive outbreaks. In 1975 and 1976, infestations were particularly high in wheat, rye and oats. Corn was the most heavily damaged crop in 1978, and Untung (1978) argued that the 1978 outbreak should be rated the most serious in the agricultural history of the state. Control of the armyworm has largely consisted of monitoring field crops for early detection of outbreaks, followed by insecticide applications (Ruppel 1979a; Ruppel and Bird 1981). However, timing is a problem, since treatments are often applied too early for light infestations or too late for heavy larval feeding (Untung 1978).

The Armyworm's Natural Enemy Complex

It is well-known that most insects have numerous natural enemies which are diverse in characteristics. This is true also with P. unipuncta, since many workers have noticed that whenever it became abundant many natural enemies appeared (see, for example, Riley 1883; Slingerland 1897; Criddle 1914; Baker 1915; Gibson 1915a; Knight 1916; Mickel 1932). Large numbers were found to attack armyworm eggs, larvae and pupae.

Coincident with the outbreaks, many observers have reported on the incidence of parasitism, but have given little attention to

host-parasitoid relationships and their possible value in natural control. Parasitism studies of non-outbreak armyworm populations are rare. Thompson (1945) compiled an extensive list of insect enemies of major pests including P. unipuncta, as found in the earlier literature. More recently, Breeland (1958) and Guppy (1967) published rather specific and comprehensive accounts of dipterous and hymenopterous armyworm parasitoids. These two groups, as well as diseases (viruses, bacteria and fungi), have long been considered to be the chief factors in population reduction of the armyworm at outbreak times (Slingerland 1897; Knight 1916; Mickel 1932). In his two year study in Tennessee, Breeland (1958) observed, in the first year, that Diptera and Hymenoptera were almost equally represented, 52% of all reared parasitoids being Diptera, and 48% Hymenoptera. In the second year, however, parasitic Hymenoptera made up 92%. Studying the armyworm in Ontario, Guppy (1967) pointed out that, of the 69 species of parasitoids noted, Hymenoptera were nearly twice as numerous as Diptera (43 and 26 species, respectively). Most of the Hymenoptera were Braconidae, with 5 genera and 18 species, and Ichneumonidae, with 13 genera and 20 species. The Diptera were largely Tachinidae, with 16 genera and 24 species. In Michigan, Untung (1978) reared 9 parasitoid species from his field samples.

In the genus Apanteles, a large genus endoparasitic on various Lepidoptera (Muesebeck 1921; Clausen 1962), A. militaris is often reared from field-collected larvae (e.g., Baker 1915; Gibson 1915b; Treherne 1916; King and Barber 1921; Vickery 1925; Schaffner and Griswold 1934). In Tennessee, Breeland (1958) found A. militaris to be the most predominant hymenopterous parasitoid, accounting for 27%

and 36% parasitism in two years of study. This species was also found the most abundant armyworm parasitoid in the southeastern portion of South Dakota (Calkins and Sutter 1976). Similar reports emphasizing its abundance or constancy (e.g. Baker 1915; Knight 1916; Pond 1960; Guppy 1967) reinforce the general assumption that this is indeed one of the most common native parasitoids of P. unipuncta. In Michigan, A. militaris was also the most prevalent hymenopterous parasitoid recovered by Untung (1978).

A. militaris* is a gregarious parasitoid native to North America, being widely distributed in the eastern part where it attacks several noctuid hosts (Muesebeck et al. 1951). It is fairly abundant in the North Central region and can also be found in the southern U.S. The biology of A. militaris was first reported in detail by Tower (1915) following a study in Lafayette, Indiana. Additional information can be found in Breeland (1958), and Calkins and Sutter (1976).

Apanteles ruficrus, with which A. militaris has been compared in this study, is also a gregarious larval endoparasitoid recorded from a number of noctuids and pyralids in Europe, Asia, Africa, Australia and New Zealand. Hafez (1947) studied the biology and life cycle in Egypt. He reported that it is very abundant in areas where its main host, Agrotis ipsilon Hbn., is prevalent. Willcocks (1937) attributed an important role in the control of some Agrotis and Leucania species in Egypt to this parasitoid. Further aspects of the reproduction and

*In his recent attempt at reclassifying the Microgastrinae, Mason (1981) has split the old "Apanteles" and placed both A. militaris and A. ruficrus in the tribe Cotesiini; militaris has been transferred to the genus Glyptapanteles Ashmead 1905, and ruficrus to the genus Cotesia Cameron 1891.

development of A. ruficrus are discussed later with respect to the results obtained in this study.

Aspects of Biological Control Relevant to This Study

A reduction in the use of chemical pesticides and the search for more ecological approaches to insect pest control have long been advocated, as shown in the works of early entomologists (e.g., Woodworth 1896, 1908; Smith 1941; Michelbacher 1945, among others). In more recent times, the increasing complexity of crop protection problems coupled with those induced by heavy chemical usage (e.g., insecticide resistance, resurgence of target pests, destruction of beneficial insects, adverse effects on non-target organisms, environmental contamination, etc.) have stimulated a greater interest in the use of ecological principles; this has resulted in the development and implementation of integrated pest management with biological control as a key component. Today, biological control constitutes a central element in most integrated control programs (Corbet and Smith 1976).

Since its emergence in the late 1800's, the practice of biological control has undergone over the years a distinct dichotomy encompassing either the introduction and manipulation of exotic entomophagous insects (classical biological control) or the management of indigenous natural enemies* (naturally-occurring

*In this review the terms natural enemy, parasitoid and predator are often used interchangeably, as are host and prey.

biological control). Although the possibilities for conservation and augmentation of naturally occurring biological control are many, most of the world effort until recent years was concentrated on "classical" biological control, the applied phase involving the discovery, importation and establishment of exotics (Huffaker et al. 1976). The main objective of "classical" biocontrol has long been the search for effective enemy species in the region where the pest originated for colonization in the areas invaded by the target pest. In many instances this objective has been achieved through the selection and importation of one or more natural enemies. The ecological principles involved in the importation of foreign species also apply to indigenous pests wherein natural enemies can be obtained from closely related pests abroad and imported to hopefully regulate a new pest (DeBach 1974).

Despite a number of critical analyses and new insights into the practice of selecting biological control agents contributed by several investigators (e.g., Force 1972, 1974, 1975; Price 1972, 1973; Ehler 1977, 1978, 1979; Miller 1977, 1980), the search for suitable natural enemies remains, as a whole, a rather empirical process. Indeed, in most applied biological control programs selection has been conducted on the basis of Smith's (1929) recommendations, that is, by utilizing an association of different species of natural enemies for each host. This practice of multiple-species introductions against the opposing idea of a single "best species" has become a matter of intense debate among modern biological control workers (see Turnbull and Chant 1961; Watt 1965; Turnbull 1967; van den Bosch 1968, 1971; Huffaker et al. 1971; Pschorn-Walcher 1977).

Since there are studies which provide empirical support for either view (e.g., Force 1974; Ables and Shepard 1976; Ehler 1977, 1978; Miller 1977) the controversy is not likely to be fully resolved soon. Bartlett and van den Bosch (1964) and, more recently, Zwölfer et al. (1976) have reviewed and discussed foreign exploration for biological control in considerable detail. Zwölfer et al. (1976) summarized important general criteria that may help in selecting natural agents for introduction. The subject was also covered extensively by DeBach (1974) who developed a series of recommendations regarding biological control importation principles, policies, and practices, most of which are still valid (see also DeBach 1971a).

Simmonds (1972) and Messenger et al. (1976) concede that seldom can one forecast with confidence the outcome of any introduction. The main reason is because it is impossible to outline all the biological characteristics necessary for effectiveness of a natural enemy in any particular instance. If, however, the attributes of successfully introduced parasitoids are compared to characteristics of those which have failed, some properties emerge which are common to the most effective species. Some of the characters pertinent to the effectiveness of a parasitoid or predator have been listed by Douthett and DeBach (1964), Huffaker et al. (1971) and Huffaker (1974). It may be useful to recapitulate some of them: (1) a marked adaptability to the varying physical conditions of the environment; (2) adequate searching and dispersal abilities to find a suitable host or habitat; (3) a high reproductive capacity relative to that of its host (or prey). Other desirable qualities include power of prey consumption and intrinsic properties such as a high degree of host specificity,

synchronization with host life history, discriminative ability, high survivability during host-free periods, and special behavioral traits which may alter its performance as related to density or dispersion of its own population (see also Messenger et al. 1976; Zwölfer et al. 1976). The first three attributes listed above are also needed by good colonizers according to Mayr (1965). Messenger et al. (1976) have warned that it is not to be expected that all the desirable attributes listed above will be simultaneously present in any parasitoid or predator. It is generally agreed that among these the prime requisite for an effective insect enemy would be a high searching capacity, i.e., the ability to find its host when the host is scarce (Huffaker et al. 1976). As parasitoids and predators are successful to a greater or lesser extent in finding host/prey, searching efficiency can be a very important parameter to evaluate their performance in biological control programs. Valuable discussions on parasitoid searching can be found in early papers (e.g., Nicholson 1933; Laing 1937; Walker 1937; Smith 1939; Thompson 1939), but more extensive assessments of searching ability and behavior and their bearing on biocontrol have, in recent times, been made by Doutt et al. (1976), Hagen et al. (1976) and Huffaker et al. (1976).

In an analysis of the concept of r- and K-selection as proposed by MacArthur and Wilson (1967), Force (1972) concludes that for biological control purposes early colonizers or r-strategists are more likely to be effective because of their high reproductive potential, high powers of dispersal, and ability to tolerate harsh conditions (see Pianka 1970, 1972, for a more complete list of the attributes characteristic of r- and K-strategists). Hence, a high

reproductive rate (intrinsic power of increase) would be a very important additional feature, especially in unstable, often disturbed environments such as agroecosystems. Using the systems analysis approach, Hassell (1978) adds to the list of characteristics of an ideal parasitoid for biocontrol the ability to aggregate in patches of high host density. He explains that the high search rate leads to a greater depression of the host equilibrium, whereas the aggregation ensures that this equilibrium will be stable.

Doutt (1964) and Doutt and DeBach (1964) have characterized the two basic types of natural enemies: parasitoids and predators. A parasitic insect (parasitoid) can usually be distinguished from a predator by the fact that the former develops in or on a single host individual whereas the latter must consume more than one host (prey). In contrasting these two forms, a notable feature stands out: males, females and immature stages of predators are all usually engaged in locating and consuming prey, whereas it is only the adult female parasitoid that searches for hosts, and that is for oviposition rather than to consume them, although some species do host-feed. More reliable, efficient, regulating parasitoids or predators are ones that show a reciprocal density-dependent relationship with their host or prey (Huffaker and Messenger 1964). This means the host will be regulated by its enemy, and the enemy is in turn limited by the number of hosts available.

In more recent review articles, Doutt et al. (1976) and Hagen et al. (1976) further discuss some of the host relationships of predators and parasitoids. Some of the most relevant aspects of early investigations on the dynamics of parasitism and predation (e.g.,

DeBach and Smith 1941, 1947; Ulliyett 1943, 1945, 1949a, 1950; Burnett 1951, 1953, 1954, 1956, 1958) are the abundance of the parasitoid (or predator) or the abundance of the host (or prey) as they relate to searching efficiency. Both parasitoid and host densities have been shown to affect the parasitoid's rate of reproduction through the success of the parasitoid in finding hosts. Looking into the factors associated with these parameters, Solomon (1949) recognized two basic responses of predators/parasitoids to prey/host density: (1) a numerical response, which is a change in predator/parasitoid numbers in response to a change in prey/host density; and (2) a functional response, which is a change in the number of prey consumed per predator (or of hosts attacked per parasitoid) in response to a change in prey/host density. Hassell (1966) proposed the terms "reproductive" and "behavioral" to respectively describe both responses. These are expressed in terms of changes in the percentage of parasitization or predation. In a series of classic papers, Holling (1959a, 1961, 1965, 1966) explored the terminology introduced by Solomon (1949), identifying and quantifying several of the components of the functional responses. During succeeding years many investigators have examined and expanded upon his approach in showing biological implications of the functional response. Some have found additional examples of organisms exhibiting a functional response (e.g., Messenger 1968; Griffiths 1969; Murdoch 1969) while others have discussed the importance of this response in the dynamics of populations (see Murdoch and Oaten 1975, for a review). Huffaker et al. (1968) show graphically four different types of functional responses of parasitoids and predators to host or prey density.

However, the basic types are only three: linear, convex and sigmoid (Hassell 1978).

So far, such behavioral or functional responses of entomophagous insects have proved essential in systems analysis for modeling host-parasitoid interactions, since they can provide a description of the behavior of parasitoids in relation to host density (Hassell 1978). Recognizing that this is not true of the behavior of predators, Huffaker et al. (1976) caution that it is the numerical response, and not the functional response itself, that is the usual indicator of their control and regulatory power. In assaying the performance of a parasitoid one has first to learn how it performs as an individual, i.e., the way in which it searches for hosts, perceives them, and finally accepts or refuses them for attack. It is such functional responses of individuals rather than the response of a population which are essential for a clear understanding and proper approach to modeling of host-parasitoid interactions. Modeling may in turn lead to greater insight and to development of more realistic strategies and tactics of pest control (Huffaker et al. 1971; Stark and Smith 1971). Hassell (1978) discusses in detail the three functional responses earlier referred to and explains why parasitoids, rather than predators, make convenient experimental subjects for the modeling of host-natural enemy interactions.

In dealing with further aspects of evaluation of the impact of insect enemies, DeBach and Huffaker (1971) and, more recently, DeBach et al. (1976) have provided excellent reviews on a variety of comparative experimental methods and techniques which may additionally be employed by biological control workers (see also DeBach

and Bartlett 1964). One of their conclusions is that, aside from the various methods of evaluation of effectiveness, both the functional and the numerical responses constitute essential tools in assessing the full regulating potential of a given insect enemy.

METHODS AND MATERIALS

Host and Parasitoid Rearing

All rearing and experiments were conducted at $23.0^{\circ}\text{C} \pm 1.5^{\circ}\text{C}$, 40-60% RH, and a photoperiod of 16 hr L : 8 hr D, using fluorescent 35-watt bulbs. A. militaris and A. ruficrus were continuously reared in the laboratory from April 1977 to May 1981 on P. unipuncta. The host stock culture was annually renewed with hundreds of armyworm larvae collected in Mid-Michigan infested corn areas. The A. militaris culture was formed with adults emerging from these field-collected larvae. The A. ruficrus culture was renewed with additional adults imported from Pakistan in 1978 and 1979. Simultaneous maintenance of all three insect cultures required a high degree of coordination and was handled as follows.

For rearing the armyworm, a combination of the procedures described by Pond (1960) and Guppy (1961) was used. Larvae and moths were initially reared in large cages measuring 61.0 x 61.0 x 30.5 cm with front, back and bottom made of wood. The sides and top were made of Plexiglas and had about 30 holes 2.5 cm in diameter, evenly spaced and covered with nylon screening for ventilation. However, following a disease problem in November 1977 a better rearing method was found wherein larvae were reared in 59.1 ml clear plastic cups (standard

cup or vial).^{*} Usually no more than two larvae were held per cup. Although labor increased considerably, dampness and sanitary conditions were more carefully monitored. The new method completely eliminated the previous problems associated with excess moisture. Armyworm larvae were fed daily on fresh barley leaves (variety Lakeland) which were cut from young plants 10-15 cm tall and placed in each cup. The old foliage and frass were removed daily to prevent or minimize contamination. Prepupae were placed on slightly moist sterilized soil sifted into 147.9 or 236.6 ml wax cardboard containers.^{**} They were usually grouped 10 individuals per dish. Containers were covered with a petri dish top and kept in a secluded place away from light until adults emerged. On the day of emergence adult moths were transferred to metal screen sleeve cages measuring either 30.5 x 30.5 x 30.5 cm or 45.7 x 45.7 x 45.7 cm for mating and oviposition. Usually 20 to 40 moths of both sexes were held per cage. A 10% honey solution and tap water were available from several cotton wads in the dishes; the solution was changed every other day to avoid contamination. Barley seedlings planted in squat containers were replaced every three days in the cages for continuous egg deposition by the moths. These seedlings rather than wax paper strips as used by other workers (Pond 1960; Calkins and Sutter 1976), were excellent sites for egg-laying. Egg clusters found on the seedling blades were

^{*}Supplied by Thunderbird Container Corporation, 128 Thunderbird Dr., El Paso, TX 79912.

^{**}Supplied by Continental Can Co., Palatine, IL 60067.

collected and transferred to 472 ml Ball[®] wide-mouth jars* covered with a fine nylon cloth for hatching and early larval development. The leaf material placed in each jar seemed to provide adequate moisture for eclosion. A few additional fresh leaves were placed into the jars as soon as newly hatched larvae appeared.

The procedures reported by Calkins and Sutter (1976) for rearing A. militaris proved to be fairly satisfactory. However, larger, 354.9 ml clear plastic cups with a 7.6 cm diameter petri dish bottom glued to the top worked best as propagating cages. Each parasitoid cage had three holes 2.5 cm in diameter. The hole in the bottom was covered with a fine metal screen for ventilation; the other two openings were for supplying a 10% honey solution and tap water from foam sponges. These solutions were replaced every other day to avoid bacterial and/or fungal growth. Offspring from no more than two or three cocoon masses were usually held per container, to reduce excessive crowding, while still allowing for some genetic diversity. After emergence, the wasps were usually allowed 3-5 days for mating, after which a group of females, taken in small numbers from several cages, were sexed and used to parasitize new hosts. Armyworms for parasitization were usually available from the main stock culture as 3rd and/or 4th instars. They were segregated two per cup (59.1 ml standard cup) with one female mated wasp. The average exposure time was 24 hours, and females of A. militaris were usually 2- or 3-days old when selected for oviposition. For continuous maintenance of the parasitoid culture this procedure had to be repeated at 3- or 4-day

*Supplied by Ball Corporation, Muncie, IN 47302.

intervals. During incubation for parasitoid emergence parasitized hosts were always fed fresh barley daily.

For rearing A. ruficrus essentially the same technique was used. The host exposure method was also very similar to the one described previously for A. militaris, but the host lots were comprised mostly of 2nd and/or 3rd instars, and the wasps were usually older (4-7 days). Moreover, since parasitism by A. militaris was seen to be greater than by A. ruficrus, a larger number of host larvae were exposed to the latter within the same 3- to 4-day period. Both parasitoids are in general rather sensitive to rough handling; therefore, a mouth-operated aspirator was always used to collect them prior to counting and sexing them under a microscope. As is to be expected, during the five year period several modifications on the exposure technique of the host to the parasitoids were tried and progressively introduced as better methods were found.

Preliminary Tests With A. ruficrus

Two types of preliminary tests were conducted with the newly-imported A. ruficrus before any comparative studies with a native parasitoid species were undertaken. They consisted of: (1) crossing tests, and (2) host range tests.

The crossing tests were conducted as a routine check of the reproductive isolation of this parasitoid from its native "congener" A. militaris chosen for comparison. The procedure used was as follows. To prevent emerging adults from normally mating, 1 or 2 days prior to emergence a number of cocoons were isolated from their

original clusters, and placed singly into standard cups. Each cup was supplied with a small piece of a foam diSP0[®] plug saturated with honey water for parasitoid nourishment. Following adult emergence, the parasitoids were sexed, and virgin females of one species were transferred into a cup cage with unmated males of the other species obtained in a similar manner. The groups were then allowed free mating for 2 days, after which 20 healthy and active females were randomly picked from each population to make up the experimental groups. They were introduced singly into standard vials, each female being given a 3rd instar armyworm larva as a host for a period of 24 hr. Twenty additional females were taken from each group and segregated with males of their own kind to function as controls. These also each received a 3rd instar host larva for parasitism. Experimental conditions were the same for both groups. After having been exposed to parasitoids, the hosts were reared one per cup until the emergence of F₁ progeny or pupation of the host larva. Daily observations were made on each individual larva, and following parasitoid death, all F₁ progeny were examined microscopically to determine species and sex, as well as to detect any hybridization.

The host range tests were designed to investigate any relationship between A. ruficrus and potential noctuid hosts other than P. unipuncta. Their purpose was to check for the suitability of different hosts among the armyworm-like complex of pests in the Mid-Michigan area and to compare the acceptability of the armyworm relative to other possible host species. Host acceptability was essentially gauged by comparing parasitization rates for three cutworm species exposed to attack by A. ruficrus in a confined

situation (59.1 ml small cups). Early instars of the variegated cutworm, Peridroma saucia (Hübner), the black cutworm, Agrotis ipsilon (Hufnagel), and the spotted cutworm, Amathes c-nigrum (L.), were chosen because of their superficially close resemblance to the target host, and because of their availability and relative abundance among cutworm species in Michigan. Following rearing and exposure procedures similar to those described for P. unipuncta, larvae of these cutworms were usually used as prospective hosts when they reached the 3rd larval instar. As usual, the parasitoid-host ratio remained 1:1 per container for a full 24-hour period. At the end of each test the surviving females were held as a group while being given fresh food for 1 hr or so. Then, another batch of females was randomly picked among these wasps for confinement with 3rd instar armyworms for another 24 hr; these last armyworms served as controls. The size of the control test (n) was usually half the cutworm sample because of parasitoid mortality in the previous test. Following the same procedure described for armyworms, all the caterpillars used as potential hosts were individually reared in standard vials, fresh barley foliage being regularly served at about the same time daily and always in excess of the amount consumed by the larvae. In rearing large noctuid larvae in small cups, free moisture accumulation may be a critical factor, rendering them more susceptible to diseases or, sometimes, interfering with molting (Pond 1960). Thus, uncut plastic lids used in the first 24 hr of the tests to prevent parasitoid escape from the vials were later replaced with lids cut to improve aeration for the larvae.

Comparative Tests Between A. *militaris* and A. *ruficrus*Host Size Preference Tests

The main objectives of this study were to identify differential parasitism among the various armyworm instars and to note the effects of differently aged parasitoids on each instar. Host size preference was investigated throughout the first week of adult parasitoid life by exposing each of the six larval instars of P. *unipuncta* to females of both parasitoid species. Host larvae of each instar were selected from the stock culture, based on measurements of their head capsules (see Breeland 1958). All armyworm larvae used were apparently healthy, well-formed and uniform in size within each instar. They were individually confined with a female wasp, presumed to be fertilized, in 59.1 ml jelly cups for 24 hrs. A. *ruficrus* wasps ranged in age from 1 to 7 days whereas it was more difficult to obtain large numbers of A. *militaris* 5 days or older due to their shorter adult life span. The females presumably mated had been previously fed honey and water, but they had not oviposited. As usual, in the days subsequent to exposure, larvae were reared in isolation, always being provided with abundant fresh food. Observations were taken daily until successful parasitization, pupation of the host or death from unknown causes occurred. Parasitized hosts were held until emergence of adult parasitoids, which were counted and sexed.

It should be noted that these tests were conducted in a very limited environment where, as a result, real parasitoid searching was not involved. Under conditions of extreme confinement, excess egg

deposition by parasitoids may often lead to superparasitism with host death as a consequence. To investigate such a possibility microscopic dissections were performed on host larvae found parasitized and on several others dying from causes which could not be clearly determined. The parasitoid larvae they contained were counted, but not added to the total number of emerging mature larvae.

Data collected in these tests also provided useful information on the estimation of several other parameters associated with parasitoid reproduction and development (see below).

Throughout the text these tests are referred to as "vial tests" or "confined tests" to differentiate them from another situation where parasitization took place in large cages within which hosts were widely dispersed and therefore intensive search by the ovipositing females was required.

Functional Response Tests

Parasitoid searching is an important factor of natural control. During this study, it was assumed to be a most important parameter in appraising relative attack efficiency. The functional response, as defined by Holling (1959a,b, 1961, 1965, 1966), was thought to be appropriate for assessing both the parasitoids' searching abilities and their general regulatory properties.

A "cage ecosystem" was designed to simulate field conditions within which host and parasitoids would interact as naturally as possible. A series of tests was conducted in which known densities of the host and parasitoids were varied, and the resulting rates of apparent parasitism were measured. Each test was replicated six

times, the time between replications dictated by the availability of the organisms to be used. Different combinations of parasitoid densities (5 and 10), host densities (1, 2, 4, 10, 20 and 40) and host instars (2nd, 3rd and 4th) were examined for each species. Tests employing five A. ruficrus females were not carried out, and all scheduled tests using 10 A. ruficrus against host densities equal to or lower than 20 were discontinued since no parasitism was repeatedly obtained.

In designing this artificial cage system, the duplication of natural ecosystem details such as ground features, physiological condition of the plant, spacing, microenvironment, etc. was a critical and challenging endeavor. To minimize experimental error, many preliminary tests were conducted and data collection was not started until all the technical procedures seemed to have been brought under an acceptable degree of control.

These tests were conducted in two wooden cages each measuring 213.4 (length) x 91.4 (width) x 30.5 (height) cm (total floor area: 1.95 m^2), with a fine mesh nylon screen on two sides and the top. Each cage had six hinged doors, each one measuring 58.4 x 17.8 cm. Three doors on one side of the cage opened to the outside and permitted full access to any point in the cage interior, making plant handling an easy task while the three other doors were not used. Wooden flats of barley seedlings planted in rows were positioned in the cage as shown in Figure 1. Each flat measured 50.8 x 35.6 x 7.6 (depth) cm (inside measurements) and was filled with sterilized soil. The seedlings were sown in three rows about 17.5 cm apart; there were about 10 plants per row. The plants were first utilized when they

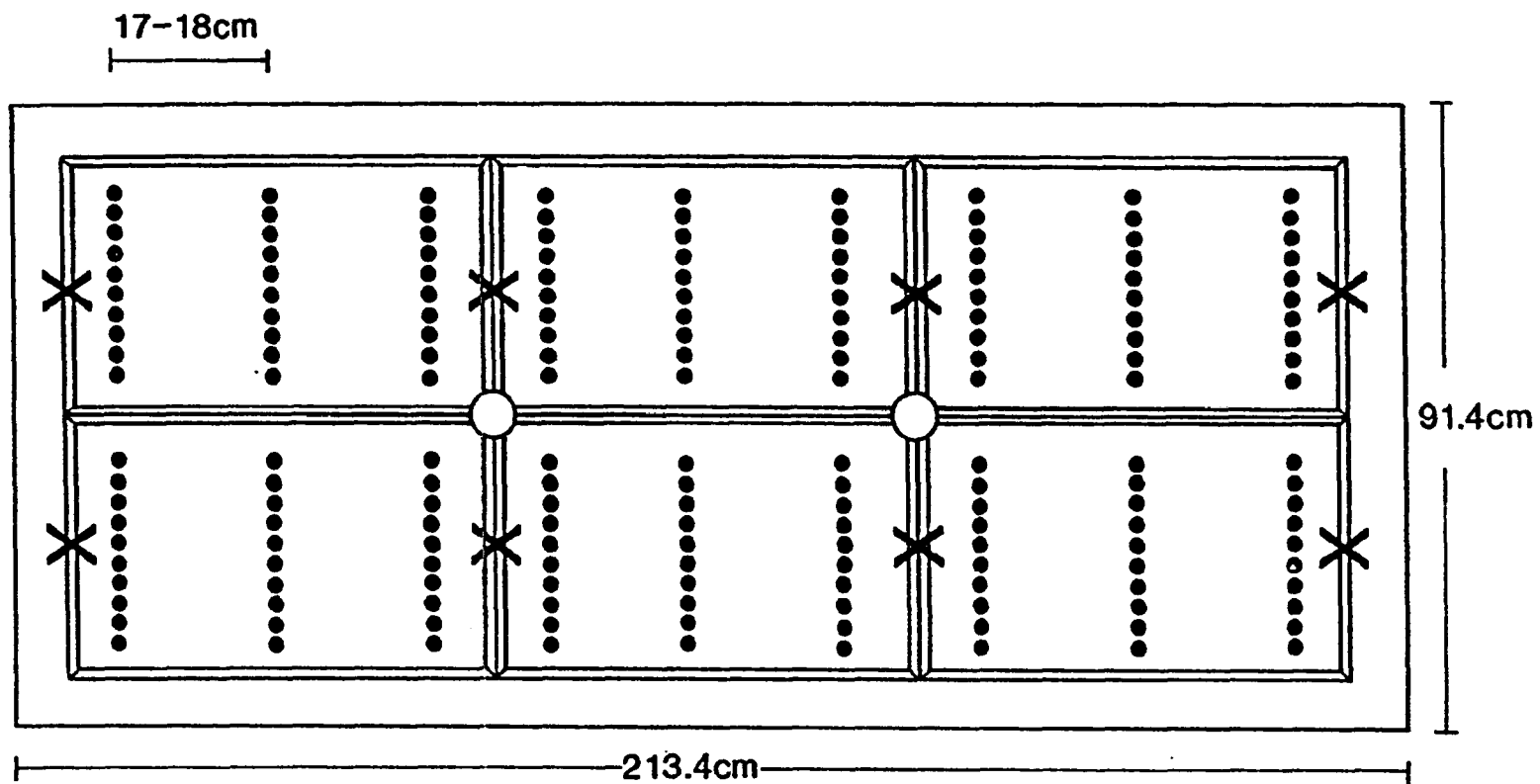


Figure 1. Schematic representation of the distribution of flats planted with barley within experimental cage (Note: 6 flats per cage, 8 parasitoid food sources (X), and 2 water sources (O)).

were 10 days old and ca. 15-20 cm in leaf length. They were usually very succulent only for two consecutive test days which required a new batch of fresh plants to be used every other day. Also, they were last watered no later than 10-12 hours before tests were begun to minimize soil dampness and to keep RH inside the cages similar to humidity of the rearing room ($50\% \pm 10\%$). Both cages were illuminated by fluorescent lights and covered with a white drop cloth for decreased brightness. Light intensity, as measured by a GE triple range 214 light meter, was in the 140-150 ft-c range. A fan was turned on some 9-10 m away from the cages, creating a gentle air current through the cage.

Armyworm hosts for each test were selected at 2nd, 3rd or 4th instars as described earlier, since these stages were found to be more susceptible to parasitoid attack. They were distributed throughout the cage area at random release sites. For each test, the sites were determined by a random double number drawing procedure which indicated row and plant position within each row. All together there were a total of 180 distinct locations to which a host larva could be randomly assigned (e.g., 2.9 = row 2, position 9; 15.3 = row 15, position 3, etc.). As each random site was selected, a green plastic ring (collar) 5 cm high by 9 cm in diam was placed around the corresponding plant (or group of plants). Each larva was positioned near the plant stem surrounded by the collar, and a bit of vaseline was rubbed on the top edge of the collar to prevent armyworm escape. Eight standard cups containing a sponge soaked in honey solution and two other cups with cotton wads in water were placed at fixed sites on the flats to serve as a food source for the parasitoids during the

8-hr test. Once the flats contained the proper number of hosts (the host density required for each test), they were transferred into each cage and arranged next to each other according to the setup in Figure 1.

Age of the parasitoid females used in these tests varied from 2-4 days for *A. militaris*, and from 4-8 days for *A. ruficrus*. After females and males of each species had been selected for each test (an equal number of males was always released into the cages with the females), they were held together for about 30 min, and then released into the experimental cages containing armyworms. The two daily tests always started in the morning with the release operation and lasted exactly 8 hr, usually being dismantled in the early evening. During the entire period the armyworm hosts were available for parasitization by females of whatever species was searching within the cage. At the end of the exposure period, all flats were quickly removed from inside the cages and were visually inspected for recovery of the exposed caterpillars, a process which was facilitated only by the presence of collars and damaged plants. Although most of the larvae were found, losses were inevitable, for often they hid themselves very effectively or were able to cross the imposed barrier. All recovered larvae were reared in single cups until pupation, death or parasitoid larvae appeared.

During the experiment, many larvae died due to unknown cause(s). Unparasitized hosts usually pupated on schedule, in which case they were separated from the experimental group and reared separately. Cocooned parasitoid larvae issuing from killed hosts were held in tight-lidded cups until they emerged. Cocoons and adult wasps were

later counted to determine sex ratios, emergence rates, and to estimate the average egg deposition per larva attacked.

Reproduction and Development

The experiments described previously where susceptible armyworm instars were exposed under confined (small cups) or simulated field conditions (cages) provided all of the basic data for analysis and comparisons of the reproductive and developmental characteristics of A. militaris and A. ruficrus. Further information, including field population data, were available only for the native A. militaris through observations on parasitoids emerging from field-collected caterpillars. By making daily observations on these and other lab-exposed armyworms it was possible to study the parasitoids' life cycle, including such major physiological events as their reproductive capacities (fertilization, fecundity and oviposition) and developmental times.

Several measures of parasitism which are directly or indirectly associated with parasitoid reproduction have been analyzed, such as the number of hosts parasitized by instar, the number of parasitoid eggs laid per unit time, the number of parasitoid eggs laid and adults produced per host larval instar and per host exposed, and parasitoid emergence rates. The average number of eggs laid per instar per host was estimated based on counts taken of the number of cocoons spun by emerging mature larvae. The percentage of male and female progeny was determined under the microscope by examining the proportion of both sexes among all adults emerging from each cocoon mass. The cocoons and males and females of each parasitoid species

possess diagnostic characters which make their separation possible. Average emergence rates were always computed from rates recorded among adult wasps emerging from single cocoon masses. The multiple interactions of parasitoid and host density relative to oviposition rate and F_1 progeny production were compared with the number of hosts successfully parasitized by both species.

With regard to development, before generation times of A. militaris and A. ruficrus were determined, a compilation was made of pertinent data on developmental times from the available literature. The total duration of their life cycles was assumed as being divided into two developmental periods: (1) the period from parasitoid oviposition in the host to larval emergence; and (2) the average length of the "pupal" period, i.e., the number of days spent by the parasitoid outside of the host to adult eclosion. These periods were both measured and compared for both species. In this study all developmental data are referred to the host instar in which each parasitoid deposits its eggs. This was done to show whether parasitoid mean generation times were influenced by the host instar attacked rather than by temperature alone, whose effects are already well documented (Hafez 1947; Calkins and Sutter 1976). This effect was investigated separately for each developmental period noted previously.

Internal Competition Tests

In this series of tests multiple parasitism was artificially induced by bringing armyworm hosts and parasitoids together in a small glass chamber, and allowing females of each species to oviposit

in the same host larva. The process was alternated allowing one species or the other to oviposit first.

They were preceded by pilot tests to assess: (1) the general susceptibility of the various instars to the procedure; (2) their ability to bring successful parasitism to term; and (3) the feasibility of using apparent ovipositor insertion as an indicator of effective parasitization. This consisted of letting the female insert her ovipositor just once in the body of an armyworm larva. For both parasitoids, the action is in general readily visible due to the posture assumed by the female when "stinging" (ovipositing in) the host. It should be emphasized that each female was allowed to thrust its ovipositor in just once, after which the organisms were promptly separated.

First, 2nd and 3rd instar larvae were selected for this test because of both parasitoids' known preference for early instar larvae, and hence a naturally quicker attack, a most desired feature during these tests.

The main steps in the exposure procedure were as follows. First, adult females of each species were sexed and then, one at a time, were placed in a small chamber consisting of a glass 1 ml straight-sided shell vial containing an armyworm larva. This caused both organisms to stay in almost direct contact for a short while. Parasitoid attack usually occurred within the first few minutes of confinement. Following the stinging act the female was discarded and the stung armyworm larva was reared and observed.

Four different time intervals between host exposure to one species or the other were tested: less than 1 hr (simultaneous exposure), 24, 48 and 96 hrs.

Upon spinning cocoons A. *militaris* can easily be distinguished from A. *ruficrus* by characteristics of the cocoon and/or by morphological features of the subsequently emerged adults.

RESULTS AND DISCUSSION

Host and Parasitoid Field Survey

Observations on the Target Host

Even though the development of appropriate sampling methods has been used as a probable means to enable one to understand the armyworm's patchy dispersion (Untung 1978), its local and regional distribution are still very poorly understood. Localized outbreaks are often characterized by their unpredictability. As a rule, it is difficult to find armyworms in the same area(s) where destructive populations were noted the year before.

In the outbreak areas, caterpillars are abundant and can be obtained in large numbers. However, it is more common for P. unipuncta to occur, year after year, in widespread endemic (non-outbreak) populations. Under these circumstances, they may occur at such low numbers that the capture of a single larva takes hours of sweeping with a net. In either situation, the exact location(s) where populations will occur in the future cannot be predicted.

These and other phenology-related problems may pose difficulties to the biological control worker who needs to select an area for parasitoid release, and to subsequently monitor for establishment and dispersal.

A 200-ha area 6 km NW of St. Johns, Clinton Co., Michigan, (T8N R3W Sec 25), including several no-till corn fields, was selected for release and monitoring of A. ruficrus. Armyworms are well known to have an oviposition preference for grasses over other plants (Breeland 1958, Guppy 1961), and field observations reveal that they often concentrate in no-till corn areas with much grass. One farmer in the area customarily planted no-till corn using a minimum of pesticides. In three of his fields, which were regularly visited in May-June over a four season period (1978-1981), armyworms consistently appeared in low to moderate numbers feeding on young corn. Where the grasses were prevalent among the corn, armyworm populations were usually moderate to large.

The fact that armyworm larvae were found at non-outbreak levels in the same no-till fields in four successive years suggested the existence of a resident population which could be used for monitoring dispersal of introduced natural enemies. In contrast, nearby corn fields which were tilled over the same four year period did not harbor as many larvae as the no-till fields. This observation also corroborates the findings by Untung (1978) who suggested that armyworms overwinter in Michigan.

Field Parasitism

Limited observations on armyworm parasitoids were conducted at the St. Johns site. These consisted of randomly collecting ca. 300-500 larvae every season and holding them in the laboratory for parasitoid emergence.

Over a three year period (1981 not surveyed), A. *militaris* was found to be more abundant than any other parasitoid. In 1980, for example, a parasitoid survey in three adjoining corn fields revealed that A. *militaris* alone accounted for up to 54.4% of the parasitism (Table 1). Most of the host larvae were collected as late instars.

Parasitism of other host developmental stages, however, often varied from place to place and from year to year. In July 1978, for instance, in a small area of a corn field at Gull Lake, Kalamazoo Co., Michigan (T1S R9W Sec 9), under attack by outbreaking armyworms, field collections of late instar larvae and pupae showed that the tachinids Archytas *apicifer* (Walker) and Triachora *unifasciata* (Robineau-Desvoidy), both larval-pupal parasitoids, were predominant. In June of 1979 T. *unifasciata* alone was the more prevalent parasitoid at St. Johns. Another tachinid, Winthemia *rufopicta* (Bigot), always ranked high, close to A. *militaris*, among larval parasitoids encountered in moderate to high outbreak host populations (see also Untung 1978).

This characteristic variability in the temporal and spatial distribution of both host and parasitoids, added to a limited knowledge of the armyworm's ecosystem, renders natural enemy management options impractical or, at best, very difficult at this time. Despite high rates of parasitism and an undeniable impact caused by native parasitoids on armyworm populations, their effectiveness to control sudden localized outbreaks is poor. Based on our past experience, it appears that natural enemies of the armyworm will not prevent periodic outbreaks; however, insecticides alone may not be the best solution. Pesticides are effective tools when utilized judiciously in

Table 1. Armyworm Larvae Parasitized by A. *militaris* in No-Till Corn Near St. Johns, Clinton Co., Michigan (T8N R3W Sec 25)

Field No.	Collection Date	Parasitism Range (No./25 larvae)	No. Parasitoids/ 25 Larvae ($\bar{X} \pm \text{S.D.}, n = 5$)	Percent Parasitism
I	6/17/80	3 - 8	4.6 ± 1.9	18.4
II	6/24/80	3 - 11	6.4 ± 3.0	25.6
III	7/12/80	12 - 17	13.6 ± 2.1	54.4

IPM programs, but excessive use can cause undesirable effects (e.g., development of resistance and cross resistance) or may be detrimental to natural enemies, increasing the chances for more frequent or severe outbreaks. Such problems frequently necessitate further insecticide use and increase the costs of crop production. The opportunity exists to try different control approaches such as the colonization of foreign natural enemies of known potential.

Foreign Parasitoid Importation

Throughout its long history of outbreaks and injury to crops referred to earlier, the armyworm has never been the object of a formalized biological control project. There are apparently no records prior to 1977 of introducing foreign natural enemies to improve control of the species in the continental U.S. (Clausen et al. 1977).

The success obtained with new strains of A. ruficrus different from those already established in New Zealand (Cumber et al. 1977, Mohyuddin and Shah 1977) has demonstrated for armyworms the validity of a principle which is now becoming widely accepted; the matching of parasitoid and host strains is critical for effective biological control. Several different "strains" of a parasitoid should therefore be introduced to obtain maximum genetic variability. In this way, it is more likely that a suitable genotype for a particular situation can be found, thus increasing the chances for establishment (Simmonds 1963).

Parasitoid shipment followed by laboratory propagation and periodic field colonization of A. ruficrus in Michigan was started in 1977. Live specimens were first sent from Lahore, Pakistan, via Newark, Delaware, to our insectary at Michigan State University, East Lansing, in April 1977. The live material screened by the U.S.D.A. quarantine facility (Beneficial Insects Research Laboratory, Newark, DE) was intended for immediate field release as well as for future study and evaluation. These first shipments consisted of a relatively small lot: 327 females and 220 males. Some adults (255) were immediately released at the Michigan State University Kellogg Gull Lake Biological Station, whereas the remaining individuals were used to start a laboratory culture. Additional shipments were received in May 1978 (39 adults; 29 females and 10 males) and May 1979 (1212 adults; 776 females and 436 males). On the shipment form it was stated that Agrotis spp. were the usual hosts in Pakistan and that the host plant was Solanum tuberosum.

Typically, newly-imported stocks were allowed to mate with individuals of the old lab culture for one or two generations before release. Several small colonies were subsequently separated from the insectary population and periodically released throughout the season in grassy fields of the University campus and/or in other areas in the central part of the state which seemed satisfactory in meeting habitat-host requirements. Colonization releases were usually made in the early morning or late afternoon.

In 1977, only adults were released, but, from 1978 to 1980, mass-parasitized armyworm larvae of varying sizes were also liberated in areas where armyworms had been detected (Appendix 1). Prior to

release, "pre-exposed" caterpillars had been confined with a large number of wasps in a 3,785 ml (1 gallon) glass jar for 1-2 days for mass parasitization. It was thought that by releasing preparasitized larvae the chances for survival and establishment would be maximized.

In the 1978-80 period, frequent host surveys were made, usually between May and August, but A. ruficrus was not recovered, despite the emergence of several other native hymenopterous parasitoids from field-collected armyworms. Perhaps the species was unable to adapt to this new habitat or host. Although able to parasitize P. unipuncta under laboratory conditions, A. ruficrus does not appear to have the potential for surviving and attacking field armyworms. This assumption is further supported by data collected in laboratory tests designed to assess the parasitoid's general searching ability (see page 57). Unfortunately, climatic tolerances and host relations in the field could not be verified, although the A. ruficrus source populations came from the plains in Pakistan and not the foothills.

Crossing Tests

Since A. ruficrus constituted a first introduction to this country, crossing this species with "congeneric" forms, such as A. militaris, was thought to be a possibility. Since the Pakistan species had been reared successfully on P. unipuncta for several generations, showing good adaptability to this non-natural host, these preliminary tests were conducted to determine the genetic and taxonomic individuality of both species, i.e., to confirm or exclude the possibility for laboratory or field hybridization.

Despite their multiple similarities, both species can be readily differentiated by the color of their hind coxae and the color and arrangement of their cocoons. The hind coxae are yellow in A. militaris and black in A. ruficrus. Cocoons are white and closely packed forming in general a single mass in A. militaris, and are yellowish in color and loosely grouped in A. ruficrus. The sexes of both parasitoids can be distinguished by the ovipositor and the length of the last five antennal segments which are somewhat shorter in the females.

It was noted that when virgin females of one species were placed with males of the other species, all offspring consisted of males having characteristics identical to those of the female parent (Table 2). Both A. militaris and A. ruficrus are known to be arrhenotokous species, i.e., unfertilized females give rise, parthenogenetically, to a generation of males (Hafez 1947, Tower 1915). The results thus indicate that cross fertilization did not take place. During their early male-female confinement period, males of both species were attracted to females of the other species; they often chased and tried to mate with the females. Judging from the final results, however, these attempted matings were unsuccessful as fertilization (or hybridization) did not occur.

It is also noteworthy that females which did not mate with males of the other species, laid more eggs than those which had a chance to mate with males of their own species (Table 2).

Table 2. Results of Attempted Crosses Between A. militaris and A. ruficrus^a

Observation/Rearing Outcome	♀ <u>A. militaris</u> x ♂ <u>A. ruficrus</u>	<u>A. militaris</u> Control	♀ <u>A. ruficrus</u> x ♂ <u>A. militaris</u>	<u>A. ruficrus</u> Control
Total Number of				
Hosts Parasitized (n)	15	13	14	11
Hosts Dying	4	6	6	7
Hosts Pupating	1	1	0	2
Average Number ^b of				
Cocoons Produced/Host	145.1 ± 15.4	96.7 ± 20.8	53.6 ± 7.6	47.5 ± 10.7
Adults Emerged/Host	122.5 ± 14.6	76.6 ± 15.5	48.4 ± 7.1	43.8 ± 10.7
Average Percent ^b of				
Female Offspring/Host	0.0	11.1 ± 4.9	0.0	49.6 ± 8.0
Male Offspring/Host	100.0	88.9 ± 4.9	100.0	50.4 ± 8.0
Emergence Rate (%)	84.4	79.2	90.3	92.2

^a20 host larvae used per test.

^bMean ± S.E. (n = no. of parasitized host larvae).

Host Range Tests

After P. unipuncta had proved a viable factitious host for A. ruficrus, under laboratory conditions, three other Michigan cutworms were also evaluated for host suitability, namely: (1) the variegated cutworm, Peridroma saucia (Hbn.), probably the most important cutworm on vegetables; (2) the black cutworm, Agrotis ipsilon (Hfn.), a major corn pest and reported as a satisfactory host in Egypt (Hafez 1947), and (3) the spotted cutworm, Amathes c-nigrum (L.), which is less important than the other two species.

Compared with Pseudaletia as a host, early instars (2nd and 3rd) of these noctuids were less vulnerable to A. ruficrus, thus revealing their limited possibility as alternate hosts (Table 3). Low parasitization rates were followed by very few parasitoid larvae pupating. From a total of 15 cocoons produced from three parasitized P. saucia, for example, only two larvae reached the adult stage. From two parasitized A. ipsilon, only seven larvae and three adults emerged (data not shown in Table 3). In contrast, significantly higher values of 54.1 (S.D. = 31.7) cocoons and 50.1 (S.D. = 31.0) emerged parasitoids resulted from control armyworms in the whole test (n = 34).

The results are somewhat surprising with respect to parasitism of the black cutworm, since the original hosts in Pakistan were Agrotis spp., and A. ipsilon was also a satisfactory host in Egypt (Hafez 1947). However, the possibility of different species or strains of the parasitoid is substantial since the systematics of Apanteles is poorly known (Mason 1981).

Table 3. Suitability of Three Cutworms as Alternate Hosts for A. ruficrus Compared with P. unipuncta

Percentage of Hosts	<u>P.</u> <u>saucia</u> (n = 80)	<u>P.</u> <u>unipuncta</u> (n = 40)	<u>A.</u> <u>ipsilon</u> (n = 50)	<u>P.</u> <u>unipuncta</u> (n = 25)	<u>A.</u> <u>c-nigrum</u> (n = 40)	<u>P.</u> <u>unipuncta</u> (n = 20)
Parasitized	3.8	35.0	4.0	40.0	0.0	50.0
Dying from Unknown Cause	5.0	55.0 ^a	12.0	52.0 ^a	10.0	45.0 ^a
Pupated	91.2	10.0	84.0	8.0	90.0	5.0

^aMost died from superparasitism.

Parasitized cutworms exhibited early signs of parasitism through low food consumption. They also looked somewhat smaller than their unparasitized siblings.

Some larvae died during rearing due to unknown cause(s), but most of the cutworms pupated within 2-3 weeks. It is possible that most larval and some pupal mortality may be connected with parasitism, resembling what happened to the armyworms (see the next section on host size preference) as a consequence of parasitoid development or of other adverse effects due to parasitoid oviposition (Vinson and Iwantsch 1980).

Comparative Studies Between A. *militaris* and A. *ruficrus*

Host Size Preference

A. *militaris*

In studying parasitic associations among lepidopterous species, few workers have stressed the importance of relating rates of parasitism found to the specific host instars attacked. In South Dakota, larvae of P. *unipuncta* were exposed to A. *militaris* females for a 4-hr period by Calkins and Sutter (1976) who studied the effect of host instars on the laboratory biology of this parasitoid. Even though all six larval instars were used in their preference tests, no parasitoid larvae ever emerged from armyworms exposed to attack during the 1st, 2nd or 6th instars. Effective parasitization was greatest among 3rd instar larvae (70%) and 4th instars (52%). They also found that the parasitoid larvae always emerged from 6th instar hosts regardless of the host instar originally attacked.

Working with the same organisms, but under slightly different conditions, particularly in relation to duration of exposure, the present data show that parasitization rates may vary considerably. For example, it appears that just by changing exposure duration from 4 to 24 hrs, some of the apparently "immune" instars reported by Calkins and Sutter (1976) may be attacked and successfully parasitized, producing viable offspring (Table 4). The data show no marked difference among rates of parasitism when age of parasitoid is the variable considered. The parasitoid attacks the whole range of larval instars (even those reportedly unattacked by Calkins and Sutter (1976)), but with a variable degree of success.

It is probable that, in the course of the experiment, a few larvae were "stung" after having molted into the next developmental stage. However, this was probably avoided by excluding those hosts exhibiting signs of imminent molt.

Considering all the larvae parasitized in these tests (149), the majority of parasitism was found among 4th, 3rd and 2nd larval instars, in decreasing order of preference. Fourth instar larvae were the most heavily parasitized (70.0%); third instars ranked next (63.3%). Thus, under confined conditions, A. militaris has a broad attack behavior, showing the highest success against 2nd, 3rd and 4th instars, reduced success against 1st and 5th instars, and the least success against 6th instars (only 5% were successfully attacked). The data also show that with increased length of exposure it is possible to obtain higher parasitism rates covering the complete range of larval instars.

Table 4. Armyworm Instars Successfully Parasitized by A. militaris According to Age of Host and Age of Parasitoid

Armyworm Instar ^a	Parasitoid Age in Days						TOTALS	
	ONE		THREE		FIVE			
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
1st	9	45.0	2	10.0	5	25.0	16	26.7
2nd	12	60.0	7	35.0	12	60.0	31	51.7
3rd	13	65.0	12	60.0	13	65.0	38	63.3
4th	13	65.0	16	80.0	13	65.0	42	70.0
5th	7	35.0	7	35.0	5	25.0	19	31.7
6th	1	5.0	0	0.0	2	10.0	3	5.0

^aNumber of larvae per instar per test was 20.

A. ruficrus

Using mostly Agrotis larvae as the available host, Hafez (1947) reported that 3rd and 4th instars appear to be the most suitable larval instars for effective parasitization by A. ruficrus. He found that this parasitoid may also lay its eggs in 1st and 2nd instar larvae, but the host is usually killed. Utilizing P. unipuncta as the host, this study reveals a definite preference for oviposition in 1st through 3rd instar larvae (Table 5). Second instars showed the highest apparent susceptibility to parasitoid attack (43.8%), followed by 3rd instars (40.0%).

In this test series, a total of 480 armyworm larvae were used, and 5th or 6th instars were never successfully parasitized. This compares favorably with Hafez's (1947) findings where 5th instar Agrotis larvae were rarely attacked and 6th instars never attacked. The means per instar per test of larvae parasitized by A. ruficrus (Table 5) are well below those previously reported for A. militaris (Table 4). Parasitism by A. ruficrus also appears to be relatively independent of the parasitoid's age, at least within its 1st week of adult life. However, unlike A. militaris, it shows a greater discrimination when ovipositing, usually preferring a narrower range of host sizes.

It is probable that percent mortalities among early host instars attacked by each parasitoid may actually be higher than shown, if hosts dying from unknown cause(s) during the incubation phase are also considered.

Tables 6 and 7 summarize a collection of data much wider in scope, recorded to show the impact of parasitism and rearing

Table 5. Armyworm Instars Successfully Parasitized by A. ruficrus According to Age of Host and Age of Parasitoid

Armyworm Instar ^a	Parasitoid Age in Days								TOTALS	
	ONE		THREE		FIVE		SEVEN ^b			
	Freq.	%	Freq.	%	Freq.	%	Freq.	%	Freq.	%
1st	4	20.0	5	25.0	5	25.0	6	30.0	20	25.0
2nd	8	40.0	12	60.0	5	25.0	10	50.0	35	43.8
3rd	9	45.0	9	45.0	6	30.0	8	40.0	32	40.0
4th	2	10.0	2	10.0	1	5.0	1	5.0	6	7.5
5th	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
6th	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

^aNumber of larvae per instar per test was 20.

^bTest series with 7-day old females was possible for A. ruficrus due to its longer life span than A. militaris

Table 6. General Susceptibility and Subsequent History of P. unipuncta Larvae Exposed in Various Stages to A. militaris for a 24-hr Period^{a,b}

Armyworm Instar	Parasitoid Age (days)	Successfully Parasitized			Unexplained Deaths			Surviving Larvae		
		Freq.	Tot.	%	Freq.	Tot.	%	Freq.	Tot.	%
1st	1	9			4			7		
	3	2			16			2		
	5	5			13			2		
			16	(26.7)		33	(55.0)		11	(18.3)
2nd	1	12			8			0		
	3	7			13			0		
	5	12			6			2		
			31	(51.7)		27	(45.0)		2	(3.3)
3rd	1	13			4			3		
	3	12			8			0		
	5	13			6			1		
			38	(63.3)		18	(30.0)		4	(6.7)
4th	1	13			1			6		
	3	16			2			2		
	5	13			1			6		
			42	(70.0)		4	(6.7)		14	(23.3)
5th	1	7			6			7		
	3	7			3			10		
	5	5			8			7		
			19	(31.7)		17	(28.3)		24	(40.0)
6th	1	1			1			18		
	3	0			1			19		
	5	2			4			14		
			3	(5.0)		6	(10.0)		51	(85.0)

^aNumber of larvae per instar per test was 20.

^bPercentages for totals in parentheses.

Table 7. General Susceptibility and Subsequent History of *P. unipuncta* Larvae Exposed in Various Stages to *A. ruficrus* for a 24-hr Period^{a,b}

Armyworm Instar	Parasitoid Age (days)	Successfully Parasitized			Unexplained Deaths			Surviving Larvae		
		Freq.	Tot.	%	Freq.	Tot.	%	Freq.	Tot.	%
1st	1	4			15			1		
	3	5			7			8		
	5	5			14			1		
	7	6			7			7		
			20	(25.0)		43	(53.8)		17	(21.2)
2nd	1	8			12			0		
	3	12			6			2		
	5	5			13			2		
	7	10			8			2		
			35	(43.8)		39	(48.7)		6	(7.5)
3rd	1	9			11			0		
	3	9			10			1		
	5	6			8			6		
	7	8			3			9		
			32	(40.0)		32	(40.0)		16	(20.0)
4th	1	2			8			10		
	3	2			3			15		
	5	1			7			12		
	7	1			5			14		
			6	(7.5)		23	(28.7)		51	(63.8)

Table 7. (Continued)

Armyworm Instar	Parasitoid Age (days)	Successfully Parasitized			Unexplained Deaths			Surviving Larvae		
		Freq.	Tot.	%	Freq.	Tot.	%	Freq.	Tot.	%
5th	1	0			2			18		
	3	0			3			17		
	5	0			2			18		
	7	0			4			16		
			0	(0.0)		11	(13.7)		69	(86.3)
6th	1	0			0			20		
	3	0			1			19		
	5	0			1			19		
	7	0			0			20		
			0	(0.0)		2	(2.5)		78	(97.5)

^aNumber of larvae per instar per test was 20.

^bPercentages for totals in parentheses.

procedures on host development. They include the data for successful parasitism classified according to host developmental stage and parasitoid age, as earlier examined (Tables 4 and 5), as well as the quantification of two other rearing outcomes, after host larvae have been exposed and incubated for parasitoid emergence. In addition to effective parasitism, the other possible outcomes are under the headings "unexplained deaths" and "surviving larvae". The former entails armyworm larvae dying after they were exposed to parasitoid females. The latter refers to larvae which pupated normally, showing no apparent signs of parasitism.

In both Tables 6 and 7, the number of deaths due to unknown cause(s) tends to decline gradually as one goes from the first to the last instar. Among the A. militaris-exposed host group (Table 6), 1st instar deaths were 55%, later dropping to 10% for 6th instars. In the A. ruficrus group (Table 7) values for this sort of mortality were rather similar to those presented above with 53.8% for 1st and 2.5% for 6th instar larvae.

The general pattern of this unknown mortality is as follows: in the group of larvae exposed to A. militaris (Table 6), about 57% of deaths occurred within the first week after exposure, 35% in 1 to 3 weeks, and finally approximately 8% died after the third week. Among the group that died after 3 weeks, there was one 1st instar larva which lived 33 days and died as a 4th instar. This is exceptionally long considering that other 1st instar larvae seemingly unaffected by parasitism pupated in 16-23 days after exposure. In the second group (Table 7), 75% died within 1 week after exposure, approximately 20% in 1 to 3 weeks, and only 5% were alive after the third week. Many

larvae in this group likewise exhibited a decreased rate of growth prior to death. Initially, these armyworms seem to be healthy; however, they stopped feeding and, after a variable number of days, died.

The real cause for death could not be determined, but it is suspected that death of some of these larvae, particularly those larvae which lived longer but grew little or none, may be associated with superparasitism, rather than natural infections. One reason for this belief is the greater number of unexplained deaths among early instar larvae as opposed to a lower number of unexplained late instar deaths where control mortality values were similar. Moreover, observations made through dissections of dead larvae showed that many were parasitized, and parasitic larval forms were sometimes seen in great numbers (Table 8). Incidentally, many parasitoids were also found inside caterpillars from which parasitoid larvae had exited, showing that the emergence process was not 100% successful (Table 9).

The larvae which somehow avoided parasitism in both groups are also shown in Tables 6 and 7. These data, together with the data on unexplained mortality discussed previously, indicate that late instar armyworm larvae are more resistant to attack than early instar larvae. The reasons for this increased resistance have not been totally elucidated, but it may be due to increased thickness of the cuticle of older larvae (Tower 1915; Calkins and Sutter 1976). The potential for parasitism avoidance and subsequent pupation is apparently greater among those late instar larvae exposed to A. ruficrus, but it could also be due to a lack of interest on the part of the parasitoid.

Table 8. Results of Dissections on Dead Armyworm Larvae After Exposure Under Confined Conditions to A. *militaris* or A. *ruficrus*^a

Host Sample No.	Larvae Exposed to <u>A. <i>militaris</i></u> ^a			Larvae Exposed to <u>A. <i>ruficrus</i></u> ^b		
	Instar at Exposure	Days Alive After Exposure	No. of <u>A. <i>mil.</i></u> Larvae Found	Instar at Exposure	Days Alive After Exposure	No. of <u>A. <i>ruf.</i></u> Larvae Found
1	6th	13	0	1st	22	87
2	2nd	23	118	3rd	13	61
3	5th	15	0	3rd	14	73
4	5th	12	138	4th	12	0
5	5th	11	0	4th	12	0
6	6th	11	150	4th	4	0
7	5th	13	125	5th	7	0
8	3rd	19	0	5th	9	0
9	4th	17	0	2nd	15	65
10	4th	14	97	5th	10	0
11	-	-	-	3rd	11	0
12	-	-	-	2nd	18	42

^aDead larvae dissected mostly as late instars.

^bExposure time was 24 hr.

Table 9. Results of Dissections on Armyworms Parasitized by A. militaris or A. ruficrus After Completion of Parasitoid Larval Emergence and Cocoon Spinning

Host Sampled No.	<u>A. militaris</u> Larvae		<u>A. ruficrus</u> Larvae	
	Emerged and Cocoons Spun	Dissected Out	Emerged and Cocoons Spun	Dissected Out
1	258	11	121	5
2	93	0	49	0
3	134	4	49	1
4	69	0	11	1
5	120	0	40	0
6	48	7	24	0
7	156	57	23	3
8	21	0	14	1
9	62	0	42	0
10	78	0	50	1
11	226	26	69	0
12	112	0	28	0
13	93	211	16	3
14	109	158	87	4
15	157	1	102	5
16	189	105	85	0
17	188	143	47	0
18	198	1	101	14
19	207	1	107	4
20	2	407	57	0
21	212	9	18	1
22	232	40	-	-
23	65	98	-	-
24	34	107	-	-
25	97	36	-	-

Greater escape rates among 1st instars were probably due to the ability of the small larvae to hide more effectively under the cut barley leaves. To avoid this difficulty only three barley blades were supplied as larval food for the small 1st instar armyworms.

Mortality rates among controls as a whole varied considerably and were null among 6th instars. The mean mortality of armyworm larvae used in the control population in both experiments was 14.3% (S.E. = 2.8; n = 210).

The results of these tests, conducted as a required preceding step to other experiments (see the next section), may also have some relevance for implementation of successful biological control. For example, when it comes to optimization of biocontrol or natural enemy augmentation programs entailing mass-rearing and parasitoid release, tasks wherein high parasitization rates are often required (Chambers 1977), information on differential parasitism by instars may be of great value. By knowing in advance which host instars are the most susceptible to attack, hosts can be mass-reared and exposed at the stage(s) of greatest vulnerability.

Responsiveness to Host Density (Functional Responses)

The number of progeny left by insect parasitoids is often determined not so much by their potential egg production as by the number of host insects which they are able to find and parasitize. Two important variables affecting the number and distribution of parasitoid progeny are, therefore, the density of the host population and the number, or density, of female parasitoids searching for

suitable hosts (DeBach and Smith 1941, 1947; Burnett 1951, 1953, 1954).

In this section, the effects of variation in parasitoid and host density on the rate of parasitization when females of both parasitoids were searching for host larvae released in a laboratory cage, are examined. Each species was introduced separately with caged armyworm larvae. Both cage ecosystems were considered large enough (1.95 m^2 surface area) to simulate field conditions and empirically measure the comparative performance of female wasps in terms of their searching efficiency. Parasitoid attack rates in response to controlled host densities were compared using their functional responses.

The presentation of these data is made in two steps. First, the functional responses of both Apanteles species are discussed and statistically compared, taking into account only the number and percentage of hosts successfully parasitized (apparent parasitism), that is, those from which viable parasitoid progeny emerged (see page 60). In the second part, secondary effects of parasitization, which were noted by dissections on dead host larvae, are also incorporated into the responses of both parasitoids, and the values represent hosts actually discovered by the wasps (effective parasitism) (see page 70). This correction was thought necessary because a considerable number of host larvae dying from apparently parasitism-unrelated deaths were in reality parasitized.

Initially, it was thought that in order to compare the searching characteristics of both parasitoids and their relative effectiveness this general test scheme would be followed. First, in a series of

tests in vials, all host larval instars would be exposed to parasitization as a check for host acceptance and/or discrimination (see page 45). Based on the results of these tests, the main experiment would then be conducted with preferred hosts. A satisfactory basis for comparisons of parasitoid search efficiency would thus be obtained by evaluating the attack rates on instars most likely to be parasitized.

In the initial tests, a variety of different sized cages and several exposure times were used to determine the range of physical variables. It seemed logical to use an assortment of host instars rather than just one, since previous experience had indicated that even small host size variation might result in rather variable parasitization rates. Had only one instar been selected for these tests, the results might not have shown the wide range of definable interactions which exist.

This gamut of interactions seemed, in general, well suited to the employment of a factorial design. This statistical approach has a combination of features which are very useful in an exploratory phase of research when little information is available on the problem under investigation (Gill 1978a; Steel and Torrie 1980).

Functional response tests were started in September 1980 and were completed in late April 1981. Additional field tests would have been deemed necessary had the imported species failed to produce any positive parasitism under laboratory conditions. The outcome, however, provided data attesting to the superior characteristics of the native species over the imported parasitoid. The sequence of tables

which follows shows very striking differences in their search capacity.

Primary Effects of Parasitization

Parasitoid functional responses in terms of hosts effectively parasitized were investigated using constant densities of 5 and 10 mated females. Hence, two test series were conducted for each parasitoid species. The number of hosts exposed within each series varied from 1 to 40. Hosts were supplied at one of three developmental stages: 2nd, 3rd or 4th instars. Each instar sequence was replicated six times. The duration of exposure was 8 hours.

The two parasitoids differ primarily in their relative ability to find and kill hosts. By and large, only under exceptionally high densities of both the parasitoid and the host was A. ruficrus able to find and effectively parasitize armyworm larvae. In contrast, even low host densities allowed A. militaris to effectively search and parasitize the hosts (Table 10). At practically any given parasitoid density A. militaris found increasing numbers of hosts as host density was increased. When the A. ruficrus population was reduced to 5 females, no parasitism was observed even with the highest number of hosts. Hence, tests with less than 40 hosts proved unnecessary and were later discontinued. Tables 11 and 12 contain parasitism rates for each species on 2nd, 3rd and 4th instars separately. In both cases where either 5 or 10 A. militaris wasps were searching, 3rd instar hosts were parasitized at a greater rate than the other instars. It appears that the parasitoid more readily attacks 3rd instars than 2nd's or 4th's. This result differs with the findings in the vial tests where 4th instars were more frequently attacked

Table 10. Armyworms Parasitized by A. militaris and A. ruficrus
 Females Released in a Cage with a 1.95 m² Basal Area
 During an 8 hr Period^a

Parasitoids Released	Hosts Exposed	<u>A. militaris</u>		<u>A. ruficrus</u>	
		Mean No.	%	Mean No.	%
5	1	0.0	0.0	-	-
	2	.1 ± .1	2.8 ± 2.8	-	-
	4	.3 ± .1	6.9 ± 3.4	-	-
	10	.8 ± .3	7.8 ± 2.9	-	-
	20	1.8 ± .5	9.0 ± 2.3	-	-
	40	4.2 ± .9	10.5 ± 2.3	0.0	0.0
10	1	.1 ± .1	5.6 ± 5.6	0.0	0.0
	2	.5 ± .1	25.0 ± 7.3	0.0	0.0
	4	.4 ± .1	9.7 ± 3.6	0.0	0.0
	10	1.9 ± .1	19.4 ± 5.9	0.0	0.0
	20	3.4 ± .6	17.7 ± 3.1	.1 ± .1	.6 ± .6
	40	4.4 ± 1.0	14.0 ± 2.6	.7 ± .4	1.7 ± 1.0

^aMean ± S.E. of 18 replicates (6 reps. each using 2nd, 3rd or 4th instars).

Table 11. Average Number of Armyworms Parasitized by *A. militaris*
Females Released in a Cage with a 1.95 m² Basal Area
During an 8 hr Period

Parasitoids Released	Hosts Exposed	Hosts Parasitized by Instar ^a		
		Second	Third	Fourth
5	1	0.0	0.0	0.0
	2	0.0	0.0	.2 ± .2
	4	0.0	.7 ± .3	.2 ± .2
	10	.8 ± .3	1.2 ± .8	.3 ± .2
	20	1.2 ± .5	3.3 ± 1.0	.8 ± .4
	40	4.2 ± 1.4	4.8 ± 1.6	3.5 ± 1.9
10	1	.2 ± .2	0.0	0.0
	2	.3 ± .2	.5 ± .2	.7 ± .3
	4	.7 ± .3	.3 ± .2	.2 ± .2
	10	1.3 ± 1.0	2.2 ± 1.2	2.3 ± 1.0
	20	3.7 ± 1.0	5.2 ± 1.1	1.5 ± .5
	40	4.8 ± 1.4	7.7 ± 2.5	4.0 ± 1.3

^aMean ± S.E. of 6 replicates.

Table 12. Average Number of Armyworms Parasitized by A. ruficrus
 Females Released in a Cage with a 1.95 m² Basal Area
 During an 8 hr Period

Parasitoids Released	Hosts Exposed	Hosts Parasitized by Instar ^a		
		Second	Third	Fourth
5	40	0.0	0.0	0.0
10	1	0.0	0.0	0.0
	2	0.0	0.0	0.0
	4	0.0	0.0	0.0
	10	0.0	0.0	0.0
	20	.3 ± .3	0.0	0.0
	40	1.5 ± 1.0	.5 ± .3	0.0

^aMean ± S.E. of 6 replicates.

than 3rd's (Table 4). This may be due to factors such as the increased searching required in the large cages or different larval response. At the highest host density used (40), an average of about eight 3rd instar larvae were effectively parasitized by 10 females, whereas only half as many were parasitized when five parasitoids were tested. The attack rates were equal (Table 11). Mean numbers of hosts killed increased consistently for rising host densities equal to or greater than 10. The parasitism rates showed more irregularities at lower host densities.

Tests were conducted with A. ruficrus in exactly the same kind of experimental design and under a similar set of physical conditions. However, parasitism rates of A. ruficrus (Table 12) were much poorer than the rates observed for A. militaris (Table 11). No parasitism occurred at densities equal to or below 10 armyworm larvae per cage, when either 5 or 10 females per cage were used. The parasitoid maintained its preference of 2nd instar larvae and did not parasitize 4th instars despite their larger size and greater chance of being discovered.

Mean percent parasitism by A. militaris females associated with every number of hosts supplied is given in Table 13 for both quantities of parasitoids employed; the corresponding treatment combination means for A. ruficrus are presented in Table 14. Standard errors of the mean have been included in all tables to show the extent of variation.

Prior to any statistical treatment, an inverse sine (angular) transformation was applied to all measured percent parasitism rates, as many attack rates were zero. This transformation helped adjust for

Table 13. Average Percent of Armyworms Parasitized by A. militaris
Females Released in a Cage with a 1.95 m² Basal Area
During an 8 hr Period

Parasitoids Released	Hosts Exposed	Percent Parasitized by Instar ^a		
		Second	Third	Fourth
5	1	0.0	0.0	0.0
	2	0.0	0.0	8.3 ± 8.3
	4	0.0	16.7 ± 8.3	4.2 ± 4.2
	10	8.3 ± 3.1	11.7 ± 7.9	3.3 ± 2.1
	20	5.9 ± 2.4	16.8 ± 4.9	4.2 ± 2.0
	40	10.4 ± 3.5	12.2 ± 4.1	8.8 ± 4.8
10	1	16.7 ± 16.7	0.0	0.0
	2	16.7 ± 10.5	25.0 ± 11.2	33.3 ± 16.7
	4	16.7 ± 8.3	8.3 ± 5.3	4.2 ± 4.1
	10	13.3 ± 9.5	21.7 ± 12.5	23.3 ± 9.9
	20	19.2 ± 5.0	26.4 ± 5.7	7.5 ± 2.5
	40	12.3 ± 3.6	19.2 ± 6.1	10.7 ± 3.6

^aMean ± S.E. of 6 replicates.

Table 14. Average Percent of Armyworms Parasitized by A. ruficrus
Females Released in a Cage with a 1.95 m² Basal Area
During an 8 hr Period

Parasitoids Released	Hosts Exposed	Percent Parasitized by Instar ^a		
		Second	Third	Fourth
5	40	0.0	0.0	0.0
10	1	0.0	0.0	0.0
	2	0.0	0.0	0.0
	4	0.0	0.0	0.0
	10	0.0	0.0	0.0
	20	1.9 ± 1.9	0.0	0.0
	40	3.9 ± 2.6	1.3 ± .9	0.0

^aMean ± S.E. of 6 replicates.

variability and normalization of the distribution (Steel and Torrie 1980). A comparison was first made between parasitoid attack rates. Only the impact on 2nd, 3rd and 4th instar larvae at the highest host and parasitoid densities (40 hosts; 10 parasitoids) was tested since for host densities lower than 40 significant differences were obvious. Results of the two-factor analysis of variance comparing the attack efficiency characteristics of each species are shown in Table 15. The following can be concluded: (1) a great difference in the searching performance exists between the two parasitoid species (factor A). At a density of 40 armyworms per cage, parasitism rates were found to be highly significant, favoring the native A. militaris over the introduced species ($F = 23$; $P = .01$); (2) there was no significant difference in parasitism rate among the three armyworm instars (factor B) used; finally, (3) no significant interaction occurred between factors.

Analysis of variance was conducted for A. militaris alone, to compare percent parasitism at the two parasitoid density levels (5 and 10). Comparisons were made only for the three higher host densities (10, 20 and 40) since, for the lower host numbers tested, differences were somewhat confounded. This was largely due to the low number of hosts supplied and replicates used. A summary of this three-factor analysis is provided in Table 16. Parasitism rate (%) resulting from exposure of armyworm larvae to parasitoid densities (factor A) of 5 or 10 differed significantly ($F = 8.091$). When the number of parasitoids was doubled, parasitization increased significantly ($P = .01$). Again, a marked difference in parasitism incidence between armyworm larval instars (factor C) occurred ($F = 3.261$).

Table 15. Two-factor Analysis of Variance of Parasitism Rates by A. militaris and A. ruficrus Searching for Three Different Instars of the Host, P. unipuncta (A = Parasitoid Species; B = Host Instar)

Source	DF	SS	MS	F
AB	2	.86267E+02	.43133E+02	.632
A	1	.15686E+04	.15686E+04	22.983**
B	2	.12355E+03	.61776E+02	.905
ERROR	30	.20475E+04	.68249E+02	
TOTAL	35	.38259E+04		

**Significant at P = .01

Table 16. Three-Factor Analysis of Variance of Parasitism Rates by 5 and 10 Females of A. militaris Searching for Three Different Instars of the Host, P. unipuncta (A = Parasitoid Density; B = Host Density; C = Host Instar)

Source	DF	SS	MS	F
ABC	4	.32501E+03	.81253E+02	.637
AB	2	.11892E+03	.59459E+02	.466
AC	2	.12009E+02	.60043E+01	.047
A	1	.10316E+04	.10316E+04	8.091**
BC	4	.43030E+03	.10757E+03	.844
B	2	.27493E+02	.13747E+02	.108
C	2	.83144E+03	.41572E+03	3.261*
ERROR	90	.11475E+05	.12750E+03	
TOTAL	107	.14252E+05		

**Significant at P = .01

*Significant at P = .05

However, no significant difference occurred between the three host density levels (factor B). Also, at the test levels chosen, no significant interactions were evident among all three factors investigated (parasitoid density, host density, and host instar). For close verification of the second conclusion, above, Bonferroni procedure for non-orthogonal contrasts (Gill 1978a) was utilized to compare percent instar treatment combination means. The result of this test shows that only 3rd and 4th instars were in fact differently affected by parasitism caused by A. *militaris* ($\alpha = .05$). Differential parasitism was unimportant for comparisons involving 2nd instars.

Secondary Effects of Parasitization

Following a procedure similar to that used in the vial tests, upon completion of a cage test, all armyworm larvae found were isolated and reared for parasitoid emergence. The rearing results from exposure to A. *militaris* are shown in Tables 17 and 18 while Table 19 summarizes the data for A. *ruficrus*. All three tables have been organized according to numbers of parasitoids liberated in the cages. Data recorded for the various categories (host effective parasitism, unknown-caused deaths, pupation, and losses) are in direct correspondence with host densities and instars used.

Regarding effective parasitism (columns 3 and 4), it is clear from the cumulative frequency (total) column that an increase in both host and parasitoid density resulted in a greater rate of attack by both parasitoids. The unclear detrimental effects of oviposition and parasitism, largely included in deaths due to unknown causes (columns 5 and 6), become more evident as host density increases. Avoidance of

Table 17. Subsequent History of *P. unipuncta* Larvae Exposed at Various Densities to 5 *A. militaris* Females in Cages 1.95 m² in Surface Area for 8 Hours^a

Host Density	Host Instar	Successfully Parasitized		Unexplained Deaths		Surviving Larvae		Lost Larvae	
		Freq.	Tot.	Freq.	Tot.	Freq.	Tot.	Freq.	Tot.
1	2nd	0		0		6		0	
	3rd	0		0		6		0	
	4th	0		0		6		0	
			0		0		18		0
2	2nd	0		0		12		0	
	3rd	0		1		11		0	
	4th	1		0		11		0	
			1		1		34		0
4	2nd	0		0		24		0	
	3rd	4		2		18		0	
	4th	1		3		20		0	
			5		5		62		0
10	2nd	5		1		54		0	
	3rd	7		5		48		0	
	4th	2		4		54		0	
			14		10		156		0
20	2nd	7		8		103		2	
	3rd	20		13		86		1	
	4th	5		13		101		1	
			32		34		290		4
40	2nd	25		15		198		2	
	3rd	29		17		191		3	
	4th	21		24		192		3	
			75		56		581		8

^aSix replicates per test.

Table 18. Subsequent History of *P. unipuncta* Larvae Exposed at Various Densities to 10 *A. militaris* Females in Cages 1.95 m² in Surface Area for 8 Hours^a

Host Density	Host Instar	Successfully Parasitized		Unexplained Deaths		Surviving Larvae		Lost Larvae	
		Freq.	Tot.	Freq.	Tot.	Freq.	Tot.	Freq.	Tot.
1	2nd	1		0		5		0	
	3rd	0		0		6		0	
	4th	0		0		6		0	
			0		0		17		0
2	2nd	2		0		10		0	
	3rd	3		3		6		0	
	4th	4		0		8		0	
			9		3		24		0
4	2nd	4		1		19		0	
	3rd	2		3		19		0	
	4th	1		1		22		0	
			7		5		60		0
10	2nd	8		1		51		0	
	3rd	13		2		45		0	
	4th	14		1		45		0	
			35		4		141		0
20	2nd	22		7		87		4	
	3rd	31		9		78		2	
	4th	9		2		109		0	
			62		18		274		6
40	2nd	29		9		199		3	
	3rd	46		9		184		1	
	4th	24		24		183		9	
			99		42		566		13

^aSix replicates per test.

Table 19. Subsequent History of *P. unipuncta* Larvae Exposed at Various Densities to 10 *A. ruficrus* Females in Cages 1.95 m² in Surface Area for 8 hours^a

Host Density	Host Instar	Successfully Parasitized		Unexplained Deaths		Surviving Larvae		Lost Larvae	
		Freq.	Tot.	Freq.	Tot.	Freq.	Tot.	Freq.	Tot.
1	2nd	0		0		6		0	
	3rd	0		0		6		0	
	4th	0		0		6		0	
			0		0		18		0
2	2nd	0		1		11		0	
	3rd	0		0		12		0	
	4th	0		0		12		0	
			0		1		35		0
4	2nd	0		1		23		0	
	3rd	0		0		24		0	
	4th	0		0		24		0	
			0		1		71		0
10	2nd	0		4		56		0	
	3rd	0		1		59		0	
	4th	0		4		56		0	
			0		9		171		0
20	2nd	2		6		109		3	
	3rd	0		0		119		1	
	4th	0		0		120		0	
			2		6		348		4
40	2nd	9		6		220		5	
	3rd	3		3		234		0	
	4th	0		5		234		1	
			12		14		688		6

^aSix replicates per test.

parasitism, expressed in terms of normal pupation (columns 7 and 8), was most common and followed a general trend similar to that found in the confined tests (Tables 6 and 7). The number of hosts which could not be recovered from the cages after tests were completed (last two columns) was minimal. In only 4 of 54 tests did host losses exceed 10% of the number liberated. Although this low loss rate was thought to be irrelevant, the number of armyworm larvae lost was subtracted from those released before parasitism values, other deaths, and pupation were computed. In this way, all data discussed herein were calculated on the basis of larvae actually recovered and reared for parasitoid emergence.

As in the confined tests, superparasitism as well as other adverse effects derived from parasitoid oviposition may have accounted for some of the unexplainable deaths. Data in Table 8 suggest that the number of hosts which were found and in which eggs were deposited may be greater than previously shown. Therefore, it seems logical that new functional response values should be calculated which take into account this exacerbating parasitism effect. They are thought to be a more accurate representation of the rate of host encounters by searching females. This number can be obtained by adding to the data previously shown (Tables 10-14) the number of parasitism-associated deaths occurring among those larvae dying from unknown causes. For the computations, a 20% natural mortality value (this is greater than the 14% mean natural mortality observed in earlier tests; see page 45) was subtracted from the unexplained deaths before all mortality data were combined. The greater response is expressed in Table 20 (see Table 10 for

Table 20. Probable Number of Armyworms Found by A. militaris and A. ruficrus Females in Cage Experiments Taking into Account Secondary Effects of Parasitization^a

Parasitoids Released	Hosts Exposed	Hosts Found by	
		<u>A. militaris</u>	<u>A. ruficrus</u>
5	1	0.0	-
	2	.1 ± .1	-
	4	.5 ± .2	-
	10	1.2 ± .3	-
	20	3.3 ± .7	-
	40	6.7 ± .7	1.2 ± .3
10	1	.1 ± .1	0.0
	2	.6 ± .2	0.0
	4	.6 ± .2	0.0
	10	2.1 ± .6	.4 ± .1
	20	4.2 ± .7	.4 ± .2
	40	7.4 ± 1.2	1.3 ± .5

^aMean ± S.E. of 18 replicates (6 reps. each using 2nd, 3rd and 4th instars).

comparison); it represents the average number of hosts probably discovered and stung by females of both species. Combined mortality rates recorded for each specific instar tested are given in Table 21 (A. *militaris*) and in Table 22 (A. *ruficrus*) (see Tables 11 and 12 for comparison).

Some remarkable adaptations linking A. *militaris* to its natural host, P. *unipuncta*, were observed during this study. For example, A. *militaris* females were frequently observed hovering over the plants occupied by armyworm larvae. As the experiments were dismantled, they were often seen sitting on the plants and sometimes on the plastic ring enclosing a group of plants. Females of A. *ruficrus* usually wandered about under the cage's top screen or simply flew above the plants. Unlike A. *ruficrus*, the native parasitoid seemed to "patrol" the areas surrounded by the rings, looking diligently for prospective hosts. However, no attempt was made to quantify the time spent by the wasps on or around the plants being fed upon by the host larvae.

The results of the cage tests indicate that A. *ruficrus* is poorer in its searching and parasitizing abilities than A. *militaris*; however, on Pakistani hosts the reverse is certainly a possibility.

The cage situation was probably a nice representation of what might occur in the field (at least for A. *militaris*), considering the number of armyworms which were parasitized. In order to have a workable system (especially for recovery), some features (e.g., plant type and age, and presence of barriers to restrict armyworm movement) were unnatural, but these extraneous components did not appear to be inhibitory to either species' searching behavior. It is possible, of

Table 21. Probable Number of Armyworms Found by *A. militaris* Females in Cage Experiments Taking into Account Secondary Effects of Parasitization

Parasitoids Released	Hosts Exposed	Hosts Found by Instar ^a		
		Second	Third	Fourth
5	1	0.0	0.0	0.0
	2	0.0	.1 ± .1	.2 ± .2
	4	0.0	.9 ± .3	.6 ± .3
	10	1.0 ± .4	1.8 ± .9	.9 ± .3
	20	2.2 ± .7	5.1 ± 1.5	2.6 ± .9
	40	6.2 ± 1.2	7.1 ± 1.2	6.7 ± 1.6
10	1	.2 ± .2	0.0	0.0
	2	.3 ± .2	.9 ± .2	.7 ± .2
	4	.8 ± .3	.7 ± .3	.3 ± .2
	10	1.5 ± .9	2.4 ± 1.2	2.5 ± 1.0
	20	4.6 ± 1.0	6.4 ± 1.3	1.8 ± .4
	40	6.0 ± 1.7	8.9 ± 2.6	7.2 ± 1.9

^aMean ± S.E. of 6 replicates.

Table 22. Probable Number of Armyworms Found by *A. ruficrus* Females in Cage Experiments Taking into Account Secondary Effects of Parasitization

Parasitoids Released	Hosts Exposed	Hosts Found by Instar ^a		
		Second	Third	Fourth
5	40	2.0 ± .7	.9 ± .5	.7 ± .2
10	1	0.0	0.0	0.0
	2	.1 ± .1	0.0	0.0
	4	.1 ± .1	0.0	0.0
	10	.5 ± .3	.1 ± .1	.5 ± .2
	20	1.1 ± .6	0.0	0.0
	40	2.3 ± 1.5	.9 ± .6	.7 ± .4

^aMean ± S.E. of 6 replicates.

course, that A. ruficrus may have responded more abnormally than A. militaris.

Although little is known about armyworm dispersion, it is believed that a clumped distribution would simulate more closely its field distribution. Although the host release was random, the final distribution often reflected varying degrees of aggregation. This was due to the fact that several larvae were placed in the same space surrounded by the ring, more so when a large number of larvae had to be used.

Time of exposure employed in functional response and similar studies varies considerably (see, for example, Hassell 1978). After having experimented with 24 and 12 hr, it was believed that an 8-hr exposure would be just as appropriate, since within this shorter period the parasitoid response could be measured even for very low host densities (e.g., at one host, for A. militaris). A relatively short exposure time may also have avoided effects due to early parasitoid mortality and superparasitism. Indeed, parasitoids are less likely to survive to the end of long exposures, and it is practically impossible to find and hence record the number of females alive after each test.

Also, there are not many models incorporating the effects of competition (Hassell 1978). Thus, it is unfortunate that because of time limitations a combination of both parasitoids' responses could not be tested. Future research therefore should explore the effects of this relationship by testing the two species at the same time with the host.

Parasitoid Reproduction

The number of eggs that Apanteles species are capable of depositing is usually large. Their fecundity depends largely on the intrinsic reproductive capacity of each species, but oviposition rates are markedly influenced by host population density as well, the number of parasitoid progeny being partly determined by how many hosts the parasitoid can find. Some of these relationships are shown by the following data. Several measures of parasitism per unit time such as the number of hosts parasitized, the number of parasitoid eggs laid, the number of eggs laid per host exposed, numbers of female and male progeny, etc. are described and analyzed.

The data included in this section come from the two laboratory test situations earlier described where armyworm hosts were either isolated singly with one female wasp of each species within a standard vial for 24 hr ("vial tests"), or were released on barley plants grown in flats and enclosed in a screen cage with a known number of females for an 8-hr period ("cage experiments"). Additionally, real field data for A. militaris are also compared with the results obtained in the laboratory. In general, sample sizes for drawing conclusions about the reproduction of A. ruficrus were by necessity smaller.

Before discussion of the observations a clear distinction must be made between the two laboratory designs. In the small vial, the parasitoid was more likely to find the host because of the close confinement. In the cage, however, a parasitoid clearly had greater difficulty finding a host as it had to search extensively for it.

Information related to parasitism by A. *militaris* and showing mean numbers of F_1 progeny emerged from 2nd-, 3rd- and 4th-stage host larvae is presented in Tables 23, 24, and 25, respectively. Similarly, fecundity and progeny production data for A. *ruficrus* are given in Tables 26 to 28; they result from parasitism under the same confined or simulated field conditions. The confined test figures in all tables were computed from data of experiments discussed earlier (see page 45), involving mated females of varying ages, whereas the cage study data refer only to parasitism information collected where the host density was 40 and the parasitoid density was 10 (see page 57). In both cases, averages computed from counts of cocoon numbers produced from a single larva were used to estimate the number of eggs laid per parasitized armyworm per instar, under the conditions mentioned. Actual oviposition rates could be higher since all eggs laid would not necessarily complete development.

In his account of the biology of A. *militaris*, Tower (1915) included only a few notes on mating and oviposition. Calkins and Sutter (1976) reported that 3 to 226 adult A. *militaris* emerged per host with an average of 71 parasitoids emerging from 3rd, 22 from 4th, and 81 from 5th instar hosts. Second instars would not parasitized. Under similar conditions, this study found an average of 79, 111 and 82 adult A. *militaris* emerging from single 2nd, 3rd and 4th instar larvae, respectively. For A. *ruficrus*, averages were smaller with 57, 43 and 39 adults emerging from 2nd, 3rd and 4th instar larvae, respectively.

Calkins and Sutter (1976) also noted that with surplus hosts available the mean number of hosts parasitized by one female A.

Table 23. Average Number of Progeny Produced by Exposure of 2nd Instar Armyworm Larvae to A. militaris

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	31	29
Average Number ^a of		
Cocoons Produced/Host	94.0 ± 10.1	26.2 ± 3.1
Adults Emerged/Host	78.6 ± 9.6	20.4 ± 2.2
Average Percentage ^a of		
Female Offspring/Host	28.3 ± 4.3	55.6 ± 4.0
Male Offspring/Host	71.7 ± 4.3	44.4 ± 4.0
Average Emergence Rate ^a (%)	81.4 ± 2.8	81.3 ± 1.9
Sex Ratio of Progeny (♀/♂)	.4	1.3

^aMean ± S.E. (n = no. of parasitized host larvae).

Table 24. Average Number of Progeny Produced by Exposure of 3rd Instar Armyworm Larvae to A. militaris

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	38	46
Average Number ^a of		
Cocoons Produced/Host	132.2 ± 11.3	35.1 ± 3.2
Adults Emerged/Host	111.2 ± 9.8	27.4 ± 2.5
Average Percentage ^a of		
Female Offspring/Host	18.6 ± 3.3	36.4 ± 3.5
Male Offspring/Host	81.4 ± 3.3	63.6 ± 3.5
Average Emergence Rate ^a (%)	82.8 ± 2.5	81.1 ± 2.3
Sex Ratio of Progeny (♀/♂)	.2	.6

^aMean ± S.E. (n = no. of parasitized host larvae).

Table 25. Average Number of Progeny Produced by Exposure of 4th Instar Armyworm Larvae to A. militaris

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	42	24
Average Number ^a of		
Cocoons Produced/Host	110.5 ± 8.0	47.4 ± 3.8
Adults Emerged/Host	81.6 ± 6.4	33.9 ± 2.9
Average Percentage ^a of		
Female Offspring/Host	16.8 ± 3.3	39.1 ± 6.7
Male Offspring/Host	83.2 ± 3.3	60.9 ± 6.7
Average Emergence Rate ^a (%)	74.4 ± 2.1	71.9 ± 3.6
Sex Ratio of Progeny (♀/♂)	.2	.6

^aMean ± S.E. (n = no. of parasitized host larvae).

Table 26. Average Number of Progeny Produced by Exposure of 2nd Instar Armyworm Larvae to A. ruficrus

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	35	9
Average Number ^a of		
Cocoons Produced/Host	66.9 ± 6.9	17.6 ± 1.7
Adults Emerged/Host	56.9 ± 5.9	15.7 ± 1.5
Average Percentage ^a of		
Female Offspring/Host	47.6 ± 3.2	41.7 ± 6.1
Male Offspring/Host	52.4 ± 3.2	58.3 ± 6.1
Average Emergence Rate ^a (%)	87.1 ± 2.0	89.3 ± 2.4
Sex Ratio of Progeny (♀/♂)	.9	.7

^aMean ± S.E. (n = no. of parasitized host larvae).

Table 27. Average Number of Progeny Produced by Exposure of 3rd Instar Armyworm Larvae to A. ruficrus

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	32	3
Average Number ^a of		
Cocoons Produced/Host	46.6 ± 5.1	26.3 ± 6.7
Adults Emerged/Host	42.6 ± 4.9	21.7 ± 5.4
Average Percentage ^a of		
Female Offspring/Host	53.4 ± 3.9	57.6 ± 7.6
Male Offspring/Host	46.6 ± 3.9	42.4 ± 7.6
Average Emergence Rate ^a (%)	91.1 ± 1.6	82.7 ± 2.0
Sex Ratio of Progeny (♀/♂)	1.1	1.4

^aMean ± S.E. (n = no. of parasitized host larvae).

Table 28. Average Number of Progeny Produced by Exposure of 4th Instar Armyworm Larvae to A. ruficrus

Observation (Numbers/Percent)	Vial Tests	Cage Experiments
Hosts Parasitized (n)	6	0
Average Number ^a of		
Cocoons Produced/Host	46.2 ± 13.6	-
Adults Emerged/Host	38.5 ± 10.2	-
Average Percentage ^a of		
Female Offspring/Host	38.1 ± 10.4	-
Male Offspring/Host	61.9 ± 10.4	-
Average Emergence Rate ^a (%)	87.9 ± 3.8	-
Sex Ratio of Progeny (♀/♂)	.6	-

^aMean ± S.E. (n = no. of parasitized host larvae).

militaris was 9, and the total average progeny per female wasp was 512 (4-hr exposure period in both cases). They consider these values low and suggested that perhaps A. militaris would oviposit more eggs if allowed to do so over several days. Hafez (1947) made a similar observation for A. ruficrus. He found that the average number of Agrotis larvae parasitized by a single Apanteles female was about 5 (range 1-10) with an average number of progeny per female of 216 (range 13-490). The values measured by these investigators were based on the number of adult parasitoids emerged. The number of cocoons spun by the newly-emerged larvae is, however, a better, although still low, estimate for eggs laid, as adult emergence is never 100% effective. A great deal of larval and pupal mortality normally occurs in the cocoon, as can be seen from the rates of emergence computed for both species (Tables 23-28). Egg or larval mortality also must occur within the host before larvae spin cocoons.

The present study also shows that the average number of cocoons produced (here used to estimate both eggs laid and emerged parasitoid larvae per host) and parasitoids emerged were both significantly lower from hosts attacked in the cages than from those confined in vials. It appeared that the need to search for more sparsely distributed hosts in the cages probably accounted for the lower parasitism rates of both species. When host and parasitoid were held in close confinement the rate of parasitism per unit time tended to increase and, as a consequence, the parasitoid oviposited more often, leaving a greater number of progeny. Simulated field conditions, thus, resulted in a lower oviposition response from both species, irrespective of host instar attacked. Production of larvae and adults from

each instar was considerably less for A. ruficrus than for A. militaris. It should be noted, however, that sample sizes associated with the imported Apanteles were in general much smaller. Fourth instar caterpillars of A. ruficrus were not used because the parasitoid failed to successfully attack them in the cage. Sample sizes (n), which are the same as the total armyworms found parasitized for each instar, are of comparable magnitude among 2nd and 3rd instars, but are probably too small to warrant any valid conclusions from the cage tests conducted with A. ruficrus. Fourth instar larvae were not readily attacked by A. ruficrus under either experimental setup used.

Tables 23 through 28 also include average percentages of female and male offspring as counted from each parasitized group. These can easily be manipulated to produce desired sex ratios. Among A. ruficrus, female and male progeny approximated a 1:1 ratio more closely than for A. militaris whose brood, in laboratory tests, seem to include a smaller proportion of females.

These data are in general thought to have some biological significance as they represent the number of larvae and adult parasitoids likely to emerge and make up the next generation. A. ruficrus produces, on the average, fewer offspring (eggs, larvae and adults) than A. militaris does. The higher reproductive rates of A. militaris with a wider range of host instars are indeed a clear indication of its greater reproductive potential when attacking P. unipuncta. The higher fecundity, combined with other intrinsic characteristics, is likely to favor the native Apanteles in a more natural setting, and indeed this seems to be the case as A. ruficrus

was not recovered in subsequent years from the field after release. Even if the longer life span of A. ruficrus is considered (ca. two times that of A. militaris), total fecundity of A. ruficrus is very low compared to that of A. militaris.

To make these laboratory comparisons more meaningful, field parasitism data by A. militaris are also provided (Table 29). The parameters are similar to those discussed above and were collected among non-outbreak armyworm populations feeding on no-till corn. When compared with data in Tables 23-25, both field and cage F_1 progeny means were considerably lower than those produced under a strictly confined situation. This increases the probability that confined Apanteles females make repeated host attacks, ovipositing several times in a single individual, especially if confinement is imposed. This may, in turn, cause superparasitism to occur at a greater rate. Despite the lack of field data for A. ruficrus, a similar behavior seems to be plausible, judging from its oviposition pattern (Tables 26-28).

It may be of interest to note that the data given in Table 29 are complementary to those in Table 1 wherein armyworm data on field parasitism by A. militaris were presented.

In the past, studies have suggested a possible correlation between host size and number of parasitoid eggs laid (Vinson and Iwantsch 1980). In this study, this relationship was not apparent, if the whole instar range was considered. To illustrate this, Table 30 is provided where average production of cocoons is specified by larval instars and numbers of individuals killed. Although the number of samples was not large, one point seems noteworthy. There is

Table 29. Average Number of A. militaris Emerging from Field-Sampled Armyworm Larvae^a

Observation (Numbers/Percent)	Field Sampled & Collection Date ^b		
	I 6/17/80	II 6/24/80	III 7/12/80
Hosts Parasitized (n)	23	32	68
Average Number ^c of			
Cocoons Produced/Host	53.0 ± 6.7	39.1 ± 3.7	60.5 ± 3.7
Adults Emerged/Host	48.7 ± 6.1	36.9 ± 3.5	34.7 ± 3.0
Average Percentage ^c of			
Female Offspring/Host	65.6 ± 2.4	56.2 ± 2.9	60.9 ± 1.4
Male Offspring/Host	34.4 ± 2.4	43.8 ± 2.9	39.1 ± 1.4
Average Emergence Rate ^c (%)	93.3 ± 1.9	94.9 ± 1.2	53.5 ± 2.2
Sex Ratio of Progeny (♀/♂)	1.9	1.3	1.6

^aLate instars most prevalent in samples.

^bFive samples per field; 25 larvae per sample.

^cMean ± S.E. (n = no. of parasitized host larvae).

Table 30. Average Number of Cocoons Produced from Armyworms Parasitized (AP) When Confined in a Vial With One Female A. *militaris* for 24 Hours

Armyworm Instar	Hosts Parasitized & Cocoons Produced/Larva ^a					
	Test 1		Test 2		Test 3	
	AP	$\bar{X} \pm S.E.$	AP	$\bar{X} \pm S.E.$	AP	$\bar{X} \pm S.E.$
1st	9	49.7 $\pm$ 8.3	2	83.5 $\pm$ 37.5	5	89.0 $\pm$ 18.7
2nd	12	99.7 $\pm$ 15.0	7	92.6 $\pm$ 23.8	12	89.3 $\pm$ 17.7
3rd	13	123.9 $\pm$ 14.9	12	124.2 $\pm$ 23.4	13	147.8 $\pm$ 21.0
4th	13	83.6 $\pm$ 8.4	16	124.4 $\pm$ 16.1	13	120.2 $\pm$ 12.1
5th	7	65.5 $\pm$ 8.4	7	74.9 $\pm$ 11.6	5	69.6 $\pm$ 12.4
6th	1	258.0	0	-	2	65.5 $\pm$ 31.5

^aNumber of larvae per instar per test was 20.

clearly a trend for oviposition in 2nd, 3rd and 4th instars, as opposed to early or late instars. There is, in general, close agreement between these results and those recorded for host size preference (see Table 4). It is very difficult to find a satisfactory explanation for the highest value in Table 30, a 6th instar larva in the first test with 258 cocoons. It is better to think of this value as an exception.

Tables 31 through 36 contain additional information on the production and distribution of F_1 parasitoid progeny among larvae parasitized in the cages. The data were tabulated according to the various combinations of parasitoid species and densities tested. Rates of emergence and female : male ratios were calculated where possible. Negative attack rates and consequent failure to produce any progeny are indicated by zeros.

Especially for A. militaris, it is evident that an increase in host density resulted in a greater rate of attack with a concurrent increase in total progeny production. Adult emergence efficiency varied from about 57% to 82%, and for the largest sample ($n = 99$) was 76%. Throughout the whole experiment, regardless of host density used, progeny production always favored males. Where wasps were released to search for the highest host densities, female brood ranged from 42 to 68% of the number of males. Comparing the net output of F_1 progeny at the highest host density, A. militaris produced nearly 13 times more offspring than did A. ruficrus.

The data just described have been further subdivided to analyze the average number of cocoons (larvae) per parasitized armyworm (Tables 34-36). The mean numbers of A. militaris cocoons per

Table 31. Total Number of Armyworms Attacked When Caged with Five *A. militaris* Females for 8 Hours and the Number of F_1 Parasitoid Progeny Produced

Total Number, Rate or Ratio	Host Density ^a					
	1	2	4	10	20	40
Total Number of						
Hosts Parasitized (n)	0	1	5	14	32	75
Cocoons Produced	0	43	251	519	1250	2520
Parasitoids Emerged	0	27	177	407	868	1861
Female Progeny Emerged	0	9	89	96	264	554
Male Progeny Emerged	0	18	88	311	604	1307
Rate of Emergence (%)	-	62.8	70.5	78.4	69.4	73.8
Sex Ratio of Progeny (♀/♂)	-	.5	1.0	.3	.4	.4

^a18 replicates for each host density (6 reps. each using 2nd, 3rd and 4th instars).

Table 32. Total Number of Armyworms Attacked When Caged with Ten *A. militaris* Females for 8 Hours and the Number of F₁ Parasitoid Progeny Produced

Total Number, Rate or Ratio	Host Density ^a					
	1	2	4	10	20	40
Total Number of						
Hosts Parasitized (n)	1	9	7	35	62	99
Cocoons Produced	42	375	281	1686	2442	3511
Parasitoids Emerged	24	294	229	1343	1903	2669
Female Progeny Emerged	8	83	39	306	716	1081
Male Progeny Emerged	16	211	190	1037	1187	1588
Rate of Emergence (%)	57.1	78.4	81.5	79.7	77.9	76.0
Sex Ratio of Progeny (♀/♂)	.5	.4	.2	.3	.6	.7

^a18 replicates for each host density (6 reps. each using 2nd, 3rd and 4th instars).

Table 33. Total Number of Armyworms Attacked When Caged with Ten *A. ruficrus* Females for 8 Hours and the Number of F_1 Parasitoid Progeny Produced

Total Number, Rate or Ratio	Host Density ^a					
	1	2	4	10	20	40
Total Number of						
Hosts Parasitized (n)	0	0	0	0	2	12
Cocoons Produced	0	0	0	0	79	237
Parasitoids Emerged	0	0	0	0	58	206
Female Progeny Emerged	0	0	0	0	23	98
Male Progeny Emerged	0	0	0	0	35	108
Rate of Emergence (%)	-	-	-	-	73.4	86.9
Sex Ratio of Progeny (φ/σ)	-	-	-	-	.7	.9

^a18 replicates for each host density (6 reps. each using 2nd, 3rd and 4th instars).

Table 34. Total and Average Number of Cocoons Produced from Different Instars of Armyworms Parasitized (AP) When Caged With Five A. militaris Females for 8 Hours

Host Density	2nd Instar			3rd Instar			4th Instar		
	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c
1	0	0	0.0	0	0	0.0	0	0	0.0
2	0	0	0.0	0	0	0.0	1	43	43.0
4	0	0	0.0	4	167	41.8 ± 7.9	1	84	84.0
10	5	163	32.6 ± 6.5	7	219	31.3 ± 5.5	2	137	68.5 ± 21.5
20	7	279	39.9 ± 3.2	20	738	36.9 ± 2.0	5	233	46.6 ± 14.8
40	25	556	22.2 ± 2.1	29	836	28.8 ± 2.1	21	1128	53.7 ± 5.4

^aAP = no. of armyworms successfully parasitized.

^bTCP = total no. of cocoons produced by parasitoid

^cTCP/AP = avg. no. of cocoons per parasitized armyworm (mean ± S.E. of 6 replicates)

Table 35. Total and Average Number of Cocoons Produced from Different Instars of Armyworms Parasitized (AP) When Caged With Ten A. *militaris* Females for 8 Hours

Host Density	2nd Instar			3rd Instar			4th Instar		
	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c
1	1	42	42.0	0	0	0.0	0	0	0.0
2	2	39	19.5 ± 2.5	3	145	48.3 ± 4.1	4	191	47.8 ± 16.9
4	4	97	24.3 ± 11.1	2	98	49.0 ± 20.0	1	86	86.0
10	8	326	40.8 ± 5.0	13	804	61.8 ± 9.1	14	556	39.7 ± 7.2
20	22	721	32.8 ± 2.4	31	1297	41.8 ± 5.3	9	424	47.1 ± 7.7
40	29	759	26.2 ± 3.1	46	1615	35.1 ± 3.2	24	1137	47.4 ± 3.8

^aAP = no. of armyworms successfully parasitized

^bTCP = total no. of cocoons produced by parasitoid

^cTCP/AP = avg. no. of cocoons per parasitized armyworm (mean ± S.E. of 6 replicates)

Table 36. Total and Average Number of Cocoons Produced from Different Instars of Armyworms Parasitized (AP) When Caged With Ten A. ruficrus Females for 8 Hours

Host Density	2nd Instar			3rd Instar			4th Instar		
	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c	AP ^a	TCP ^b	TCP/AP ^c
1	0	0	0.0	0	0	0.0	0	0	0.0
2	0	0	0.0	0	0	0.0	0	0	0.0
4	0	0	0.0	0	0	0.0	0	0	0.0
10	0	0	0.0	0	0	0.0	0	0	0.0
20	2	79	39.5 ± 18.5	0	0	0.0	0	0	0.0
40	9	158	17.6 ± 1.7	3	79	26.3 ± 6.7	0	0	0.0

^aAP = no. of armyworms successfully parasitized

^bTCP = total no. of cocoons produced by parasitoid

^cTCP/AP = avg. no. of cocoons per parasitized armyworm (mean ± S.E. of 6 replicates).

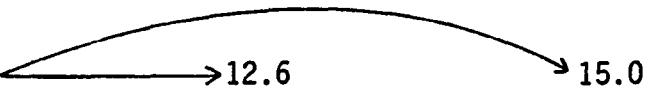
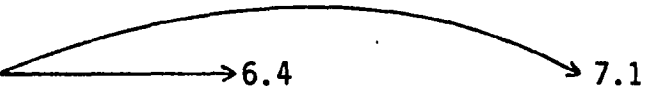
parasitized armyworm larva of the same instar do not appear to differ for either level of parasitoid density used. A similar analysis is not possible for A. ruficrus (Table 36) due to the small number of samples. When mean cocoon production was compared among different instars, there was a tendency for smaller size hosts to have fewer parasitoid larvae. This was observed when parasitoid density was either 5 or 10 wasps. Considering the reduced range of host sizes which were examined in this experiment, more eggs were laid in 3rd and 4th instar larvae than in the younger 2nd instars, which in part supports the correlation earlier mentioned between host size and number of eggs laid.

Parasitoid Development

A summary of the life cycle and developmental times as found in the literature was compiled, together with my own observations on A. militaris in Table 37. Table 38 summarizes similar data for A. ruficrus. It should be noted that these times are largely dependent upon the rearing temperature regimes. Calkins and Sutter (1976) found, for instance, that between 21 and 27°C A. militaris developmental time within P. unipuncta caterpillars decreased proportionally as the temperatures increased. Their reported values were: ca. 31.5 days at 21°C, 20 days at 24°C, and 12.6 days at 27°C. They noted that the parasitoid developed moderately well at high temperatures, but armyworm mortality increased substantially with higher temperatures.

Table 39 shows the average days from parasitoid oviposition in the host to emergence; the data were tabulated according to host

Table 37. Duration of *A. militaris* Life Cycle from Egg to Adult from Literature and Author's Observations^a

Developmental Stage	Duration in Days According to Author		
	Tower (1915) ^b	Calkins & Sutter (1976) 27°	Rolim (1983) 23°
Egg	5.5		15.0
1st Stage	3.3		
2nd Stage	5.0		
3rd Stage ^c	2.5		7.1
Pupa ^c	9.0		
Adult ^d	-	6 - 7 ^{d1}	4 - 8 ^{d2}
Overall Life Cycle	25	17 - 30 ($\bar{x}$ = 19.0)	18 - 26 ($\bar{x}$ = 22.1)

^aLab-reared on *P. unipuncta* host.

^bNo temperature record; experiments conducted in laboratory but under conditions as like those outside as possible; time spent in the cocoon was measured in an outdoor insectary.

^cDevelopment within cocoon.

^dProvided with food (d1 = raisins; d2 = 10% honey water mixture); 50% mortality.

Table 38. Duration of A. ruficrus Life Cycle from Egg to Adult from Literature and Author's Observations^a

Developmental Stage	Duration in Days According to Author	
	Hafez (1947) 26.5°C	Rolim (1983) 23°C
Egg	5.0	} → 14.1
1st Stage	5.0	
2nd Stage	3.5	
3rd Stage ^b	0.5	} → 5.5
Pupa ^b	5.2	
Adult ^c	-	8 - 16
Overall Life Cycle	-	17 - 21 ($\bar{x}$ = 19.6)

^aLab-reared on A. ipsilon (Hafex 1947) or P. unipuncta (Rolim 1983).

^bDevelopment within cocoon.

^cProvided with 10% honey water mixture; 50% mortality.

Table 39. Developmental Times from Oviposition to Parasitoid Larval Emergence from Various Armyworm Instars^a

Instar Attacked	<u>A. <i>militaris</i></u>		<u>A. <i>ruficrus</i></u>	
	Cocoon Masses ^b	Time in Days ($\bar{x} \pm \text{S.E.}$)	Cocoon ^b Masses	Time in Days ($\bar{x} \pm \text{S.E.}$)
1st	16	18.8 $\pm$.6	20	15.1 $\pm$.7
2nd	31	17.7 $\pm$.5	35	14.7 $\pm$.4
3rd	38	15.8 $\pm$.4	32	13.1 $\pm$.3
4th	42	12.3 $\pm$.2	6	12.0 $\pm$.3
5th	19	11.9 $\pm$.2	-	-
6th	3	12.0 $\pm$.0	-	-
Totals	149	-	93	-
Overall Average ($\bar{x}$)	-	15.0 $\pm$.3	-	14.1 $\pm$.3

^aReared at 23.0 $\pm$ 1.5 °C^bSame as no. of parasitized host larvae.

instar and parasitoid species. It is apparent that an inverse relationship exists between host instar (or size) and number of days spent in the host larva, i.e., it takes longer for the parasitoid larva to develop in early than late instar hosts, probably due to more food being available in larger larvae. Similar observation seems to apply to A. ruficrus except that data for 5th and 6th instars are lacking, as host larvae were not parasitized.

Shortly before emerging from its host the Apanteles larva molts into a 3rd instar larva. This instar usually spins a cocoon on the back of its host, and pupates in ca. 2.5 days (A. militaris), or less than one day (A. ruficrus) (Tables 37 and 38). It takes about 30 min for an emerging larva to leave its host, and most of them do it at the same time. When the larva has emerged halfway it starts spinning its silken cocoon. Cocoon-spinning is completed in 1-2 hr. Calkins (1977) found the total time for cocoon construction to be ca. 100 min, and Hafez (1947) estimated that A. ruficrus spent about 120 min. Externally, the cocoons are whiter and closely packed for A. militaris, and yellowish, loosely connected for A. ruficrus. Adults of both species from single cocoon masses usually emerge within 12 hr. or less. Hafez (1947) observed that among A. ruficrus, male wasps usually emerged first.

The time spent by the 3rd instar and the pupa in the cocoon was also recorded (Table 40). In contrast to what was noted for duration of the egg and early larval period, the average length of the pupal stage (including 3rd instar larvae and prepupae) was not influenced by the host instar in which the larvae originated. This time averaged about 7 days for A. militaris and 5.5 days for A. ruficrus.

Table 40. Developmental Times Between Parasitoid Larval Emergence from Various Armyworm Instars to Adult Parasitoid Emergence^a

Instar Attacked	<u>A. <i>militaris</i></u>		<u>A. <i>ruficrus</i></u>	
	Cocoon _b Masses	Time in Days ($\bar{x} \pm \text{S.E.}$)	Cocoon _b Masses	Time in Days ($\bar{x} \pm \text{S.E.}$)
1st	16	7.3 $\pm$.1	20	5.6 $\pm$.1
2nd	31	7.0 $\pm$.1	35	5.5 $\pm$.1
3rd	38	7.1 $\pm$.1	32	5.7 $\pm$.1
4th	42	7.4 $\pm$.5	6	5.2 $\pm$.3
5th	19	7.2 $\pm$.1	-	-
6th	3	6.7 $\pm$.3	-	-
Totals	149	-	93	-
Overall Average ($\bar{x}$)	-	7.1 $\pm$.1	-	5.5 $\pm$.1

^aReared at 23.0 $\pm$ 1.5 °C.

^bSame as no. of parasitized host larvae.

The mean developmental time from egg to adult of each species was determined by adding the time from oviposition until the 3rd instar emerged (Table 39), and the time spent inside the cocoon (Table 40). The total developmental time found by Calkins and Sutter (1976) for A. militaris ranged from 17 to 30 days and averaged 19 days at 27°C (Table 37). In the present study, the total egg to adult developmental period varied from 18 to 26 days and depended on the host instar attacked in addition to temperature; it averaged 22.1 days at 23°C. According to Hafez's (1947) observations the egg to adult developmental period for A. ruficrus was about 19-20 days (Table 38). Although adult A. ruficrus lived longer than A. militaris, the egg to adult time of 19.6 days at 23°C was somewhat shorter.

Induced Internal Competition

Internal competition is a behavioral trait often observed among parasitic wasps developing concurrently within the same host. It may occur as a result of superparasitism or multiparasitism. In either case, some sort of competition or conflict or repressive action occurs among the parasitoid larvae which affects their development and survival. In some cases, this may result in total suppression of one species by the other (Salt 1961; Fisher 1971).

In this experiment, 1st, 2nd and 3rd instar armyworm larvae were individually exposed to multiple parasitism in a small glass chamber. (1 ml straight-sided shell vial). Females of each parasitoid were allowed to oviposit once in the same host larva, one species or the other ovipositing first. Exposures were either simultaneous (0-1 hr

group) or conducted over 24-, 48- or 96-hr intervals. General superiority was assumed for the species which managed to survive under supposedly competitive conditions and which gave rise to unmixed progeny in more frequent cases. The results showing which species survived and emerged in each case, and their respective frequencies, are discussed below.

A. ruficrus seemed to be a better larval competitor inside the host, having a noticeable advantage whenever it oviposited first (Table 42). If, however, A. militaris was the first to attack, A. ruficrus offspring were predominant only when the exposure was almost simultaneous (Table 41). As exposure intervals were greater than 24 hr, A. ruficrus development was suppressed.

Although competition may have played a significant role in deciding which species emerged first, total developmental time determines early or late emergence. Thus, the apparent competitive ability exhibited by A. ruficrus may hinge upon its shorter developmental time (see Tables 37 and 38). There is, however, some doubt concerning the outcome of larval competition between the two species, and one should be totally aware that this discussion is still too simplistic to provide a satisfactory explanation for the observed results. In assessing their relative performances, these tests should be considered less relevant than the parasitoid functional response study.

It may also be of interest to observe that the instances of mixed species were rare. The fact that only one species generally emerged could have been determined by competitive elimination or simply by restraint from oviposition in hosts already containing a

Table 41. Parasitization of Early Instar Armyworm Larvae Following an A. militaris - A. ruficrus Exposure Sequence^a

Instar Exposed	Hours Between Exposures	Parasitoid Species Emerged ^b and Number of Cocoons Produced				Other Unknown Deaths ^c	Unaffected Host Larvae
		<u>A. mil.</u>	$\bar{x} \pm \text{S.E.}$	<u>A. ruf.</u>	$\bar{x} \pm \text{S.E.}$		
1st	0 - 1	0	-	3	12.7 $\pm$ 5.8	17	0
	24	4	30.5 $\pm$ 3.8	4	27.3 $\pm$ 5.4	12	0
	48	14	37.9 $\pm$ 3.1	1	105.0	5 [3]	0
	96	8	32.0 $\pm$ 4.7	3	41.7 $\pm$ 10.7	9 [2]	0
2nd	0 - 1	0	-	5	17.6 $\pm$ 3.5	15	0
	24	9 (1)	39.3 $\pm$ 4.1	2	10.5 $\pm$ 3.5	9 [2]	0
	48	14	26.1 $\pm$ 3.7	1	13.0	5	0
	96	8 (1)	36.5 $\pm$ 7.7	0	-	11	1
3rd	0 - 1	0	-	9	29.6 $\pm$ 5.7	11	0
	24	2	14.5 $\pm$ 2.5	8 (3)	21.8 $\pm$ 7.0	9	1
	48	11 (1)	28.9 $\pm$ 4.4	4	31.3 $\pm$ 5.1	5 [1]	0
	96	4	64.0 $\pm$ 9.2	0	-	16 [8]	0

^a20 host larvae used per test.

^bValues in parentheses indicate frequency of mixed offspring; the prevalent species is recorded first.

^cValues in brackets indicate frequency of host deaths between two successive exposures.

Table 42. Parasitization of Early Instar Armyworm Larvae Following an A. ruficrus - A. militaris Exposure Sequence^a

Instar Exposed	Hours Between Exposures	Parasitoid Species Emerged and Number of Cocoons Produced				Other Unknown Deaths ^b	Unaffected Host Larvae
		<u>A. ruf.</u>	$\bar{x} \pm S.E.$	<u>A. mil.</u>	$\bar{x} \pm S.E.$		
1st	0 - 1	7	15.6 $\pm$ 2.5	0	-	13	0
	24	12	17.3 $\pm$ 1.4	0	-	8	0
	48	18	20.6 $\pm$ 1.1	0	-	2	0
	96	16	20.8 $\pm$.9	0	-	4 [4]	0
2nd	0 - 1	7	17.3 $\pm$ 3.7	1	56.0	11	1
	24	3	27.7 $\pm$ 2.0	0	-	17	0
	48	12	20.8 $\pm$ 1.1	0	-	8	0
	96	10	26.2 $\pm$ 2.3	0	-	10 [4]	0
3rd	0 - 1	5	27.6 $\pm$ 7.7	0	-	15	0
	24	3	19.3 $\pm$ 7.7	2	63.5 $\pm$ 21.5	15	0
	48	11	25.7 $\pm$ 1.5	0	-	8 [3]	1
	96	8	22.1 $\pm$ 2.2	0	-	12 [11]	0

^a20 host larvae used per test.

^bValues in brackets indicate frequency of host deaths between two successive exposures.

different kind of parasitoid egg. A ruficrus reportedly cannot distinguish parasitized from nonparasitized Agrotis hosts (Hafez 1947). Thus, the last hypothesis cannot be supported, at least for this species. Also, in accepting the first hypothesis one is led to believe that a larger number of larvae might have escaped competition, thus making mixed progeny more frequent; however, that was not what occurred. The second hypothesis (deterred oviposition) would seem, thus, more attractive although oviposition by each female parasitoid participating in the tests apparently did take place.

A more crucial aspect, however, is that the technique may be faulty as an experimenter can never be totally sure that females have actually laid eggs to make this a valid test. Although the experiment raises interesting questions on the biology and physiology of the species involved, the method used is admittedly unsatisfactory to answer many of these questions. Additional anatomical and physiological studies and dissections are deemed necessary if competitive interactions and developmental processes taking place internally in the parasitized host are to be explained. Dissections of larvae at various stages of their development are of utmost importance to disclose some of the intricacies involved, and may help explain why an "unfit" parasitoid (see page 57), under certain conditions, may be reproductively superior to an otherwise "more effective and well-adapted" one.

Tables 41 and 42 also include unexplained host deaths (including those occurring between successive exposures) and pupation as outcomes of the incubation phase. The number of mature parasitoid larvae constructing cocoons provides an estimate of eggs laid by

individual females of both species in one quick insertion of the ovipositor which often lasts less than 5 seconds. The number of eggs per initial insertion averaged 34 for A. *militaris* when this parasitoid attacked first, and 21 for A. *ruficrus* when it attacked first (weighted means, not shown in tables). For the former species, Tower (1915) gave a range of 8-72 eggs in one oviposition; for the latter, Hafez (1947) reported an average of about 26 eggs for 9 Agrotis larvae.

Implications for Biological Control and General Recommendations

For many years great financial losses to agriculture have been caused by the armyworm. In Michigan, interest has increased since 1975 due to unusually frequent yearly outbreaks.

Many independent factors may have contributed to the present population status of this pest. Some of them have been identified, and should be given further attention in future studies, as they may be major obstacles in the design and implementation of armyworm management programs. The following are worth noting:

- (1) The difficulty of detecting certain life stages (i.e., adults, eggs, 1st and 2nd instars) in the field. This is a frequent cause of sudden crop damage (Riley 1883; Slingerland 1897). Armyworm infestations usually go unnoticed until the caterpillars have reached later instars and food consumption is at its greatest point. The characteristic hiding behavior coupled with the pest's habit of moving from one field to another, make it particularly difficult to assess regional densities and to monitor the spatial and temporal

distributions of armyworm populations (Untung 1978), as essential prerequisite for effective control.

(2) P. unipuncta is also known for its polyphagous feeding behavior; its larvae have been reported to feed on small grains, corn, sorghum, grasses, beans, forage crops, vegetable crops and even a few fruit crops. With such a wide range of hosts, application of adequate control measures is not always easy. This problem may be further complicated by climatic fluctuations which may cause larval populations to move from grassy areas or low-value crops to adjacent, more economically important ones.

(3) Little information on where armyworm populations originate in outbreak and non-outbreak years is available. A better understanding of its general life history (especially early season development) is critical for the selection of an efficient control strategy.

(4) Being a multivoltine species, armyworm population dynamics are complex, making some management strategies less available or economically unfeasible.

These are associated problems which generally point to a lack of information on the dynamics of armyworm populations and of its ecosystem. This has resulted in the practice of an "insurance"-type of control where treatments are often improperly applied, making insecticide applications ineffective and environmentally damaging.

There have been suggestions that more frequent localized outbreaks might be due to the greater use of insecticides which kill off large numbers of parasitoids and predators which normally may control the species (e.g., Breeland 1958). At present, however, the

cause(s) of localized outbreaks are unknown. In the future, a more thorough study of armyworm biology, particularly with reference to its habits and seasonal synchronization should be pursued. This will help determine the real cause(s) of outbreaks while providing future workers with additional data for increased management options.

An area which has received very little attention and where the lack of data is particularly critical is the study of relationships between the armyworm and its many natural enemies. Furthermore, the abundant and varied complex of parasitoid species attacking armyworms provides a good opportunity to study the interaction of parasitoid guilds that is particularly relevant to the theory and practice of biological control of insects in temporary ecosystems (see Ehler and Miller 1978). One species which may be of great interest due to its close association with the armyworm is A. militaris. The high searching characteristics of this insect (see page 57), allied with an apparently high natural ability to reproduce and catch up with small increases in the host population, make it a desirable organism for studying host-parasitoid interactions both in the field and laboratory. It is hoped that this study has contributed to a better understanding of some factors governing these host-natural enemy interactions.

In general, satisfactory chemical control measures are available to the farmer, but timing of application is frequently a problem owing to the sporadic nature of armyworm outbreaks. Moreover, even though insecticide usage may be regarded as a dependable, rapid and effective way to combat this pest, the search for less damaging environmental control options should continue. It appears that

pesticide usage can best be reduced by increasing the efficiency of natural control agents. Hence, it is my opinion that the biological control component should be integrated with other control measures.

It is unfortunate that the introduction of A. ruficrus did not result in successful establishment. The door is open, however, for additional introductions of new strains of A. ruficrus and/or different species into Michigan, as well as other areas in the country. I basically concur with van den Bosch's (1968) statement that unsuccessful introductions should never be regarded as a failure of the biological control method, but only as a failure of establishment of certain species in some target areas. There is probably considerable potential for applying biological control to P. unipuncta, not to mention other major noctuid pests; however, the chances of success will be greater if the approach of multiple introductions is used. It should be noted that attempted establishment of A. ruficrus into this country did not have the multiple characteristics of many other biological control projects. Contrary to a typically "classical" approach, whereby many different parasitoids are usually introduced at once, only one promising parasitoid species was imported and assessed in this project. Some empiricism may also have been involved in this particular study, but this is not a shortcoming per se, since the very practice of biological pest control has essentially had an empirical origin and fortuitous establishment of exotic natural enemies is not all that uncommon.

Recently, techniques have been proposed that can assist in selecting the best species for introduction into an area with a known

species composition and distribution (Price 1972; Ehler 1978). The use of these methods may also provide the basis for a scientific assessment of the results of future biological control projects. In a most interesting analysis of how a sequential r- K-strategist series of parasitoids might evolve with a host insect, Force (1972) noted that to control pests in disturbed environments (agricultural, etc.), the preferred natural enemies should be r-strategists. These organisms are viewed as better colonizers than K-strategists (see MacArthur and Wilson 1967, Pianka 1970, for discussions on the r- and K-selection concept). Some researchers (e.g., Ehler 1979) have further stressed the need for detailed studies prior to any introduction. These studies should indeed improve our understanding of general competitive interactions in endemic parasitoid guilds, thus allowing for more rational decisions concerning new introductions. As to the continued use of biological control, DeBach (1974) notes that, as a rule, no geographic area, crop or pest insect should be prejudged as being unsuitable for biological control. This has been a basic guideline for many biological control workers. He also shows impressive figures on the number of undescribed natural enemies. Among the parasitic Hymenoptera alone, he estimates that only about 25% of all the species have been described (see also Sabrosky 1955; Schlinger and Doutt 1964). This means that "we have just begun to scratch the surface in the search for insect natural enemies" (DeBach 1974), and that a tremendous potential exists for their increased use in applied pest control.

More specifically, Mason (1981) mentions that braconid parasitoids are poorly known, and the 1300 or so species of Apanteles

thus far described, represent only a fraction of their real number. Based on these estimates, one cannot help but hypothesize that the potential of Apanteles species and their ecotypes in biological control of noctuid pests is much greater than presently attained.

An evaluation of the results provided by biological control research also shows that in every area where this method has been rigorously applied, major successes have occurred (Munroe 1971). Rather than the climate, crop or pest, major success has often been directly related to the research and funds that are utilized (DeBach 1964; Simmonds et al. 1976). Intensive, well-supported programs are, of course, likely to be more successful than isolated small projects.

Accordingly, if biological control of a lepidopterous pest be the ultimate objective of future projects, a sequence of introductions of parasitoids of known value, such as outlined by Force (1972) would be advised. That, of course, would imply increased financial support since more intensive laboratory and field evaluation of all species concerned will be required.

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APPENDIX 1

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1983-2

Title of thesis or dissertation (or other research projects):

Laboratory Comparison of the Potential of Apanteles ruficrus
Haliday and Apanteles militaris Walsh (Hymenoptera: Braconidae)
for Control of the Armyworm, Pseudaletia unipuncta (Haworth)
(Lepidoptera: Noctuidae) in Michigan

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums: None

Investigator's Name (s) (typed)
Antonio Edilton Rolim

Date June 1983

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Species or other taxon	Label data for specimens collected or used and deposited	Number of:						
		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other * Museum where deposited
<u>Pseudaletia unipuncta</u> (Haworth)	Michigan State University campus, lab culture		5					M.S.U.
<u>Apanteles militaris</u> Walsh	Michigan State University lab culture reared from local populations of <u>Pseudaletia unipuncta</u> (Haworth). 1977-1982, A. E. Rolim					1 via	1 via	M.S.U.
<u>Apanteles ruficrus</u> Haliday	Michigan State University lab culture from Lahore, Pakistan, CIBC-PAK-77-1128. BIRL-77-58. From <u>Agrotis</u> sp.					1 via	1 via	M.S.U.

(Use additional sheets if necessary)

*COCOONS

Investigator's Name(s) (typed)

Antonio Edilton RolimVoucher No. 1983-2

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Date June 1983Curator [Signature]Date 22 June 1983

APPENDIX 2

Appendix 2

Table A. Field Releases of *A. ruficrus* Adults and Mass-Parasitized Armyworm Larvae in Michigan (1978)

Date	Release Site	Approximate Number Released	
		Wasps	Armyworms
6-13	T4N R2W Sec 36 *	400	-
22	T6S R7E Sec 25 (?)	200	500
29	T4N R2W Sec 36 *	400	1000
7-02	Ibid.	200	500
04	Ibid.	400	-
15	Ibid.	600	-
19	T1S R9W Sec 9	800	-
21	T4N R1W Sec 19 *	200	500
26	T1S R9W Sec 9	600	-
27	T4N R1W Sec 19 *	200	500
29	T4N R2W Sec 36 *	200	500
8-03	Ibid.	400	1000
08	Ibid.	200	500
19	T4N R1W Sec 19 *	100	500
20	Ibid.	200	500
25	Ibid.	200	500
9-08	T4N R2W Sec 36 *	600	1000
17	Ibid.	400	1000
27	Ibid.	100	500
10-04	Ibid.	600	1000
Totals		7000	10000

*MSU Campus.

Appendix 2

Table B. Field Releases of *A. ruficrus* Adults and Mass-Parasitized Armyworm Larvae in Michigan (1979)

Date	Release Site	Approximate Number Released	
		Wasps	Armyworms
6-26	T4N R1W Sec 19 *	100	500
7-02	T4N R2W Sec 36 *	200	1000
11	T8N R3W Sec 25	200	1000
14	T4N R1W Sec 19 *	200	500
20	T4N R2W Sec 36 *	200	500
8-05	T4N R1W Sec 30 *	400	1000
07	T4N R1W Sec 19 *	100	500
20	T4N R2W Sec 36 *	600	1500
31	T4N R1W Sec 30 *	400	1000
9-03	T4N R2W Sec 36 *	400	1000
10	Ibid.	800	1500
12	T4N R1W Sec 30 *	400	1000
14	Ibid.	200	1000
17	T4N R2W Sec 36 *	200	500
22	Ibid.	400	1000
26	Ibid.	400	1000
10-03	T4N R1W Sec 19 *	200	500
09	T4N R2W Sec 36 *	400	500
Totals		5800	15500

*MSU Campus.

Appendix 2

Table C. Field Releases of A. ruficrus Adults and Mass-Parasitized Armyworm Larvae in Michigan (1980)

Date	Release Site	Approximate Number Released	
		Wasps	Armyworms
6-17	T8N R3W Sec 25	200	1000
23	T4N R2W Sec 36 *	100	1000
7-08	T8N R3W Sec 25	2000	-
12	Ibid.	500	1000
22	T4N R2W Sec 36 *	100	1000
25	T8N R3W Sec 25	100	1000
28	Ibid.	1000	2000
8-05	T4N R2W Sec 36 *	1000	-
12	Ibid.	1000	-
16	Ibid.	500	1000
27	Ibid.	1000	3000
9-05	Ibid.	500	2000
12	Ibid.	100	1000
21	Ibid.	200	1000
29	Ibid.	1000	500
10-05	Ibid.	2000	500
11	Ibid.	2000	1000
18	Ibid.	2000	1000
Totals		15300	18000

*MSU Campus