HOST-PARASITE INTERACTION BETWEEN *APHELINUS ASYCHIS* (WALKER), AN IMPORTED PARASITE, AND THREE APHID SPECIES OF SORGHUMS

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Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
July 1970

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PREFACE

Recent concern over pesticides and environmental contamination by pesticides has placed more emphasis on biological control as a means of arthropod control. Several states (i.e., California, Indiana, Missouri, etc.) have had success in biological control attempts by more effectively utilizing native and introduced parasites and predators. In the summer of 1968, Oklahoma sorghum fields became highly infested with a possible new greenbug biotype. By February 1969, Oklahoma State University initiated a state project to investigate biological control of this sorghum pest. Laboratory evaluation of this greenbug pest along with various parasites and predators was given first priority in order to insure that later field tests would have more validity in any eventual biological control success.

Doctor R. D. Eikenbary, Associate Professor of Entomology, was selected as Investigations Leader for this project. I was fortunate enough to be working under Dr. Eikenbary in another research project and was asked to participate in the research presented in this thesis. Words cannot express my appreciation for all the advice and constructive ideas received from my major adviser throughout this current research as well as in the past. His guidance, encouragement and assistance in preparing this manuscript are sincerely appreciated. More important, I feel Dr. Eikenbary has endeavored to prepare me for a profession in entomology by stimulating my interest in publication and proposal writing as well as giving me a broad background in several areas of research and teaching.

Special appreciation is extended to Professor R. R. Walton for his suggestions and guidance in my teaching experiences and in preparing this manuscript.

Doctor Edward E. Sturgeon, Head, Forestry Department, was kind enough to serve as a member of my committee and offer excellent advice in preparing this manuscript.

I want to thank Dr. J. A. Hair, Associate Professor of Entomology, for his help in this thesis preparation. He, too, has endeavored to offer much valuable time and talent in better preparing me for a career in Entomology.

An amazing man, Dr. R. D. Morrison, Professor of Mathematics and Statistics, contributed many hours toward the statistical manipulations in this paper as well as in subsequent review of this manuscript. I also want to thank Mrs. Morrison for doing an excellent job of typing this manuscript.

Indebtedness for part of my financial support is expressed to The Society of Sigma Xi.

Meredith Oliver, Laboratory Technician, gave me much assistance in the laboratory and I want to thank her for her excellent help.

I would like to thank Jack Jackson, Dave Langston, and Susan Hight, Graduate Research Assistants, for their cooperation, advice, and assistance throughout this study.

A long-awaited appreciation is extended to my wife, Doris, who has sacrificed much in order that this manuscript could be prepared. She

has been my inspiration in both good and bad times; to her I dedicate this manuscript.

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INTRODUCTION

In 1968, outbreaks of the greenbug, *Schizaphis graminum* (Rondani), occurred on grain and forage sorghums throughout a major portion of the sorghum-producing region of the United States. Thousands of acres of young sorghum plants were killed. The severity of the greenbug attack on sorghum was given in the Cooperative Economic Insect Report, USDA (1969), which listed the estimated acreage treated for greenbug control in 1968. Those states treating the most acreage were: Texas (1,500,000 acres), Kansas (600,000 acres), Nebraska (540,000 acres), Oklahoma (300,000 acres), Colorado (150,000 acres), and New Mexico (137,000 acres). Plants in all stages of maturity were attacked. Populations of 30,000 to 40,000 greenbugs per plant were reported on large sorghum plants in some areas. Due to the suddenness of the problem, many areas were faced with insufficient supplies of insecticide and application equipment and were not prepared to treat fields when needed.

Tests showed that the insects could be transferred from grain sorghums to wheat and back to grain sorghums with no difficulty in living or reproducing on either host (Daniels, 1969). These greenbugs possibly were of the "C" biotype described by Harvey and Hackerott (1969a, 1969b) and Wood et al. (1969). Our observations indicate that the biotype attacking sorghum in the field is also the most prevalent one on wheat and other small grains. The greenbug appeared on sorghum in large areas of the sorghum-producing states again in 1969, indicating that it could be a limiting factor in sorghum production in the future.

Rising concern over wide scale pesticide use and environmental contamination has caused many to seek other means in controlling insects which damage many economically important crops such as sorghums. When parasitic Hymenoptera are used for biological control the host-parasite interaction is basically symbiotic and, since the parasites' habits have changed little over the last 100 million years, we may conclude that the newly established parasite would not become detrimental.

In biologically controlling agricultural pests such as the greenbug, one is concerned with regulating the pest population at low economic loss levels. To maintain this density the parasite must have high host-searching abilities. The parasite which requires a small amount of food for development and single host development would possibly be more efficient at low host density levels. Also, the female parasite who is the most efficient in making use of the time available to her should better survive these low host densities. High mobility of the parasite helps her to find an adequate number of hosts during a short life.

After the invasion of sorghums by the greenbug in 1968, the Insect Identification and Parasite Introduction Research Branch, USDA, initiated a search in Southern Europe for effective natural enemies. Laboratory studies conducted in Paris indicated Aphelinus asychis (Walker) would parasitize the corn leaf aphid, Rhopalosiphum maidis (Fitch). Dr. G. Remaudiere of the Pasteur Institute, Paris, France, cultured A. asychis from Iran on Schizaphis graminum (Rondani).

Material from the 2 sources appeared to be the same and eventually the Iranian stock was used for importation purposes because the Southern France-Italy stock was used for specimens. A. asychis was sent to Oklahoma State University for laboratory and field evaluations.

This parasite is similar to the one described by Hartley (1922) when he reported on the biology of Aphelinus semiflavus (Howard). A. asychis and A. semiflavus were synonymized by Ferriere (1965) and Force and Messenger (1968) concurred. Mackauer and Finlayson (1967) left A. asychis as a separate species because of possible differing geographic races or strains. The A. asychis used in these studies might be another geographic strain of Aphelinus asychis as theorized by Ramaseshiah and Dharmadhikari (1969).

Under natural conditions the innate capacity of a hymenopterous parasite to regulate the population of its host and its own species is almost impossible to prove scientifically. Many of the environmental factors can modify and obscure population regulation; but, fortunately, laboratories are available which help control many of the essential factors. Such laboratory experiments confirm the conclusions that certain hymenopterans regulate their own population as well as that of the hosts (Flanders, 1962).

A laboratory host preference study of A. asychis was initiated using 3 species of aphids growing on sorghum. Other studies including adult longevity, duration of development, sex ratio, and intraspecific competition were made at 5 controlled temperatures. Information gained from the study is to be applied in field evaluation of biological control of the greenbug.

MATERIALS AND METHODS

Host Preference

In determining insect host preference, initially, 5 constant and 2 constant-alternating temperatures were chosen: 23.9, 26.7, 29.4, 32.2, 35, 21.1-32.2, and 26.7-37.8 C. The 35 C constant and 26.7-37-8 C alternating temperatures yielded a few mummies (parasitized aphids), but no adults emerged. These 2 treatments were dropped, leaving 1 constant-alternating (12 hours low temperature and 12 hours high) and 4 constant temperatures. Temperatures were maintained in controlled environmental chambers with a 12-hour photoperiod yielding approximately 1100 ft. candles/chamber. Four-inch plastic pots planted with RS-610 sorghum plants were used in these tests (Fig. 3). Three aphid species were used (Fig. 1): a new greenbug biotype, *Schizaphis graminum* (Rondani), of primary interest because of recent widespread damage in sorghum producing areas; the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), which causes occasional damage to sorghum; and the yellow sugar cane aphid, *Sipha flava* (Forbes), which caused widespread damage to small grains in Oklahoma in 1960 and 1961 (Chada et al., 1965).

The host preference of *A. asychis* was measured by comparing the number of mummies and progeny produced from the 3 aphid species. Adult parasites were caged in 3 ways: 1) with single aphid species for the life span of the parasite; 2) with combinations of the 3 aphid species for the life span of the parasite; and 3) with greenbug + corn leaf aphid combinations for 12 hours of light and 12 hours of darkness. There were 4 possible combinations used with the 3 aphid species: sorghum greenbug + corn leaf aphid; sorghum greenbug + yellow sugar cane aphid; corn leaf aphid + yellow sugar cane aphid; and sorghum greenbug + corn leaf aphid + yellow sugar cane aphid.

Twenty-five 3rd and 4th instar nymphs were used for each aphid host for each possible combination. Ten sorghum plants were hand inoculated with nymphs by using a soft brush and were left for 2 to 3 hr to allow the nymphs to distribute themselves (Fig. 2). Each test plant was covered with a cellulose nitrate cylinder, 6 cm in diameter and 28 cm in length. Organdy cloth was used to cover the top of the cylinder and the two air movement holes (Fig. 3). A mouth aspirator (Fig. 3) patterned after Childs (1932) enabled transferral of one mated female _A. asychis_ through a hole punched in the cage covering each test pot of sorghum. The soil surface under each test plant was covered with white sand to facilitate recovery of fallen mummies and checking on the small parasite (i.e., longevity). Ten potted plants were used with each individual aphid species and each combination of aphid species. The pots were randomly placed in a controlled environmental chamber with a relative humidity of 50% ± 10% and a pre-selected test temperature. The parasites in the cages were checked each day to determine the longevity. Cages could be removed and the plant inspected because the parasite seldom moved while on the plant. This Aphelinid trait was reported by Hartley (1922) and Griswald (1929). After a few days, depending on the temperature, the blackened mummies produced by parasitization (Fig. 4) were removed daily and separated as to aphid host. The parasites from these mummies (Fig. 5) were sexed daily and recorded. A total of 350 pots were used in these studies.

Longevity

In determining the longevity of the adult female A. asychis, only freshly emerged and mated females were used. The parasites mated readily when they were confined in 2-dram vials and provided with droplets of undiluted honey (Fig. 6). After mating, the female parasite was transferred into a cage (Fig. 3) containing a sorghum plant and aphid hosts. No additional food was provided the parasite to give more validity to field studies as Force and Messenger (1968) stated that if food is not readily available in the field, the conclusions of laboratory studies where food is artificially plentiful may not be meaningful. The longevity of the parasites in these studies should approach more closely the field situation in that the adult parasite had to survive on moisture droplets on the plant or cage, honey dew from aphids, and the feeding from the puncture holes made by the ovipositor in the aphid. The combinations of aphid species and temperatures were the same as described above.

Developmental Period

To determine developmental periods of the parasites, mated A. asychis were caged separately with twenty-five 3rd and 4th instar greenbug, corn leaf aphid and yellow sugar cane aphid and allowed to parasitize for 12 hours. Then the aphid hosts were held at the experimental temperatures until the progeny of the parasite emerged. The same controlled temperatures described under insect host preference were used in this study.

Sex Ratio

To determine the sex ratio, mated female parasites were caged with twenty-five 3rd and 4th instar greenbug, corn leaf aphid, and yellow sugar cane aphid, individually. The female parasite was allowed to parasitize hosts throughout her life span. After mummies started appearing, they were collected daily, stored at the experimental temperatures, and the sex determined upon the emergence of the progeny. Only those female parasites which produced 1 or more female offspring were considered as mated in this study. Based upon previous studies, unmated female parasites produced only male offspring. The temperatures used in this study were the same as described above.

A uniformity trial, run beforehand, indicated a completely randomized design could be used within each controlled environmental chamber because of a resulting insignificant variance. Variation among pots within a temperature was used as the experimental error without sex or competition. A split-plot type design facilitated analysis when there was competition between hosts, or differences among sex, or both. The main-plots were the temperatures and the sub-plots became host and sex.

The data were then subjected to an analysis of variance. The variance shown was not independent of the mean and log counts were used for stabilization of data in each analysis (Snedecor & Cochran, 1967). All illustrations and tables present the mean response of ten pots for the particular aphid combination and temperature. Analysis was made on parasites, mummies and all possible interactions with temperature and aphid hosts.

Intraspecific Competition

An intraspecific competition study involving *A. asychis* was run at 2 constant temperatures: an optimum 23.9 and a threshold 32.2 C. Fifteen sorghum pots were used for each of 2 replications at each of the 2 constant temperatures. The plants were inoculated with fifty 3rd and 4th instar greenbug nymphs. The nymphs were allowed to distribute themselves over the sorghum plant. Three different densities of *A. asychis* were used: 2, 4, and 8 parasites per plant.

A randomized block design was utilized within each chamber (5 blocks and 3 treatments). The 3 concentrations of parasites were randomly applied to 3 pots in each block and allowed to parasitize over a 24 hour period. After appearing, the mummies produced by each combination were collected and a certain number dissected to check for superparasitism while the others were left in cups to check other factors. An analysis of variance was run on the number of mummies and parasites produced at each constant temperature. The data gathered included the parasites, developmental period, fecundity, sex ratio, efficiency, effect of crowding, and superparasitism.

RESULTS AND DISCUSSION

Host Preference

The successful attack of a host by a parasite is related to host habitat finding, host finding, host recognition and acceptance, and host suitability (Salt, 1938). One or more of these steps limits the number of species that may serve as hosts for a parasite. The parasite's pattern of searching and its nutritional requirements have a great deal to do with whether a host species will be acceptable. Flanders (1962) indicated that gravid females search first for a certain environment and later for a site of egg deposition. It is possible that unnatural hosts can be used in mass culture because the need for host-habitat finding is eliminated.

The host specificity of parasites with many potential hosts is largely dependent on host-habitat finding, while for those with few potential hosts it is largely a process of host suitability. The most important agent in regulation of insect population is a parasite which is characterized by inherent low fecundity, high host-searching capacity, a capacity based on morphological, physiological, and psychologically adaptive characteristics. The preference of the parasite for a particular host in this study was measured by the number of mummies of each aphid species produced, i.e., the greater the number of mummies of the aphid species, then the more highly preferred that species to the parasite.

Sorghum Greenbug, Corn Leaf Aphid and Yellow Sugar Cane Aphid Individual Tests

An analysis of variance of the mummies produced from these 3 aphids caged separately with A. asychis (Table I) indicates significant differences for temperature, host and host x temperature interaction. Figure 7 illustrates higher responses for the number of mummies produced as compared to the aphids in combination. One may conclude that the aphids in combination serve to provide a different environment for A. asychis with a resulting decrease in the potential for controlling a particular pest.

Sorghum Greenbug + Corn Leaf Aphid Combination

Figure 8 illustrates the number of mummies produced for each of the 2 hosts involved. The sorghum greenbug was preferred at each temperature. This preference seems to decrease with increasing temperatures. When the mummies produced are subjected to an analysis of variance (Table II) one gets statistically significant differences for the 5 temperatures, 2 hosts and host x temperature interaction. One would expect these to show significant differences because the interaction of these 2 aphids should have an effect on the number of aphids parasitized (i.e., the parasite still has to walk over and around an undesirable host). Smith (1969) reported a similar trend in that the Pteromalid parasitoid Nasonia vitripennis (Walker) showed statistically significant differences with 2 different hosts in regard to number of hosts attacked and number of eggs laid per host. The efficacy of N. vitripennis was influenced by host selection and host suitability which is the same apparently for A. asychis and its experimental hosts.

<u>Sorghum Greenbug + Yellow Sugar Cane Aphid Combination</u>

Figure 9 indicates fewer mummies produced for each temperature except for 32.2 C as compared to the preceding aphid combination. One must assume that one of the hosts had a detrimental effect on the total number of mummies produced.

An analysis of variance (Table III) of the mummies produced with these two aphids as hosts gives statistically significant differences for temperatures, hosts, and host x temperature interaction. Figure 4 further emphasizes these significant differences and gives an indication that the yellow sugar cane aphid's presence decreases the number of sorghum greenbug mummies produced without its actually being parasitized to any great extent.

<u>Corn Leaf Aphid + Yellow Sugar Cane Aphid Combination</u>

Generally, there is an even lower response for mummies produced as compared to the 2 previous aphid combinations. Again, the mean number of mummies produced remains fairly stable for the first 3 constant temperatures and drops off rapidly at 32.2 C. Figure 10 illustrates the mummies produced for this 2 aphid combination. When one compares this host preference test to the sorghum greenbug + corn leaf aphid combination the corn leaf aphid response lies midway between the responses shown with that combination. One must assume here that the techniques involved were rather uniform throughout the experiment. Again, the yellow sugar cane aphid was preferred the least by a large margin. The mummies produced at 21.1-32.2 C gave an approximate midway response from the controlled constant temperatures.

Table IV is the analysis of variance for the mummies produced by this combination, and we again have statistically significant differences for the 5 temperatures, 2 hosts, and host x temperature interaction.

Sorghum Greenbug + Corn Leaf Aphid + Yellow Sugar Cane Aphid Combination

Figure 11 indicates more mummies were produced from sorghum greenbug than the other 2 hosts. One could theorize that the yellow sugar cane aphid's presence with these two aphids could provide the stimulus for fewer mummies produced from sorghum greenbug and corn leaf aphid, as compared to previous combinations. An approximate midway response shows up with the fluctuating temperature. Table V gives the analysis of variance for the mummies produced. Again, statistically significant differences are indicated for temperatures, hosts and host x temperature interaction.

For all the above tests, Figures 7, 8, 9, 10, 11, and 12, in general, illustrate the host preference of A. asychis. The preference of A. asychis for the aphid species in descending order were: greenbug, corn leaf aphid, and yellow sugar cane aphid. This trend of preference was consistent at all temperatures, combinations of aphids, and when the parasite was caged with each aphid species individually.

The order of preference of A. asychis for the 3 aphid species in various combinations was approximately the same whether aphids were exposed to the parasites for 12 hours of light and 12 hours of darkness or for the entire life span of the parasite (Figs. 7, 8, 9, 10, 11, and 12). However, where parasites were caged with individual aphid species, preference of the parasite for the greenbug over the corn leaf aphid was not as pronounced (Fig. 7). While this difference was minimal when comparing the greenbug and corn leaf aphid, there was a uniform trend and a significant difference. Duncan's New Multiple Range Test indicated significant differences in the number of mummies produced when A. asychis was caged with the individual aphid species. This test showed the greenbug parasitized significantly more than the corn leaf aphid, and the corn leaf aphid parasitized significantly more than the yellow sugar cane aphid. In the field, A. asychis' preference for these 2 aphids may be based upon the searching behavior of the parasite and the habitat of the aphid (i.e., does A. asychis spend the most of its time searching in the whorls of the sorghum plant where the corn leaf aphid is found primarily or does it prefer to search on the under surface of the lower leaves where the highest greenbug population is found). Because of the low preference showed for S. flava in the laboratory, it is doubtful that A. asychis would parasitize this species in the field.

The varying degrees of host preference may be attributed to the nutritional value of the hosts as shown by Smith and Pimental (1969) who stated that nutrition of the host species is an important factor to consider in any population study of a parasite. One must assume that the habitat of the host and searching pattern of the parasite could also have an effect on the number of mummies produced from a particular host.

Although parasitism of the yellow sugar cane aphid was low in general, the highest parasitism of this aphid species occurred at the lowest temperature tested (23.9 C). This trend was consistent when the yellow sugar cane aphid was exposed by itself or in combination with either or both of the other aphid species. The number of aphids parasitized per cage was generally from 1-6 with a maximum of 30. The low rate of parasitism may be attributed to this aphid's large size, which makes the parasite's task of oviposition quite difficult (i.e., the aphid can drag the parasite around when the ovipositor is inserted). Also, S. flava has small spines on the dorsum (Ingram et al., 1951) which might result in less preference by the parasite. In addition, this aphid readily jumps or falls from the plant when approached by the parasite. If this aphid becomes a problem in the future, a strain of A. asychis might be developed through genetics which would parasitize this host more readily. Ingram et al. (1951) stated there were no known internal parasites of S. flava. However, Wolcott (1955) reported Lysiphlebus testaceipes (Cresson) as a parasite of S. flava in Puerto Rico. Stary (1965, 1966) reported Ephedrus plagiator (Nees) and Lysiphlebus arvicola Stary as parasites of Sipha spp. in Russia and Czechoslovakia, respectively. Jones (1915) listed Homalotylus obscurus as a parasite of S. flava. (The author of this manuscript doubts this last record.) Arnold (personal communication, Survey Entomologist, Oklahoma State University, Stillwater) surveyed for parasites of S. flava in 1968 in Oklahoma but found none.

The fecundity of A. asychis is illustrated in Tables VI and VII. The number of mummies varied by temperature, aphid combination, and interaction of temperature x aphid combination. However, there were definite trends. The greatest number of mummies was produced at 23.9 and 26.7 C when the greenbug and corn leaf aphid were in combination. Occasionally as many as 200 mummies were produced by one female. This finding compares with Hartley (1922) who stated A. semiflavus females could produce some 200 young.

Tables VI and VII are the per cent emergence of A. asychis for each aphid species. There was some difference in the per cent emergence by aphid species and temperature. The per cent emergence for the parasitized corn leaf aphid ranged from 65 to 76 per cent, greenbug from 59 to 82 per cent, and yellow sugar cane aphid from 57 to 80 per cent. In general, the highest per cent emergence for the mummies occurred at 23.9 and 26.7 C. The per cent emergence of A. asychis paralleled the emergence of the parasites of aphids on potatoes as Shands et al. (1965) estimated 60 to 90 per cent of the parasites emerged from parasitized aphids on potatoes with an overall average of 75 per cent.

Longevity

Figures 13 and 14 illustrate the mean longevity of A. asychis females caged with individual aphid species, and the mean longevity of the parasite when caged with the four aphid combinations. In general, the longevity decreased with increasing temperature and the 21.1-32.2 C alternating temperature yielded an approximate midway response. The mean longevity at 23.9 C was approximately 18 days as compared to 9 days at 32.2 C. This decline in longevity at the higher temperatures was nearly a straight line relationship from 23.9 to 32.2 C.

Maximum longevity at 23.9 C was 28 days and compares favorably to Flanders (1953) who reports Aphelinidae in general live about 30 days at 26.7 C. Schlinger and Hall (1959) reported A. semiflavus lived about 28 days at 21.1 C and 60% R. H. and less than 12 hours at 32.2 C and 25% R. H., while Force and Messenger (1964) stated that A. semiflavus lived about 29 days at 26.7 C and about 5 days at 32.2 C and 45-55% R. H. Flanders et al. (1961) reported that Coccophagus basalis Comp., a primary Aphelinid parasite of scale insects, lived 3 weeks at 26.7 C. The longevity of the parasite was about the same for the yellow sugar cane aphid, greenbug, and corn leaf aphid when caged separately at the constant and alternating temperatures. The only exception was at 32.2 C when the parasite lived about 4 days less when caged with the yellow sugar cane aphid as compared with the other two aphid species. Also, the longevity of the parasite was about the same when caged with an individual aphid species as when caged with two or more aphid species in combination. Ramaseshiah and Dharmadhikari (1969) found that A. semiflavus lived an average of 22 days when fed a honey solution. Aphelinus asychis longevity compares favorably to their findings, even though they were not fed honey after they were placed in cages for tests. One must assume that these laboratory findings approached more closely a field situation in that the parasite had to survive on moisture from the plant and its feeding on puncture holes made by the ovipositor in the young aphids. Hartley (1922) states that the A. semiflavus exhibited this same feeding trait.

Longevity determinations of A. asychis with these 3 sorghum aphid hosts was important for compiling various life table data and for correlating host and parasite life cycle patterns (Force and Messenger, 1964).

Developmental Period

Table VIII indicates the development time for A. asychis along with the standard errors. There were a few hours difference in developmental period of the male as compared to the female A. asychis. However, in all cases, the first parasites to emerge were males. Then, 1 to 2 days later, females emerged and continued to emerge for 3 to 5 days, depending upon the temperature. The parasite took about 16 days to develop at 23.9 C and approximately 10 days at 32.2 C in both the greenbug and corn leaf aphid hosts. Flanders (1953) stated that Aphelinids in general have a developmental period of 15-30 days. The findings of Force and Messenger (1964) indicate the duration of A. semiflavus and A. asychis are quite similar (about 18 days for A. semiflavus to develop at 21.1 C and 10 days at 32.2 C). The alternating temperatures gave an approximate midway response in regard to developmental time. The parasite took 1 to 2 days longer to develop in the yellow sugar cane aphid as compared to the greenbug and corn leaf aphid at the temperatures tested.

Force and Messenger (1964) reported that the more rapidly a parasite can develop to maturity, the more rapidly can it be expected to increase in numbers sufficient to decrease the population growth of the host. They further stated that determining such life factors help in calculating reproductive rates, capacities for increase, and in correlating host and parasite life cycle patterns. For example, Hunter (1909) stated that at summer temperatures, Toxoptera graminum lived about 35 days in the laboratory with an average of 55 offspring or 2.43 aphids/day. A. asychis took approximately 12 days to develop with a mean of 38 mummies produced and roughly 68% females emerging at 21.1-32.2 C. One may assume that the A. asychis, all things being equal, might overtake its host in one generation. One can see how laboratory studies may be used to help better analyze and evaluate field evaluations and the manipulations of the parasite for biological control.

Sex Ratio

Parasitic Hymenoptera are capable of increasing their host-finding abilities with decreasing host populations. An increasing number of females is usually realized with low host densities, an attribute which may account for the effectiveness of many species. Predetermination of sex in the Hymenoptera is brought about by the fact that normal males develop only from haploid eggs and normal females only from diploid eggs. In biparental species, the female is generally the result of the fertilization of the haploid egg. Stored sperm in the parent female spermatheca accomplishes this fertilization. The control of sex, therefore, is accomplished by the facultative response of the spermathecal gland to environmental stimuli associated with oviposition (Flanders, 1962).

In some parasitic Hymenoptera the oviposition posture or stance of the female can determine the sex of the deposited eggs. When the female stands on top of the host and prepares to insert her ovipositor vertically into the host, the egg will be fertilized, yielding a female. Standing beside the host and thrusting the ovipositor horizontally beneath the host's body yields an unfertilized egg. In other Hymenoptera the spermathecal gland is large enough to produce enough sperm for fertilization of all eggs. Certain temperatures, humidities and hosts inhibit spermathecal gland stimulation without affecting the number of eggs deposited.

The Hymenoptera female is blessed with a highly specialized ovipositor for depositing eggs in otherwise inaccessible hosts. Female parasites are able to prolong the number of eggs deposited per host as well as their capacity to increase the proportion of female progeny as the host population density decreases, by sex control of stored sperm. In general, the parasite's efficiency in oviposition is usually not bothered by a low host density, the host receiving no more eggs than can develop to maturity.

Sorghum Greenbug, Corn Leaf Aphid, and Yellow Sugar Cane Aphid Individual Tests

Statistically significant differences were found for temperatures, hosts, host x temperature, and sex for the parasites produced in these tests (Table IX). These results were similar to those found when the same aphid species were in combination (Table XIII).

Figure 15 illustrates parasites produced by *A. asychis* when caged with each of the 3 aphid hosts. The proportion of females remained approximately the same as obtained in the 3-host combination. The number of corn leaf aphid parasites produced increased in separate tests while the number of greenbugs remained relatively the same over all temperatures and combinations.

Sorghum Greenbug + Corn Leaf Aphid Combination

An analysis of variance was run on the parasites emerging from this 2-host combination at 5 controlled temperatures (Table X). Statistically significant differences were found for temperatures, hosts, host x temperature interaction, sex and sex x temperature interaction. This further substantiates the finding of a greater ratio of females emerging from sorghum greenbug hosts. Figure 16 illustrates the mean number of males and females produced for each host at each temperature. One interesting factor is that the female ratio is higher for the sorghum greenbug host as compared to the corn leaf aphid host.

More females were produced at 29.4 C from corn leaf aphid hosts than at any other temperature.

Sorghum Greenbug + Yellow Sugar Cane Aphid Combination

Figure 17 indicates that the male:female ratio is closer for the sorghum greenbug than in the previous sorghum greenbug + corn leaf aphid combination. The yellow sugar cane aphid mummies yielded mostly females. DeBach (1965) reported a similar finding in that *Aphycus helvolus* (Comp.) increased its proportion of females directly with an increase in host size. The parasites produced were subjected to an analysis of variance (Table XI), giving statistically significant differences for temperatures, hosts, host x temperature interaction and sex.

Corn Leaf Aphid + Yellow Sugar Cane Aphid Combination

Figure 18 indicates that the female ratio was higher for corn leaf aphid than when the corn leaf aphid was in combination with the sorghum greenbug. Again, one notes that the few yellow sugar cane aphid parasites were almost all female. An approximate midway response was shown for the fluctuating temperature.

Table XII shows the analysis of variance for the parasites emerging from these two aphid hosts and depicts statistically significant differences for the 2 temperatures, 2 hosts, host x temperature interaction, sex and sex x host interaction. The latter difference was statistically significant for the first time and one can note that in Figure 13 there was a greater ratio of female parasites emerging from corn leaf aphid hosts caged alone than from corn leaf aphids in combination with sorghum greenbug (Fig. 11).

Sorghum Greenbug + Corn Leaf Aphid + Yellow Sugar Cane Aphid Combination

Figure 19 illustrates that the female ratio is again highest for sorghum greenbug in competition with corn leaf aphid. There was a very small response for yellow sugar cane aphid, with the majority of these being female.

Table XIII gives the analysis of variance for parasites produced in this 3-aphid combination and shows statistically significant difference for the 5 temperatures, 3 hosts, host x temperature interaction and sex. There was no interaction with sex, host and temperature, as was the case for the previous combinations. One must assume here that there are no statistically significant interactions with sex in the 3-aphid combination.

Table XIV indicates the general trend in the sex ratio of *A. asychis* for combinations of aphids, and 5 controlled temperatures. Figure 20 illustrates the sex ratio of the parasite when the aphid hosts are combined for each temperature. In Figure 20 one may note a fairly predictable trend in that as the temperature increases the female:male ratio becomes smaller. The highest number of females to males occurred at the coolest temperature (23.9 C) with approximately 2.4 females to one male and at 32.2 C the ratio was nearly 1:1. In all aphid combinations and temperatures, however, there were more females than males produced. The emerging parasites were approximately 60 per cent females when averaged over all temperatures for each species of aphid. Clausen (1939) and Flanders (1942) point out that in the parasitic Hymenoptera, the sex ratio varies with the sex ratio of the host and with different hosts. Flanders (1939) reported that at a high rate of oviposition eggs may escape fertilization. He further stated that the sex ratio decreased with increased temperature. This disagrees with the A. asychis sex ratio averaged over all temperatures.

The alternating temperatures did not give a midway response for the production of females in comparison to the constant temperatures. This suggests that the high temperatures might be more detrimental to the developing parasites. Schlinger and Hall (1959) reported the production of A. semiflavus females decreased with increasing temperatures, while Force and Messenger (1964) reported all emerging A. semiflavus were males at 32.2 C. The strain of A. asychis produced over 50% females for all hosts and temperatures except in one case with the yellow sugar cane aphid at 32.2 C. However, the number of yellow sugar cane aphids parasitized was too low to draw a valid conclusion on the sex ratio of the parasites emerging from this aphid species. The major portion of parasites emerging from this aphid host were females. This is quite similar to the findings of Clausen (1939) who stated that one of the important factors influencing the sex ratio is the size of the host in which the parasite develops (i.e., large host favors female parasite).

Virgin female parasites were caged with the greenbug to determine if mating was necessary to produce female offspring. In all tests at the five controlled temperatures only male offspring were produced from virgin female parasites. The A. asychis sent from the USDA European Parasite Laboratory may well be another geographic strain than that reported by Force and Messenger (1968) who stated that A. asychis = A.

semiflavus. The main criterion used for this separation in this case is that A. asychis parasites used in this study required mating for the production of females while A. semiflavus did not.

Intraspecific Competition

Aphelinus asychis has a rather interesting method of ovipositing (Fig. 21). It usually approaches the aphid from the rear and stops when its antennae touch the prospective host. After a few seconds, it does an about-face, rises up on its legs, and thrusts the ovipositor out and downward toward the aphid. Several attempts are usually required before the parasite's ovipositor finds its mark, usually on the dorsal surface of the aphid's abdomen. If the aphid is too large, the parasite is dragged around because the barbs on its ovipositor (Hartley, 1922) keep it from releasing. One parasite in these intraspecific studies had this same problem. Another parasite, seemingly sensing the other's plight, mounted the ovipositing parasite and provided enough weight to keep the aphid from moving about.

Generally, A. asychis oviposits in a host that no other parasite is simultaneously ovipositing. However, in one instance, 2 A. asychis were seen ovipositing in the same host, one in the dorsal abdomen and the other in the dorsal thorax of the host. Hartley (1922) provided a detailed account of the oviposition behavior of A. semiflavus, and A. asychis had a great many similarities to this.

In dissections of mummies produced at both constant temperatures, no more than one egg per host was found. Hartley (1922) stated that in 3000 dissections there were only 2-3 cases when more than 1 egg was deposited per host by A. semiflavus. One must conclude that superparasitism among A. asychis did not occur in these tests.

Table XV is the analysis of variance for the mummies produced by A. asychis. The only significant difference found is in the temperature x parasite interaction. Table XVI gives evidence of the interaction in that there is a greater difference between the mummies produced by the 2 parasites per pot than at any other parasite density when comparing both temperatures. The number of mummies produced with 4 and 8 parasites per pot at both test temperatures is approximately the same. In other words, the efficiency of A. asychis did not improve appreciably with increasing parasite numbers both within and between temperatures. DeBach and Sisojevic (1960) reported that Aphytis lingnanensis Compere, a scale parasite, responded in the same way. These authors stated that the mean progeny per adult female decreased with increasing densities. One notes similarities in Table XVI where the mean progeny per adult female at 23.9 C ranges from 10-4 and from 6-2 at 32.2 C.

The sex ratio was not appreciably affected by increasing densities. It remains about 2:1 at 23.9 and a varying amount over 1:1 at 32.2 C. One may conclude that even though the efficacy of A. asychis does not increase with increasing densities and temperatures, a stable sex ratio could mean a great deal to possible success in a field situation. DeBach and Sisojevic (1960) indicated A. lingnanensis is, like A. asychis, a biparental species producing about 50% males with increasing densities. This would give it a disadvantage when comparing it to A. asychis's 2:1 ratio.

The highest number of mummies was produced with a parasite density of 8 at both temperatures. Force and Messenger (1965) found that A. semiflavus parasitized from 40-49 hosts with 3 parasites per test and from 25-40 with 1 parasite. What is indicated here is that even though more mummies are produced with increasing densities, the amount is not significant in regards to the total efficiency of each of the parasite densities.

The per cent emergence decreases with increasing parasite densities and this would lead one to believe that some of the ovipositional habits (i.e., 2 parasites parasitizing simultaneously) increase directly with density resulting in fewer *A. asychis* reaching the adult stage.

SUMMARY

Laboratory studies of _A. asychis_ were conducted on host preference, adult longevity, duration of development, sex ratio and intraspecific competition at 5 controlled temperatures. The preference of _A. asychis_ for hosts in descending order were: greenbug, corn leaf aphid, and yellow sugar cane aphid. This trend of preference for these 3 hosts was consistent for all combinations of aphid species and temperature. Adult longevity was greater at the low temperatures than at the higher temperatures. The mean longevity was approximately 18 days at 23.9 C and 9 days at 32.2 C. The duration of development time was approximately 16 days at 23.9 C and 10 days at 32.2 C for the greenbug and corn leaf aphid. Developmental time for _A. asychis_ was 1 to 2 days longer when the yellow sugar cane aphid was the host. A greater number of female progeny was produced per adult female parasite at the lowest temperature tested. An increase in temperature resulted in a greater number of male progeny per adult female _A. asychis_. Virgin females produced only male progeny.

In intraspecific tests, no superparasitism was found. The efficiency of _A. asychis_ did not improve with increasing densities. The sex ratio was not changed with increasing densities. Per cent emergence dropped off with increasing densities. The threshold 32.2 C temperature did not appreciably decrease the number of mummies produced but changed the sex ratio from 2:1 to 1:1.

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APPENDIX

Table I. Analysis of variance for *Aphelinus asychis* mummies produced from individual tests of 3 sorghum aphids at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	149	1.51**
Temperature	4	23.99**
Host	2	.40**
Host x Temperature	8	
Error A	135	

**Significant at 1 per cent level.

Table II. Analysis of variance for mummies produced by *Aphelinus asychis* with sorghum greenbug + corn leaf aphid hosts at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	99	2.33**
Temperature	4	.07
Error A	45	
		3.54**
Hosts	1	.26**
Hosts x Temperature	4	.04
Error B	45	

**Significant at 1 per cent level.

Table III. Analysis of variance for mummies produced by *Aphelinus asychis*, with sorghum greenbug + yellow sugar cane aphid hosts, at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	99	
Temperature	4	.46**
Error A	45	.03
Hosts	1	58.07**
Hosts x Temperature	4	.35**
Error B	45	.06

**Significant at 1 per cent level.

Table IV. Analysis of variance for mummies produced by *Aphelinus asychis* with corn leaf aphid + yellow sugar cane aphid hosts, at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	99	
Temperature	4	.44**
Error A	45	.02
Hosts	1	52.21**
Hosts x Temperature	4	.33**
Error B	45	.02

**Significant at 1 per cent level.

Table V. Analysis of variance for mummies produced by *Aphelinus asychis* with sorghum greenbug + corn leaf aphid + yellow sugar cane aphid hosts, at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	149	
Temperature	4	1.71**
Error A	45	.08
Hosts	2	22.16**
Host x Temperature	8	.45**
Error B	90	.06

**Significant at 1 per cent level.

Table VI. Response of *Aphelinus asychis* to 4 combinations of corn leaf aphid, sorghum greenbug, and yellow sugar cane aphid, at 5 controlled temperatures.

Temperature °C	No. Mummies Low	No. Mummies High	No. Mummies Mean	No. Parasites Low	No. Parasites High	No. Parasites Mean	Per Cent Emergence
			Corn Leaf Aphid + Greenbug				
23.9	48	201	111	30	167	82	74
26.7	45	180	118	29	148	94	80
29.4	25	173	94	20	127	69	74
32.2	8	34	15	2	29	11	69
21.1-32.2	20	101	79	13	63	51	65
			Corn Leaf Aphid + Yellow Sugar Cane Aphid				
23.9	33	90	50	28	60	38	75
26.7	38	91	55	32	76	44	81
29.4	19	80	42	15	52	30	74
32.2	6	25	11	4	14	7	64
21.1-32.2	15	60	31	10	44	22	72
			Greenbug + Yellow Sugar Cane Aphid				
23.9	49	111	76	35	110	57	75
26.7	33	140	75	25	112	58	77
29.4	20	134	73	11	130	58	79
32.2	10	27	17	8	20	10	57
21.1-32.2	40	120	67	25	90	48	71
			Greenbug + Corn Leaf Aphid + Yellow Sugar Cane Aphid				
23.9	50	148	92	39	120	68	74
26.7	20	117	85	14	92	67	79
29.4	15	138	71	12	110	52	73
32.2	5	26	11	3	14	7	60
21.1-32.2	16	112	57	14	87	36	63

Table VII. Response of <u>Aphelinus asychis</u> to corn leaf aphid, sorghum greenbug, and yellow sugar cane aphid, at 5 controlled temperatures.

Temperature °C	No. Mummies			No. Parasites			Per Cent Emergence
	Low	High	Mean	Low	High	Mean	
			Corn Leaf Aphid				
23.9	20	112	52	18	81	39	76
26.7	54	132	79	25	88	58	74
29.4	16	70	31	16	52	22	70
32.2	9	30	19	6	22	13	65
21.1-32.2	14	58	31	13	49	23	76
			Greenbug				
23.9	35	121	82	25	100	64	79
26.7	40	139	89	31	117	72	82
29.4	23	56	41	18	47	29	73
32.2	9	35	20	8	27	15	75
21.1-32.2	20	46	38	19	28	22	59
			Yellow Sugar Cane Aphid				
23.9	2	30	10	2	21	7	72
26.7	2	2	1	1	2	.8	80
29.4	1	4	1	1	3	.7	70
32.2	1	6	2	2	4	2	73
21.1-32.2	1	2	.7	1	2	.4	57

Table VIII. Effect of temperature on the development of Aphelinus asychis on 3 aphid hosts at 5 controlled temperatures.

Temperature °C	Mean Development Period (Days)		
	Sorghum Greenbug	Corn Leaf Aphid	Yellow Sugar Cane Aphid
23.9	15.8 ± .66	16.6 ± .66	17.4 ± 1.19
26.7	12.8 ± .60	12.3 ± .90	14.2 ± .94
29.4	10.6 ± .49	11.8 ± .67	12.5 ± 1.38
32.2	10.2 ± .60	9.5 ± .40	11.2 ± .28
21.1-32.2	12.5 ± .67	12.4 ± 1.45	13.0 ± .45

Table IX. Analysis of variance for Aphelinus asychis parasites emerging from individual tests involving 3 sorghum aphids at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	299	
Temperature	4	2.46**
Host	2	31.44**
Host x Temperature	8	.55**
Error A	135	.07
Sex	1	1.33**
Sex x Host	2	.07
Sex x Temperature	4	.08
Sex x Host x Temperature	8	.04
Error B	135	.05

** Significant at 1 per cent level.

Table X. Analysis of variance for <u>Aphelinus asychis</u> parasites emerging from sorghum greenbug + corn leaf aphid hosts at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	199	
Temperature	4	4.26**
Error A	45	.22
Hosts	1	6.63**
Hosts x Temperature	4	.54**
Error B	45	.13
Sex	1	1.53**
Sex x Temperature	4	.11**
Sex x Host	1	.04
Sex x Host x Temperature	4	.04
Error C	90	.02

**Significant at 1 per cent level.

Table XI. Analysis of variance for <u>Aphelinus asychis</u> parasites emerging from sorghum greenbug + yellow sugar cane aphid hosts at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	199	
Temperature	4	1.00**
Error A	45	.07
Hosts	1	74.51**
Host x Temperature	4	.79**
Error B	45	.09
Sex	1	.66**
Sex x Temperature	4	.02
Sex x Host	1	.14
Sex x Host x Temperature	4	.002
Error C	90	.02

**Significant at 1 per cent level.

Table XII. Analysis of variance for Aphelinus asychis parasites emerging from corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	199	
Temperature	4	.73**
Error A	45	.05
Hosts	1	55.65**
Hosts x Temperature	4	.73**
Error B	45	.05
Sex	1	.67**
Sex x Temperature	4	.08
Sex x Host	1	.50**
Sex x Host x Temperature	4	.04
Error C	90	.01

**Significant at 1 per cent level

Table XIII. Analysis of variance for Aphelinus asychis parasites emerging from sorghum greenbug + corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

Source of Variation	Degrees of Freedom	Mean Square
Total	299	
Temperature	4	2.22**
Error A	45	.20
Hosts	2	23.60**
Hosts x Temperature	8	.69**
Error B	90	.15
Sex	1	.93**
Sex x Temperature	4	.08
Sex x Host	2	.04
Sex x Host x Temperature	8	.05
Error C	135	.03

**Significant at 1 per cent level.

Table XIV. Per cent female *Aphelinus asychis* for all combinations of the sorghum greenbug, corn leaf aphid, and yellow sugar cane aphid at 5 controlled temperatures.

Aphids	Temperature °C				
	23.2	26.7	29.4	32.2	21.1-32.2
Caged separately with Parasite:					
Greenbug	63	57	58	53	68
Corn Leaf Aphid	64	54	68	61	52
Yellow Sugar Cane Aphid	57	50	86	44	75
Combination with Parasite:					
Greenbug and Corn Leaf Aphid	65	61	68	54	59
Greenbug and Yellow Sugar Cane Aphid	61	62	55	60	60
Corn Leaf Aphid and Yellow Sugar Cane Aphid	71	70	57	57	59
Corn Leaf Aphid, Greenbug, Yellow Sugar Cane Aphid	65	66	64	57	53

Table XV. Analysis of variance for the mummies produced by *Aphelinus asychis* in intraspecific competition studies.

Source of Variation	Degrees of Freedom	Mean Squares
Total	59	
Replications	1	81.6667
Temperatures	1	153.6000
Error A	1	187.2667
Blocks	4	157.0833
Blocks x Temperatures	4	69.5167
Error B	8	118.2167
Parasites	2	56.1167
Temperature x Parasites	2	160.5500*
Blocks x Parasites	8	88.0958
Temperature x Block x Parasite	8	88.7792
Error C	20	88.2167

*Significant at the .25 level.

Table XVI. Response of *Aphelinus asychis* in intraspecific competition studies conducted at 2 constant temperatures (23.9 C optimum, 32.2 C threshold).

Number Parasites Per Pot	Mummies			Progeny			Sex Ratio		Per Cent Emergence
	Low	High	Mean	Low	High	Mean	♀	♂	
					23.9° C				
2	11	42	26	9	38	21	14	7	80
4	18	36	21	9	30	16	11	5	79
8	15	50	23	12	43	16	11	5	70
					32.2° C				
2	8	40	18	6	30	13	7	6	72
4	11	34	23	7	25	16	10	6	70
8	11	47	23	9	36	16	9	7	70

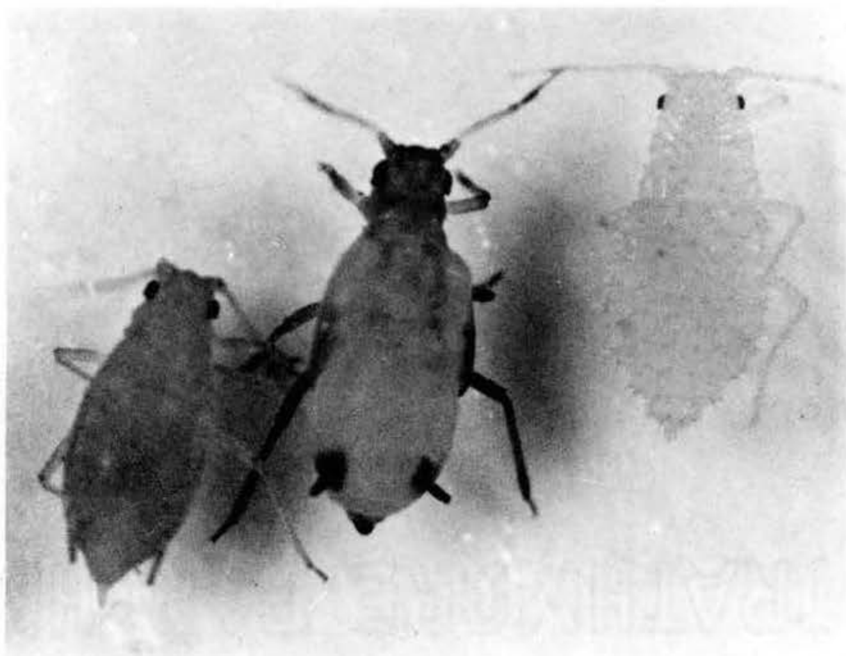

Figure 1. Aphids utilized as hosts in laboratory evaluations involving *Aphelinus asychis* (greenbug, corn leaf aphid, yellow sugar cane aphid, respectively).

Figure 2. Greenbugs dispersed on sorghum leaf 2-3 hours after hand inoculation.

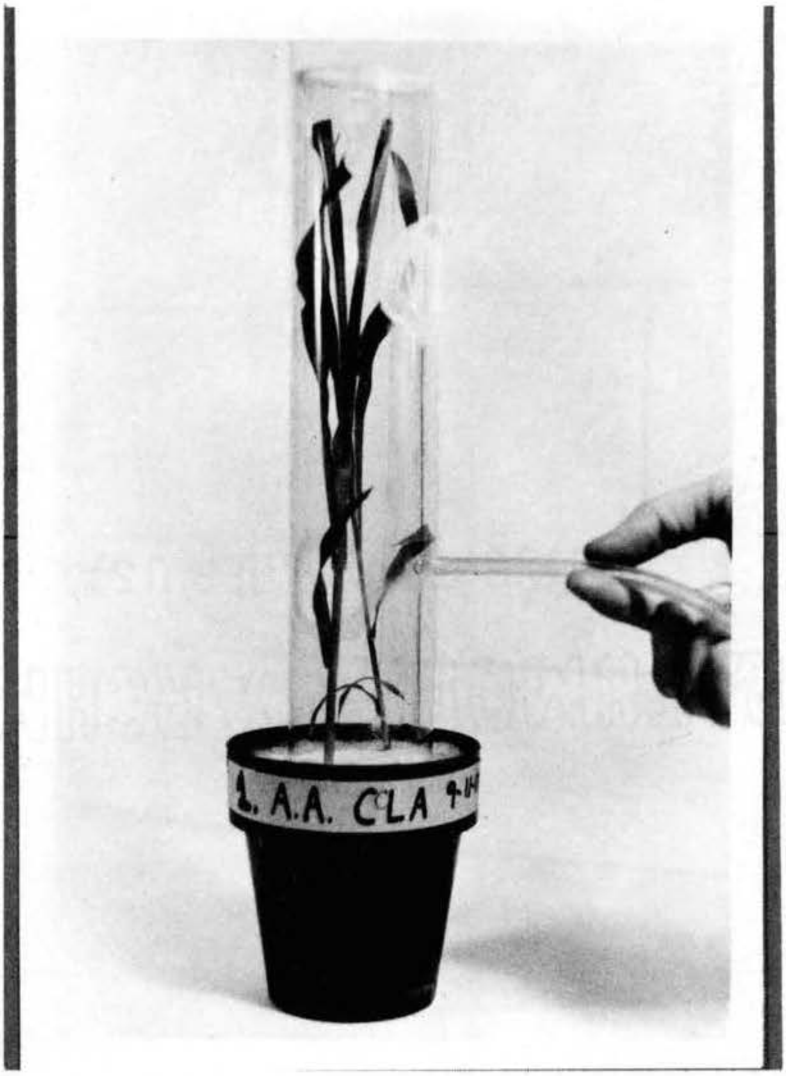

Figure 3. Sorghum plant, 4-inch pot, cellulose nitrate cage, ventilation holes, white sand and mouth aspirator utilized in studies of Aphelinus asychis.

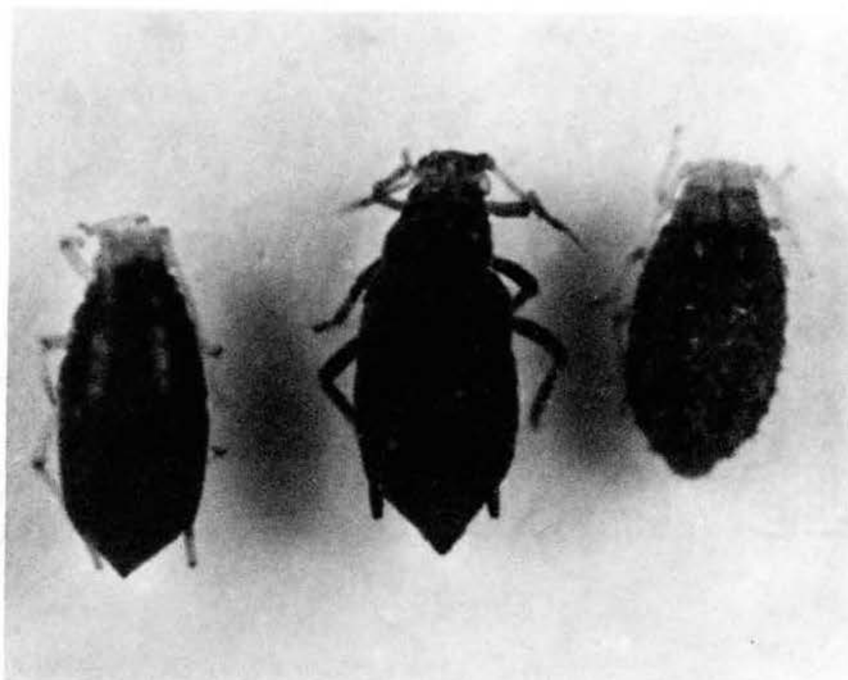

Figure 4. Mummies produced by Aphelinus asychis parasitization (greenbug, corn leaf aphid, yellow sugar cane aphid, respectively).

Figure 5. Aphelinus asychis emerging from a mummified host.

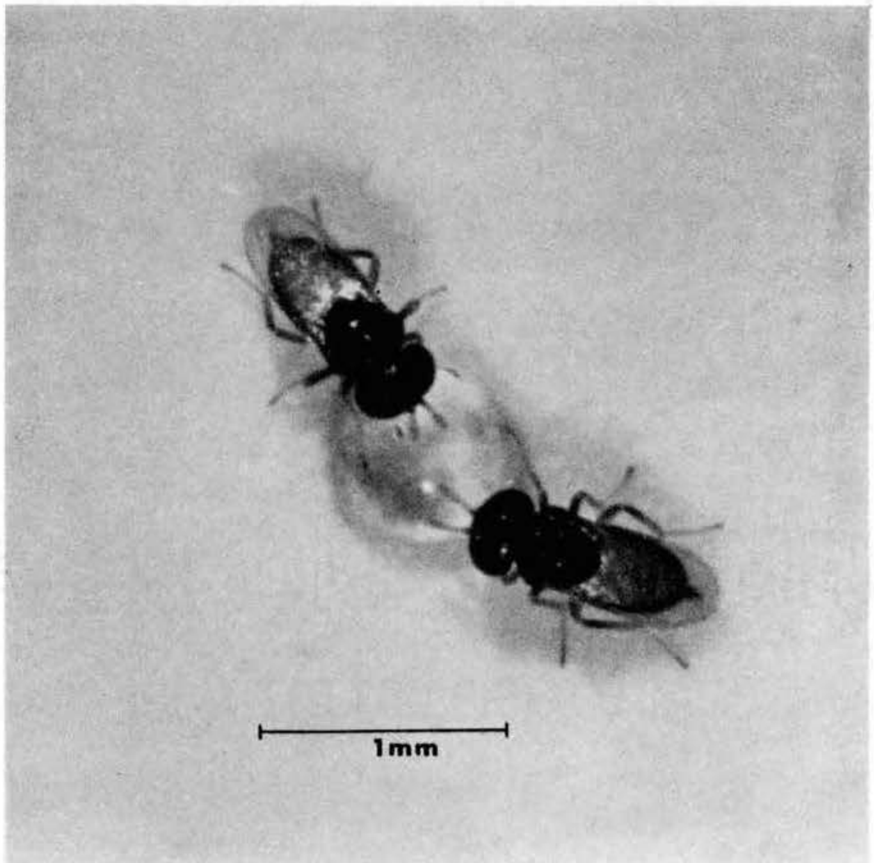

Figure 6. Aphelinus asychis females feeding on a honey droplet.

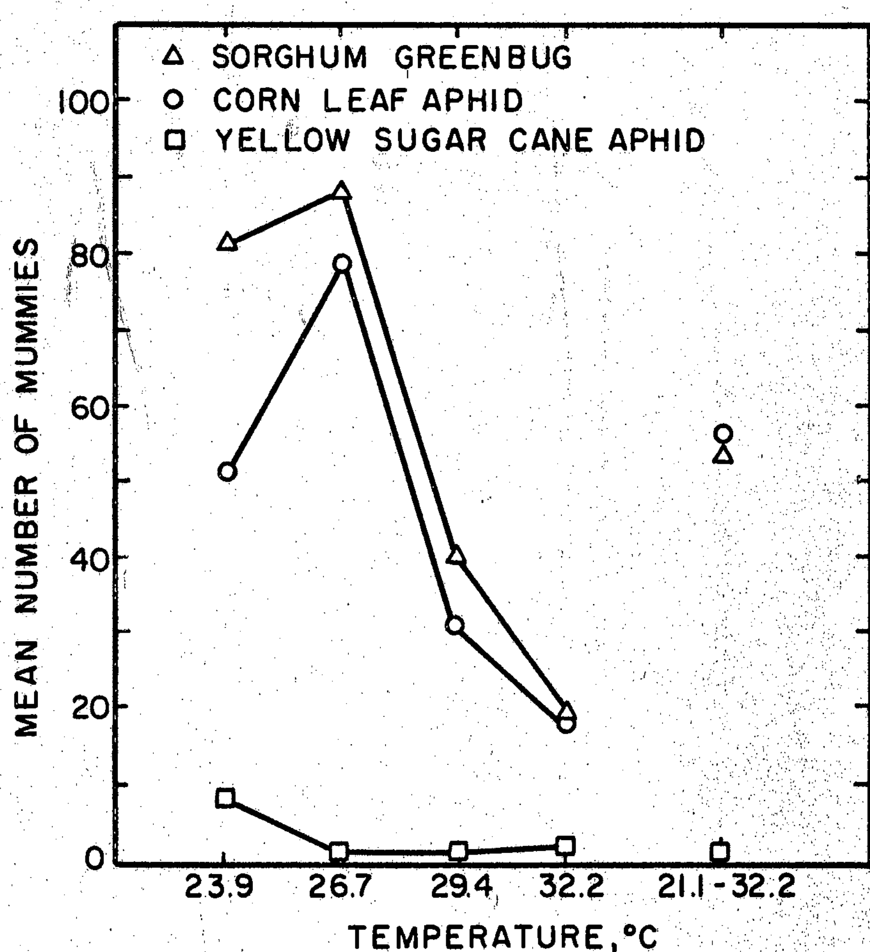

Figure 7. Mummies produced by <u>Aphelinus asychis</u> when caged with each of 3 aphid species at 5 controlled temperatures.

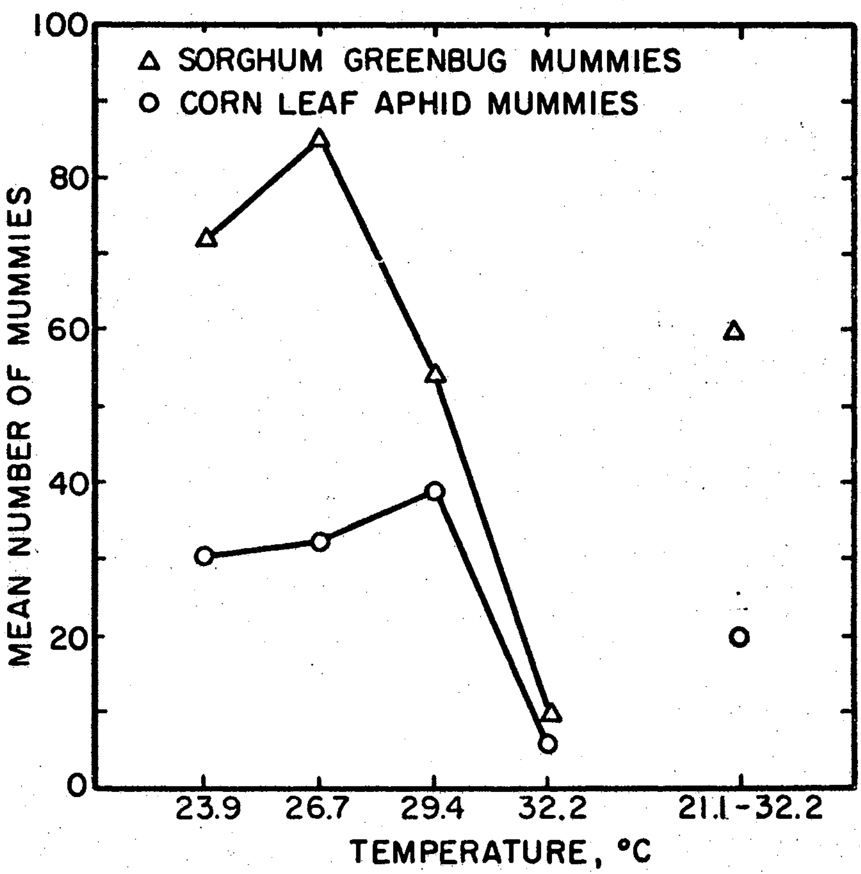

Figure 8. Mean number of mummies produced by *Aphelinus asychis* with sorghum greenbug + corn leaf aphid hosts at 5 controlled temperatures.

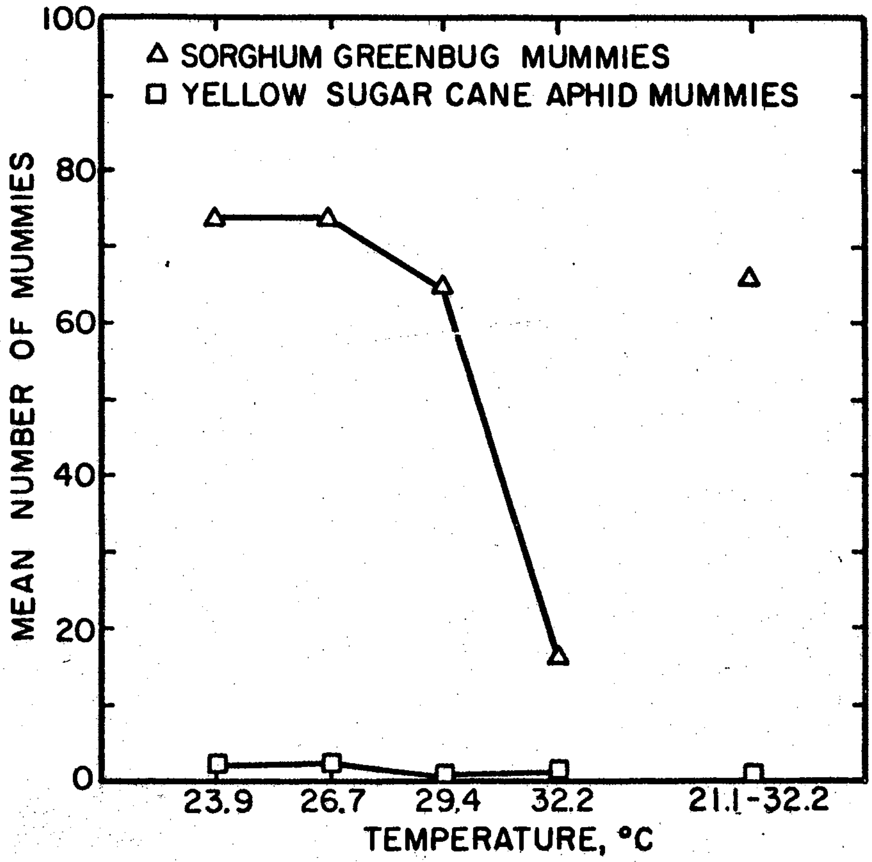

Figure 9. Mean number of mummies produced by Aphelinus asychis with sorghum greenbug + yellow sugar cane aphid hosts at 5 controlled temperatures.

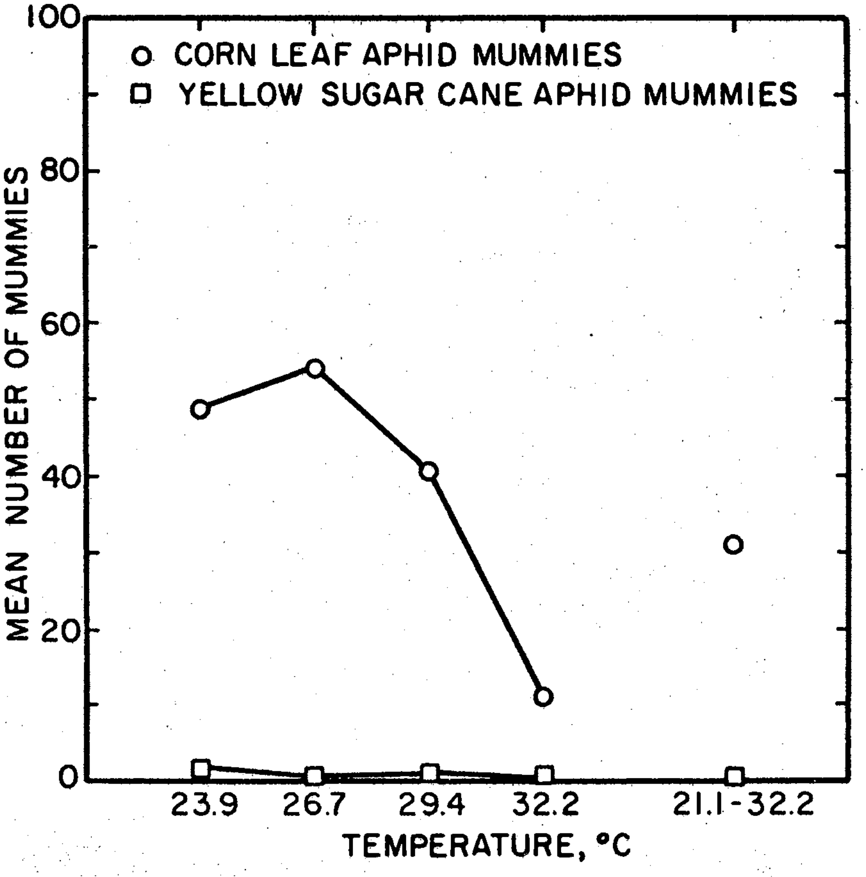

Figure 10. Mean number of mummies produced by *Aphelinus asychis* with corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

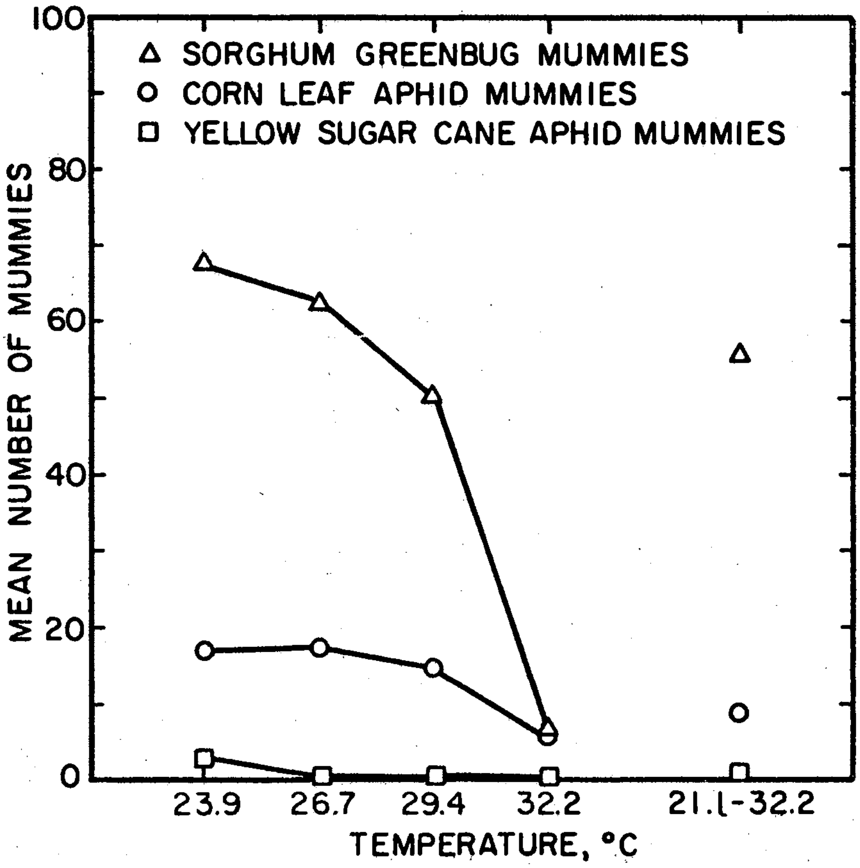

Figure 11. Mean number of mummies produced by *Aphelinus asychis* with sorghum greenbug + corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

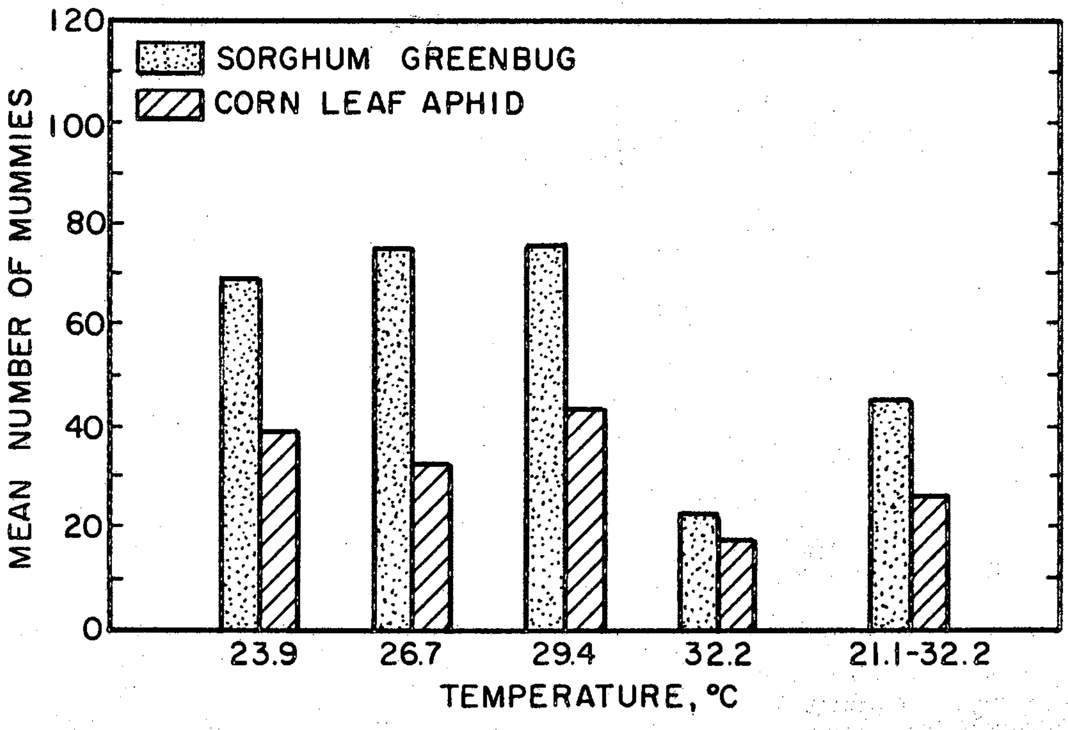

Figure 12. Mummies produced by Aphelinus asychis when caged for 12 hours of light and 12 hours of darkness with corn leaf aphid + sorghum greenbug at 5 controlled temperatures.

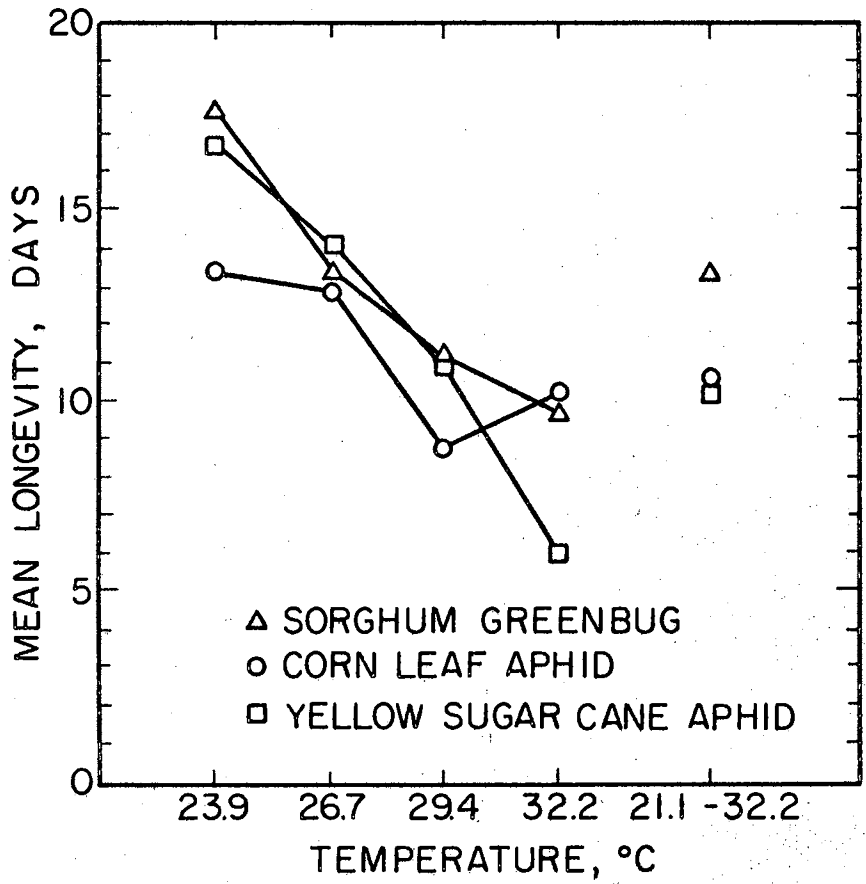

Figure 13. Mean longevity of Aphelinus asychis when caged with each of three aphid species at 5 controlled temperatures.

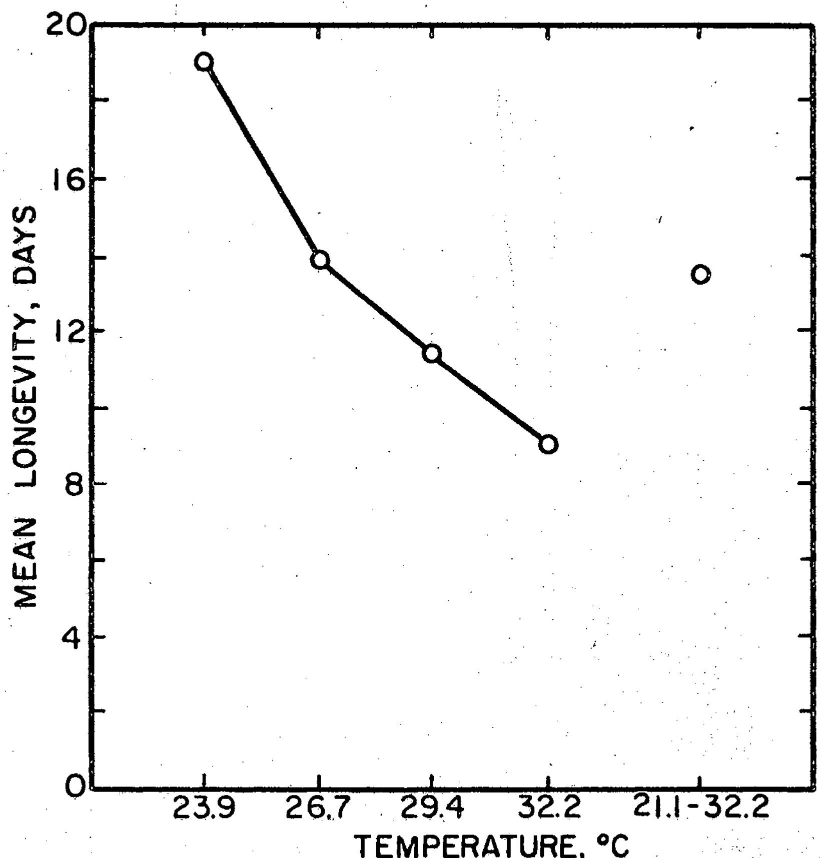

Figure 14. Mean longevity for *Aphelinus asychis* on 4 combinations of 3 aphid hosts on sorghum at 5 controlled temperatures.

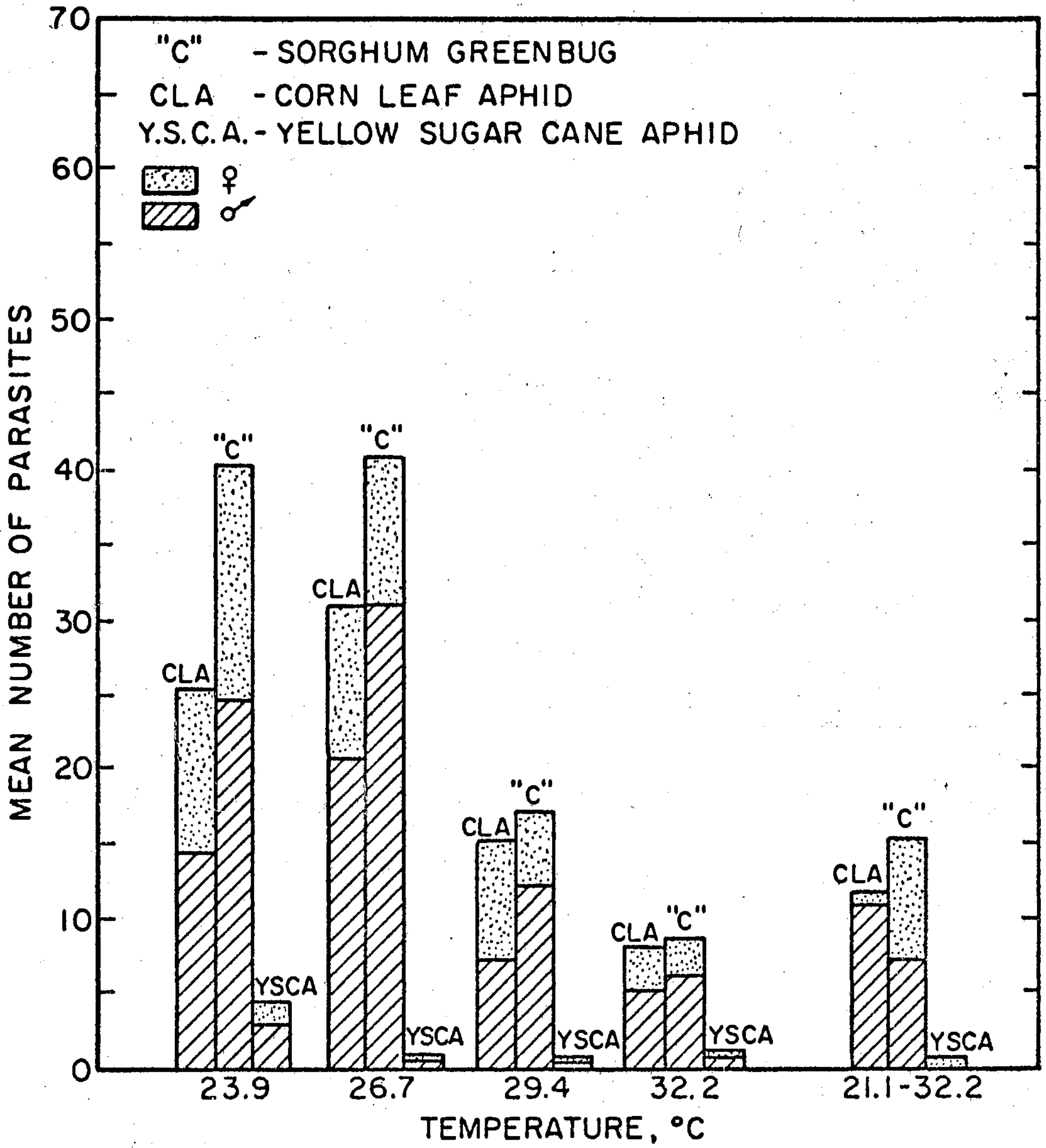

Figure 15. Mean number of male and female Aphelinus asychis emerging from individual tests involving 3 sorghum aphids at 5 controlled temperatures.

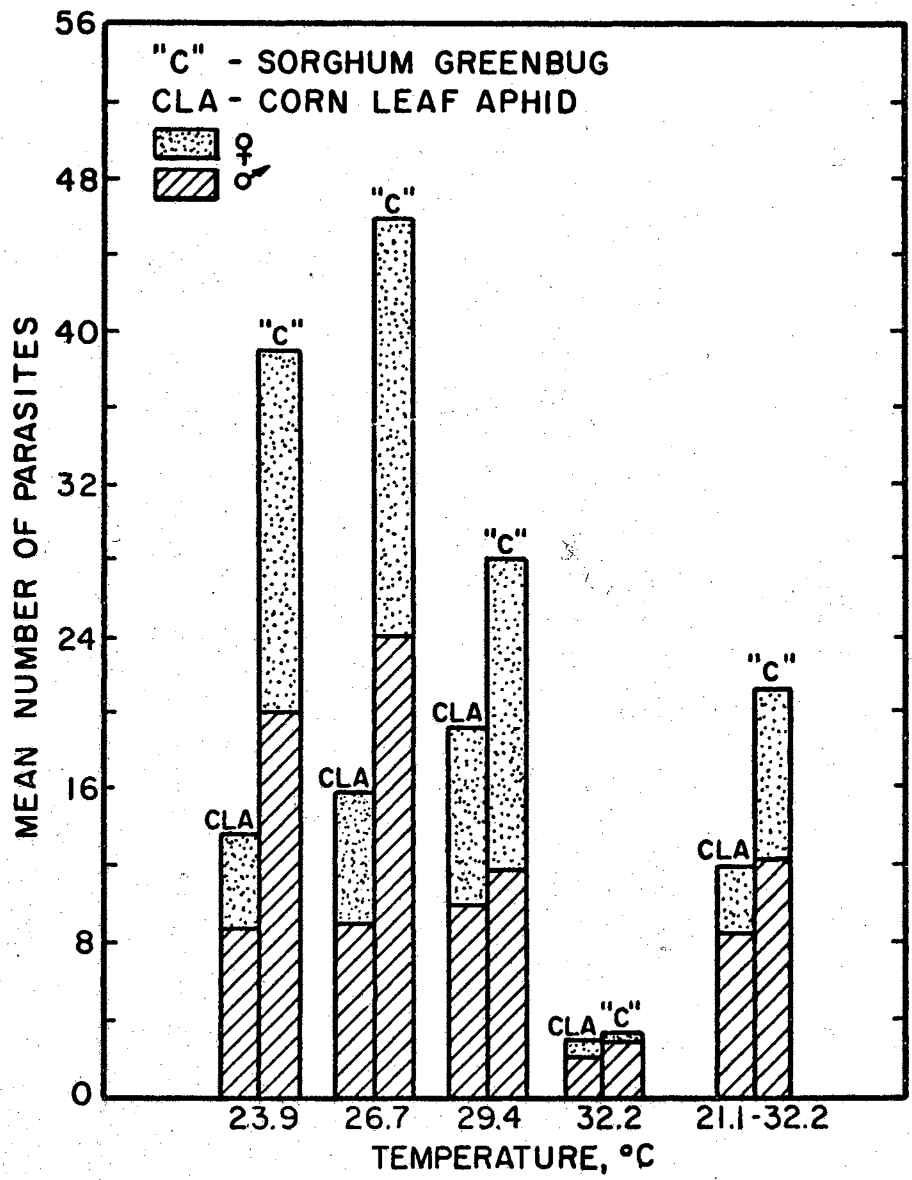

Figure 16. Mean number of male and female Aphelinus asychis emerging from sorghum greenbug + corn leaf aphid hosts at 5 controlled temperatures.

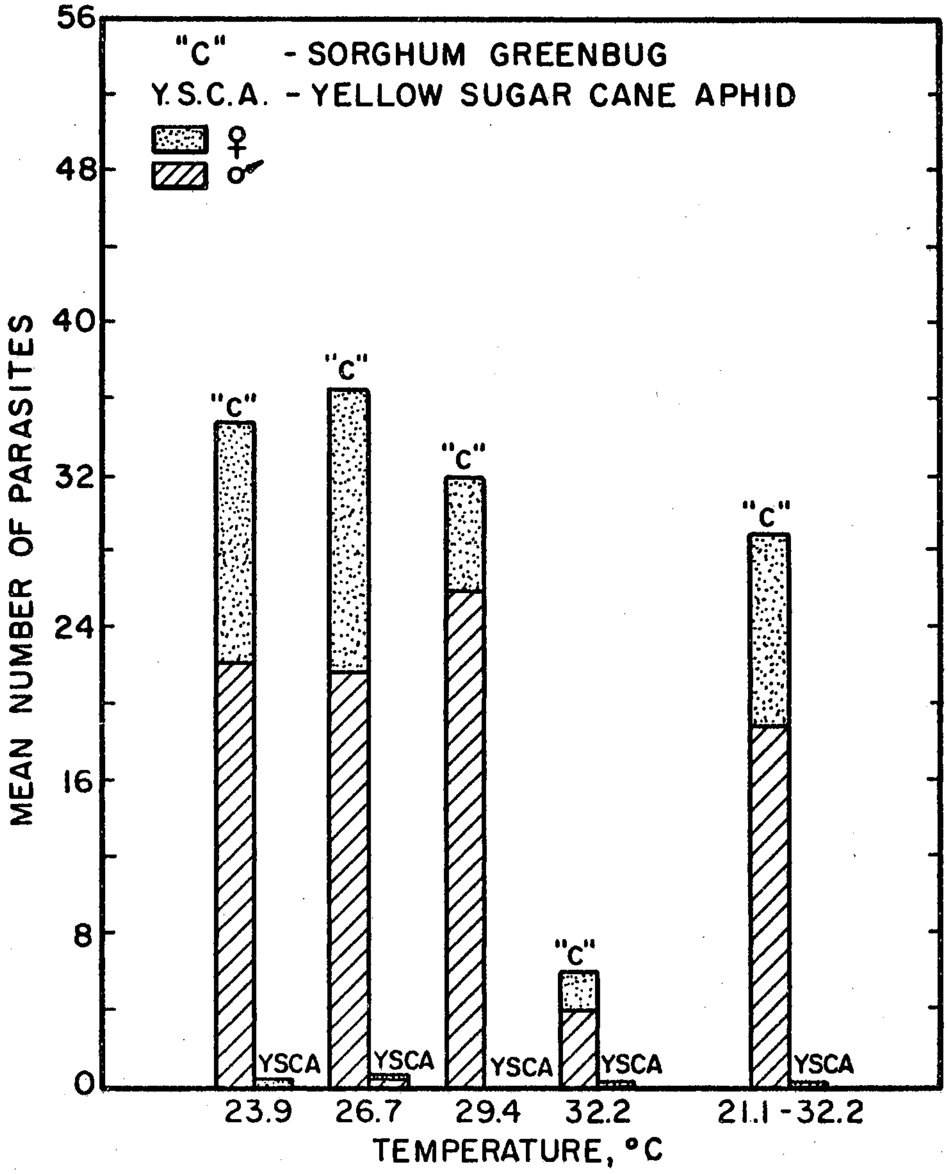

Figure 17. Mean number of male and female Aphelinus asychis emerging from sorghum greenbug + yellow sugar cane aphid hosts at 5 controlled temperatures.

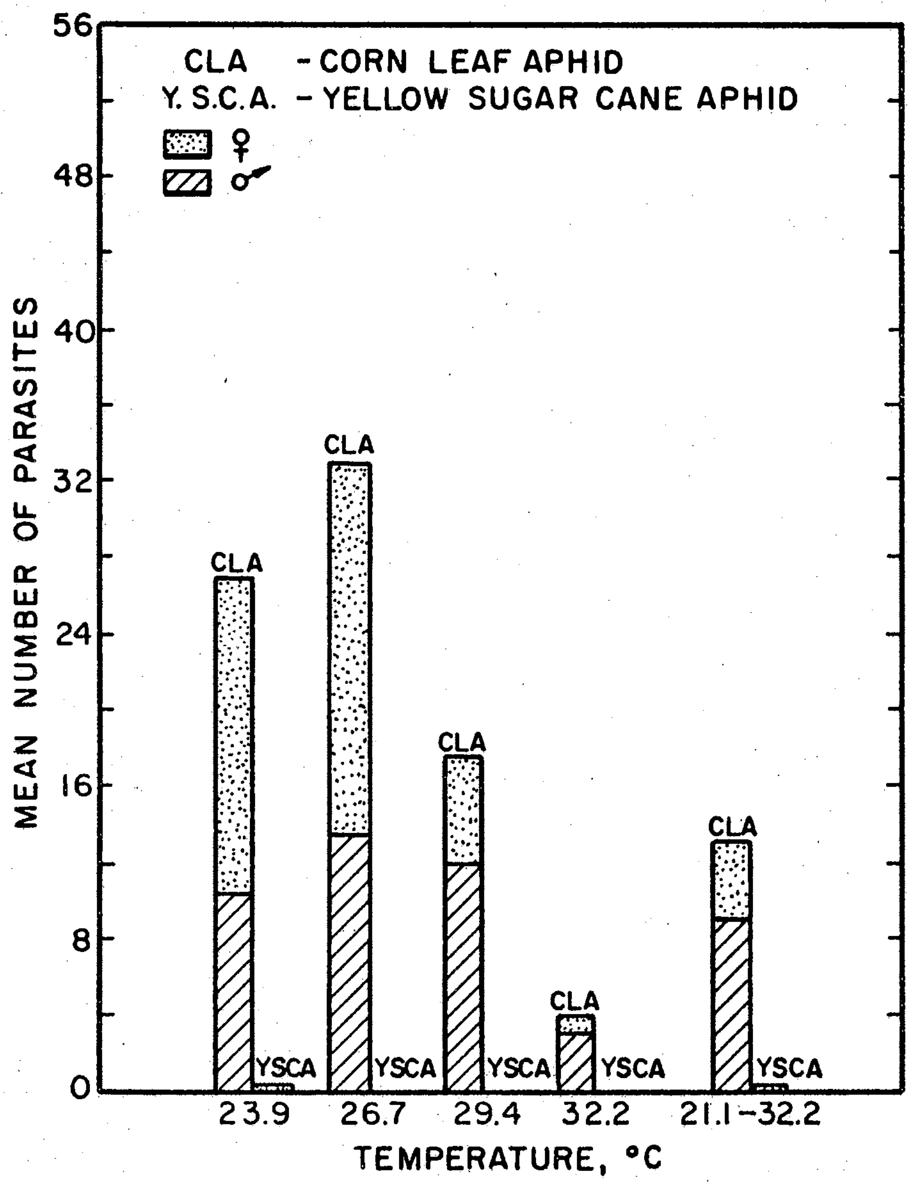

Figure 18. Mean number of male and female <u>Aphelinus asychis</u> emerging from corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

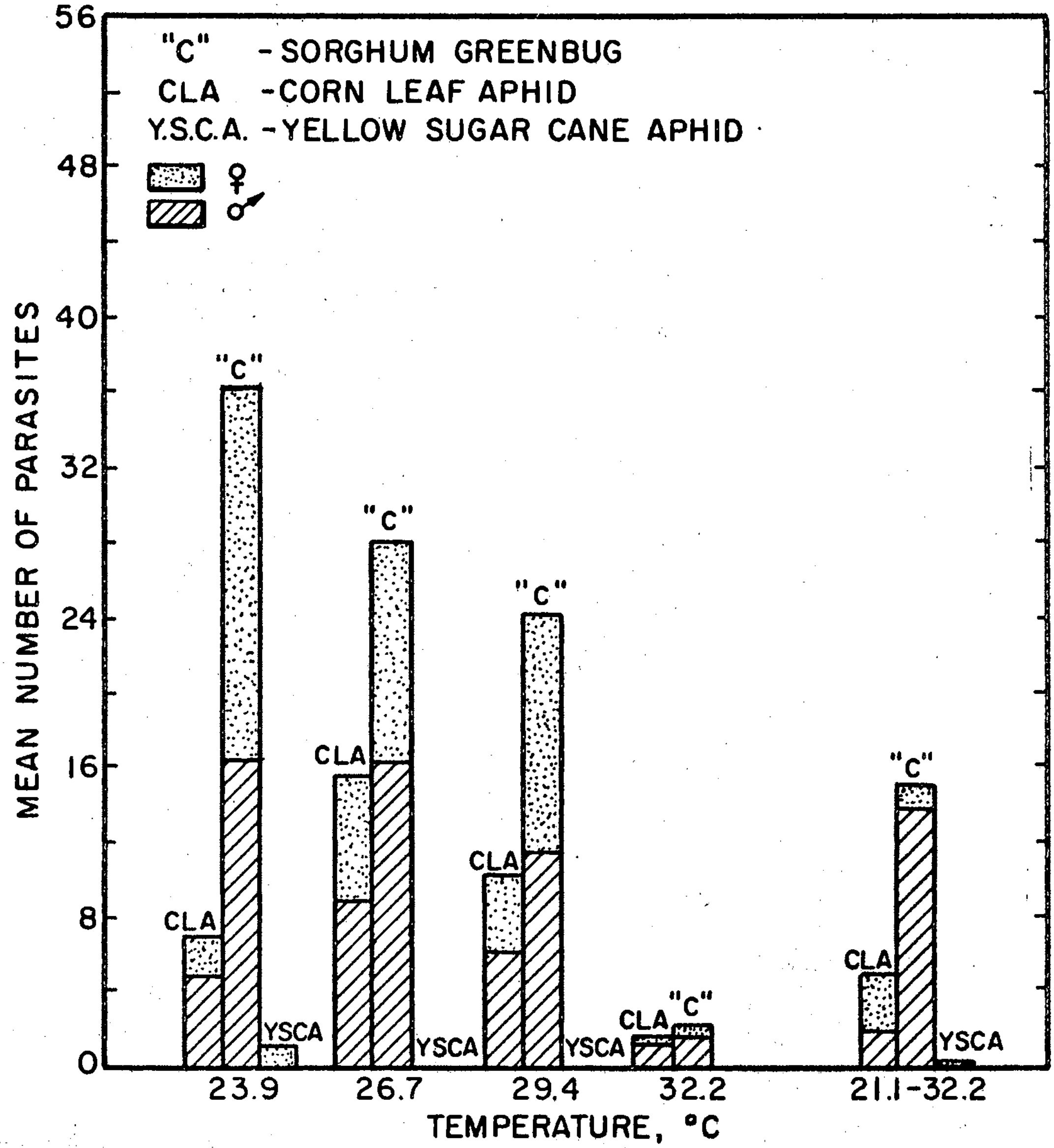

Figure 19. Mean number of male and female Aphelinus asychis emerging from sorghum greenbug + corn leaf aphid + yellow sugar cane aphid hosts at 5 controlled temperatures.

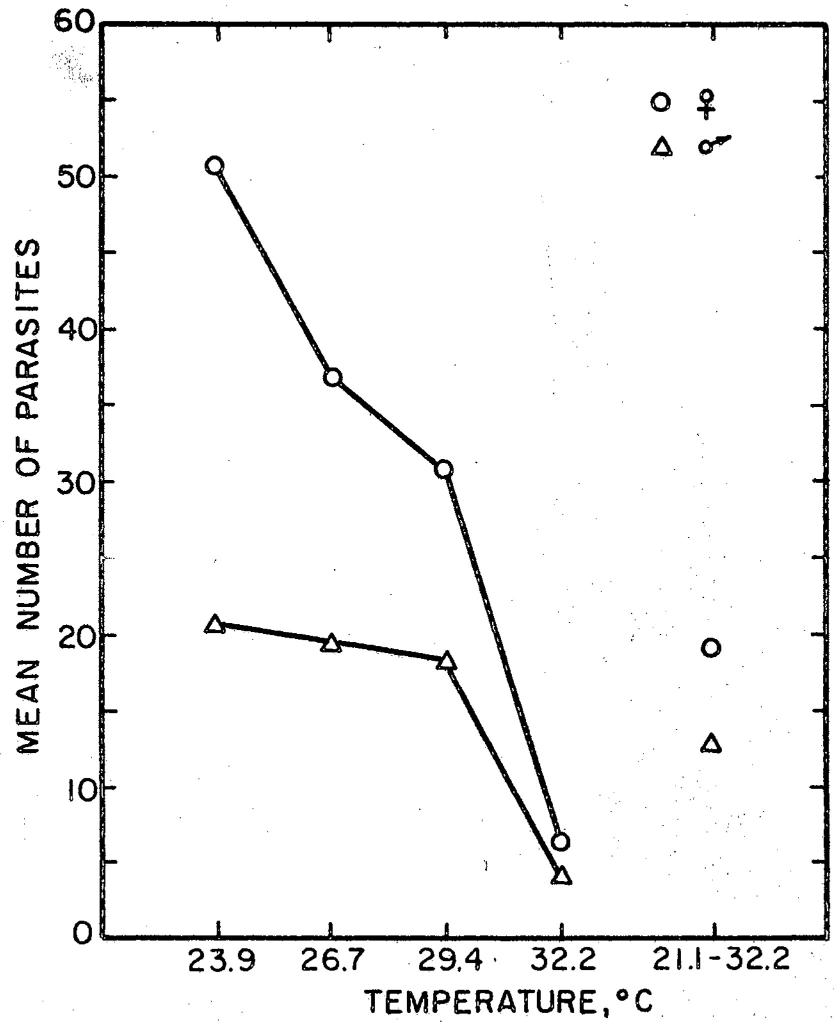

Figure 20. Sex ratio of Aphelinus asychis from 4 combinations of 3 aphid species at 5 controlled temperatures.

Figure 21. Aphelinus asychis stinging a greenbug host.

VITA

Harley Gene Raney

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Doctor of Philosophy

Thesis: HOST-PARASITE INTERACTION BETWEEN APHELINUS ASYCHIS (WALKER), AN IMPORTED PARASITE, AND THREE APHID SPECIES OF SORGHUMS

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