Aphelinus sp. nr. varipes (Hymenoptera: Aphelinidae) as a potential biological control agent of Russian wheat aphid Diuraphis noxia (Mordvilko) (Homoptera: Aphididae)
by Sherry Ellen Lajeunesse

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University
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Abstract:
Developmental rates, lower developmental threshold, and host selection among three species of aphids were determined in the laboratory for the parasitoid Aphelinus sp. nr. varipes (Foerster) (Hymenoptera: Aphelinidae). Host aphid species used were Russian wheat aphid, Diuraohis noxia (Mordvilko), western wheat aphid, Diuraphis tritici (Gillette) (which is a native species that also causes leaf rolling and which is believed to have been the primary host of the parasitoid before arrival of the Russian wheat aphid), and corn leaf aphid, Rhopalosiphum maidis (Fitch). Developmental rates were tested at five constant temperatures, 30.3°, 25.7°, 19.0°, 14.7°, and 11.3 °C. Developmental times of the wasp were found to be similar in Russian and western wheat aphids, ranging from 11.3 days at 30.3°C to 88.7 days at 11.3°C. The parasitoid lower developmental thresholds were similar in these two host species; 9.65°C in Russian wheat aphid and 9.36°C in western wheat aphid. Because of the low number of corn leaf aphids parasitized, it was not possible to compute a parasitoid development threshold in that host. In the host selection test, there were no differences in numbers of Russian wheat aphids and western wheat aphids attacked. CLA was seldom attacked. A study to estimate the continuous rate of increase was done, but due to factors which appeared to be resource limited and possibly density-dependent, it is not felt that an accurate estimate was obtained.

APHELINUS SP. NR. *VARIPES* (HYMENOPTERA: APHELINIDAE) AS A POTENTIAL BIOLOGICAL CONTROL AGENT OF RUSSIAN WHEAT APHID *DIURAPHIS NOXIA* (MORDVILKO) (HOMOPTERA: APHIDIDAE)

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

of

Master of Science

in

Entomology

MONTANA STATE UNIVERSITY
Bozeman, Montana

June 1991

N378
L1475

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGEMENTS

I thank Greg Johnson, my major professor, for the support he gave, which far exceeded the amount required or expected. I also appreciate his unerring ability to put research questions and results into perspective. Special thanks also go to my committee, each member of which has willingly and freely given his or her time beyond the call of duty: Kevin O'Neill, whose suggestions and knowledge of the literature were particularly helpful; Bill Kemp, whose perceptive questions and critiques always made me think; Bob Nowierski, who so willingly shared his expertise; Pat Munholland, who gave an extraordinary amount of time and was extraordinarily patient.

Thanks also to Mike Ivie for his timely suggestions, and to my fellow graduate students, whose good humor helped make the whole experience even more enjoyable. I also thank Lynn Wester for her assistance, willingness, and impeccable work.

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ABSTRACT

Developmental rates, lower developmental threshold, and host selection among three species of aphids were determined in the laboratory for the parasitoid Aphelinus sp. nr. varipes (Foerster) (Hymenoptera: Aphelinidae). Host aphid species used were Russian wheat aphid, Diuraphis noxia (Mordvilko), western wheat aphid, Diuraphis tritici (Gillette) (which is a native species that also causes leaf rolling and which is believed to have been the primary host of the parasitoid before arrival of the Russian wheat aphid), and corn leaf aphid, Rhopalosiphum maidis (Fitch). Developmental rates were tested at five constant temperatures, 30.3°, 25.7°, 19.0°, 14.7°, and 11.3°C. Developmental times of the wasp were found to be similar in Russian and western wheat aphids, ranging from 11.3 days at 30.3°C to 88.7 days at 11.3°C. The parasitoid lower developmental thresholds were similar in these two host species; 9.65°C in Russian wheat aphid and 9.36°C in western wheat aphid. Because of the low number of corn leaf aphids parasitized, it was not possible to compute a parasitoid development threshold in that host. In the host selection test, there were no differences in numbers of Russian wheat aphids and western wheat aphids attacked. CLA was seldom attacked. A study to estimate the continuous rate of increase was done, but due to factors which appeared to be resource limited and possibly density-dependent, it is not felt that an accurate estimate was obtained.

INTRODUCTION

In 1986, a new pest of small grains, the Russian wheat aphid (RWA), Diuraphis noxia (Mordvilko) (Homoptera: Aphididae), was found in western Texas (Webster 1987, Stoetzel 1987). Within three years, RWA spread to 17 western states and three Canadian provinces, infesting more than 64 million acres. A single RWA is considered to be an infestation, because the aphid reproduces parthenogenetically. Nearly seven million infested acres have been treated at a cost of $55 million. Estimated yield losses for 1986-88 amounted to approximately $221 million (Anonymous 1989, 1990).

Feeding damage by the aphid results in breakdown of chloroplast membranes and produces longitudinal white, yellow, or reddish lines on the leaves. The leaves of infested plants roll into a longitudinal tube, which can trap the developing grain head, resulting in a deformed, poorly filled seedhead. Other damage symptoms include reduced tillering (Walters et al. 1980, Anonymous 1989), reduction in yield (Johnson et al. 1988), and decreased cold tolerence in winter wheat (Thomas and Butts 1990). The aphids colonize inside the rolled leaf, where they are protected from most natural enemies in North America, and, to some extent, from foliar insecticides (Walters et al. 1980, Johnson 1989).

RWA was first detected in Montana in the fall of 1987. Anticipating the spread of RWA throughout Montana, a survey was conducted during 1988 to identify potential RWA natural enemies indigenous to south-central Montana (Lajeunesse and Johnson 1991). This information was necessary as a first step in the development of an integrated approach to RWA management. We were particularly interested in aphid parasites or predators that enter the leaf roll and attack the aphid there. Results of the survey showed a complex of aphid natural enemies in south-central Montana, including species of the following families: Nabidae and Anthocoridae (Hemiptera), Coccinellidae (Coleoptera), Chrysopidae (Neuroptera), Aphidiidae and Aphelinidae (Hymenoptera), Syrphidae, and Chamaemyidae (Diptera). Of these natural enemies, only the aphelinid and the larval chamaemyid were frequently found inside the rolled leaf attacking RWA. Anthocorid adults and syrphid larvae were occasionally found inside the rolled leaf.

The aphelinid wasp, Aphelinus species near varipes (Foerster) (Hymenoptera: Aphelinidae), appeared to attack many RWA, so it was chosen for further study. Prior to the arrival of RWA in central Montana, this parasitoid was found attacking the western wheat aphid (WWA), Diuraphis tritici (Gillette). The WWA is closely related to RWA and is native to North America (Blackman and Eastop 1984). The first report of the WWA causing economic damage in Montana

appeared in 1910 (Parker 1916). Feeding damage caused by WWA is similar to that caused by RWA, and includes chlorotic streaking, leaf rolling, and trapped grain heads. The wasp began to parasitize RWA when it appeared in central Montana in early summer. Results of this survey indicate that WWA was the primary host of this aphelinid before RWA arrived.

Aphelinus species near varipes is a member of a genus in which species identification is difficult. The genus is currently being revised. Until the revision is complete and methods of identification established, the population in south-central Montana will be designated as "species near", or sp. nr. (J.B. Woolley, pers. com. 1989).

Voucher specimens of this population have been placed in the Montana State University Entomology Collection in Bozeman, Montana and in the collection of the Department of Entomology, Texas A&M, at College Station, Texas. Other specimens have been placed in nitrogen cold storage for possible electrophoretic identification at Mission, Texas at the USDA-APHIS laboratory, and at Stillwater, Oklahoma at the USDA-ARS laboratory. Preliminary results of electrophoretic isozyme analyses done at the USDA-APHIS laboratory in Mission, Texas indicate differences between the Montana population of A. sp. nr. varipes and other populations of A. varipes, including populations found in Idaho, Texas, and Turkey; these differences occurred in at least two loci (D. Vacek, pers. com. 1991).

Literature Review

It is not known at this time if A. varipes found in the United States is native, naturalized (arrived accidentally in North America with the greenbug, Schizaphis graminum Rondani), or introduced (Wharton 1983, J.B. Woolley, pers. com. 1989). Wharton (1983) synonomized Aphelinus nigritus Howard, a species which had been considered native, with A. varipes (Foerster) after examinination of specimens showed no consistent differences between the two. Aphelinus varipes (Foerster) is found in many parts of the world, including Eurasia, the Middle East, the Mediterranean area, and North America (Peck 1963, Ferriere 1965, Stary 1982, Wharton 1983). In North America, Aphelinus varipes (= nigritus) was reported on greenbug in South Carolina in 1908 (Howard). Specimens of the wasp were collected in Egypt and France and introduced in California in the 1960's (Jackson et al. 1970). In 1960-62, specimens collected in Oklahoma were released in the Orange Free State and Transvaal regions of South Africa in 1960-1962, for control of the greenbug (Kfir 1983).

Little is known about the biology of A. sp. nr. varipes. It is a small, solitary endophagous parasitoid, usually less than one mm in length. The wasp kills aphids by parasitization and also by host feeding, thus functioning as both parasite and predator. Parasitized aphids turn a characteristic black with white appendages after several

days (Stary 1988). Aphids are killed by host-feeding when the wasp inserts its ovipositor then turns and feeds on hemolymph seeping from the wound. Oviposition and host-feeding are thought to be mutually exclusive in the family. The wasp is multivoltine and reproduction can be either uniparental or biparental (Stary 1988). Males are present in the Montana population, but it is not known if reproduction is also by parthenogenesis. Sex ratio of A. varipes (= nigritus) was reported to be male biased (i.e. 1.5:1 to 3.1:1) at temperatures ranging from 24°C to 32°C by Langston[1]. The sex ratio of A. sp. nr. varipes in our laboratory colonies is usually female biased (i.e. approximately 1:9).

Developmental time of A. varipes from egg to adult in the sunflower aphid, Aphis helianthi Monell, was found by Rogers et al. (1972) to take a mean of 16 days at 23.9° to 26.7°C. Developmental time of A. varipes in greenbug was found by Langston to range from 10 to 15 days at temperatures of 24° to 32°C, and 10.5 to 16 days in corn leaf aphid (CLA), Rhopalosiphum maidis (Fitch), at the same temperatures. Host aphid species for A. varipes have been noted by several authors (Howard 1908, Webster and Phillips 1912, Hartley 1922, Wood 1958, Jackson et al. 1970, Rogers

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[1] D.T. Langston. 1970. Laboratory studies of the aphid parasite, Aphelinus nigritus (Howard) (Hymenoptera: Aphelinidae). Thesis, Department of Entomology, Oklahoma State University, Stillwater.

et al. 1972, and Archer et al. 1974, Gilstrap and McKinnon 1988). In each case, greenbug or CLA were the host species most commonly selected. In this study, it was found that A. sp. nr. varipes in central Montana seldom attacks these aphid species.

Objectives

Since there appeared to be differences between the population of A. sp. nr. varipes found in Montana and those found in other areas, a study was initiated to investigate some aspects of the basic biology of the Montana wasp in order to assess the potential of this wasp as part of the natural enemy complex of RWA. Three areas of study were chosen: 1) estimation of developmental rates of A. sp. nr. varipes as a function of various temperatures and the lower developmental threshold (LDT), 2) host selection among three aphid species, and 3) determination of the continuous rate of increase. The results of these studies could yield useful information for integrated management strategies being developed for RWA.

MATERIALS AND METHODS

General

An Aphelinus sp. nr. varipes colony was initiated from wasps collected in 1989 in Stillwater County, Montana. The colony was maintained in Plexiglas (acrylic) sleeve cages, measuring 64 x 75 x 49 cm. Cage openings were covered with polyester monofilament 95 count PeCap mesh (Tetko, Inc., Briarcliff Manor, New York) with 0.1 mm openings; the wasps were able to crawl through mesh with larger openings. Air flow inside the cage was facilitated by a 9-watt axial fan mounted outside the cage over a mesh-covered opening. Temperatures inside the cage ranged from 22° to 25°C, and 40% to 60% R.H. Light was provided by two banks of flourescent tubes (General Electric F40-C50 Chroma 50) and two 60-watt incandescent bulbs, for a total intensity of 67$\mu E/m^2/sec$, measured ten cm above the soil surface of potted plants in the cage. Photoperiod was 16L:8D.

Adult wasps were released into the cage containing RWA on winter wheat, Triticum aestivum L., var. Neeley. Uninfested winter wheat plants (two-leaf growth stage) were added to the cage at weekly intervals; only half of the plants in the cage were replaced each week to minimize disruption of the wasp colony. Additional RWA were placed in the cage as needed to replace those killed by the wasps. Wheat plants destroyed by the aphids were clipped at the

soil surface and placed to one side in the cage for three weeks to allow wasps to eclose from the aphid 'mummies' attached to the plants. All wasps used in this research were reared on RWA.

Three species of aphids were used in the study, RWA, WWA, and CLA. Colonies of each species were initiated from aphids collected in south-central Montana; RWA were collected in Yellowstone County in 1988, WWA in Gallatin County in 1988, and CLA in Gallatin County in 1989. Laboratory colonies were maintained on winter wheat, Triticum aestivum L., Neeley variety, using methods similar to those described by Singh and Moore (1985) and Starks and Burton (1977). All aphids used in the studies were 2nd through 4th instars. In preliminary studies, 80 RWA (1st through 5th instars, 16 aphids/instar) were exposed to eight female parasitoids for 25 minutes and ovipositional thrusts were observed. Two 1st instar aphids were attacked, nine 2nd instar aphids, ten 3rd instars, ten 4th instars, and four 5th instars. Based on this preliminary study, results indicated A. sp. nr. varipes attacks 2nd through 4th instars with approximately equal frequency.

Developmental Study

Developmental rates of A. sp. nr. varipes were determined at five constant temperatures, 30.3°, 25.7°, 19.0°, 14.7°, and 11.3°C (±1.0°), using Model No. 3023

Conviron environmental growth chambers (Conviron Inc., Winnepeg, Manitoba). Photoperiod was 16L:8D, light was provided by VHO flourescent tubes and 60-watt incandescent bulbs for a total intensity of 125μE/m²/sec. Temperatures, measured inside the cages, decreased by 2° to 7°C during the dark phase of the photoperiod. Therefore, weighted averages of hourly in-cage temperatures were used to calculate developmental times.

Standard 100 x 10 mm polystyrene petri dishes (Falcon Inc., Oxnard, California) were used to contain aphids and wasps. A ventilation hole, one cm in diameter, was cut in the center of each lid and covered with PeCap mesh to eliminate problems with condensation and entomophagous fungi. The three ridges in the petri dish lids, which create a gap between the top and bottom portions of the dish, were trimmed off, because the wasps and aphids were able to crawl through this space. Ten excised leaf sections of winter wheat, 5.5 mm in length, were placed on firm agar [7 gm Bacto-Agar (Difco Labs, Detroit, Michigan) + 125 mg benzimidazole (Aldrich Chemical Co., Milwaukee, Wisconson) + 1000 ml distilled water] (modified from Sewell and Caldwell 1960) in each petri dish. Benzimidazole slows degradation of the chloroplasts in the excised leaf section, keeping the leaf green and healthy in appearance for up to three weeks (Sewell and Caldwell 1960).

Forty mated female parasitoids were placed in each of three petri dish cages containing 250 RWA, WWA, or CLA. The sides of the cages were sealed with Parafilm plastic film (American Can Co., Greenwich, Connecticut) to prevent aphids and wasps from escaping. The petri dish cages were placed in the laboratory at 22° to 25°C for sixteen hours, after which the surviving aphids were removed from the cages. The aphids were placed on potted wheat plants and covered with cages constructed of nitrocellulose, which is non-toxic to aphids (Starks and Burton 1977). Cages were 6 cm diameter and 45 cm tall, and similar in design to those of Raney et al. (1971). Caged plants were placed in growth chambers at one of five temperatures until mummy formation was completed. Mummies were clipped from the plants and placed in empty petri dish cages that were sealed with Parafilm and returned to the growth chamber. Cages were checked daily at 0700 hr. The process was repeated for each of the five experimental temperatures.

Host Selection Study

Ninety aphids, 30 of each species, were placed on a wheat plant in the two-leaf growth stage, then covered with a nitrocellulose cage. After three hours, 40 mated female wasps were released into the cage for two hours, then removed using an aspirator. The plants containing the aphids were put in an environmental growth chamber at 24°C

and 16L:8D photoperiod, light intensity 125μE/m²/sec. Ten pseudoreplicates were performed.

Plants with aphids were held in the growth chamber until mummy formation was complete. Mummies were clipped from the plant, sorted by species and tallied. They were then placed in petri dish cages and returned to the growth chamber where they were held until adult wasp eclosion. Emerging wasps were collected daily and tallied.

Differences in head width of parasitoids reared in RWA and in WWA were determined using an ocular micrometer mounted on a Nikon microscope. Head capsules were removed from the wasps and measurements, taken from a frontal view, were made to the nearest 0.02 mm.

Continuous Rate of Increase Study

This study was conducted in a cage 76 x 66 x 61 cm, constructed of 6 cm Plexiglas and pressed board. The cage was similar in design to the one used to rear the wasp colony, except for the dimensions and the use of pressed board with white surfaces for the floor and back of the cage. The top of the cage was scribed with 1-cm squares. The cage was placed in a Kysor-Sherer growth chamber (Warren Sherer Inc., Marshall, Michigan), photoperiod 16L:8D, light intensity was 185μE/m²/sec, measured ten cm above the surface of the soil in the planting tubes. Temperature inside the cage was 23°C.

Winter wheat was planted in 3.2 cm plastic planting tubes, (Conetainers, Stuewe and Sons, Corvallis, Oregon), eight plants per tube. There were 98 tubes per rack, for a total of 784 plants. Half of the rack of plants was replaced each week. Thus each tube of plants remained in the cage two weeks. Approximately 100 RWA were placed on each plant. More aphids were placed in the cage daily, to serve as both food and hosts for the wasps. Approximately 78,400 RWA were in the cage at the beginning of the test.

Three hundred female and male wasps of all ages, collected from the laboratory stock colony, were placed in the cage with the aphids. At weekly intervals, wasps were counted using three separate methods: 1) 80 of the 806 squares on top of the cage were chosen each week using a random numbers generator and wasps crawling on the ceiling of the cage were counted in these squares, 2) a yellow sticky trap measuring 6.2 x 3.7 cm was placed in the center of the rack of plants and left in place for five hours, and 3) wasps were attracted to the mesh-covered opening of the fan and counts of the wasps on this circular space (ten cm diameter) were made. The counts were used as relative comparisons between weeks.

Data Analysis

The developmental study data were analyzed using the SAS (Statistical Analysis System) for Personal Computers,

version 6.06 (SAS Institute 1990). A model was constructed for each of the host aphid species used, the developmental times (days) of each of the wasps were included in the models. To estimate the lower develomental threshold, (LDT), a simple linear regression was performed, regressing developmental rate (1/developmental time) against temperature. The estimate of LDT is provided by the intercept of the temperature axis, and degree-days required to complete development are calculated as the reciprocal of the regression coefficient b (Campbell et al. 1974). A confidence interval for t was calculated by performing inverse regression of x onto y, using the formula given by Draper and Smith (1981).

The host selection study data were analyzed using MSUSTAT, version 4.12 (developed by R.E. Lund, Montana State University, Bozeman, Montana, 1989). One-way ANOVA and multiple comparisons based on LSD (Student's t) at $P = 0.05$ significance level were conducted, using mummy formation data. Data from adult wasp eclosions would have included the issue of suitability of the host aphid species for the development of the parasitoid, which would be an issue different from host selection.

The continuous rate of increase study data were to be analyzed using a stochastic exponential population growth model developed by Dennis et al. (in press). The model expresses the relationship between the logarithm of

population growth increments and the corresponding time increments or intervals. This relationship is a function of two parameters, μ and σ^2; r (the continuous rate of increase) and lambda (the finite rate of increase) are both functions of μ and σ^2. This approach allows random fluctuations in population growth, as well as sampling variability, to be incorporated in the model.

RESULTS

Developmental Study

Developmental data for the wasp when RWA and WWA were the host species are given in Table 1. There is no significant difference in developmental rates or developmental threshold of A. sp. nr. varipes in comparison between RWA and WWA hosts. Developmental rates for the wasp in RWA and in WWA ranged from 89 days at 11.3°C to 11 days at 30.3°C.

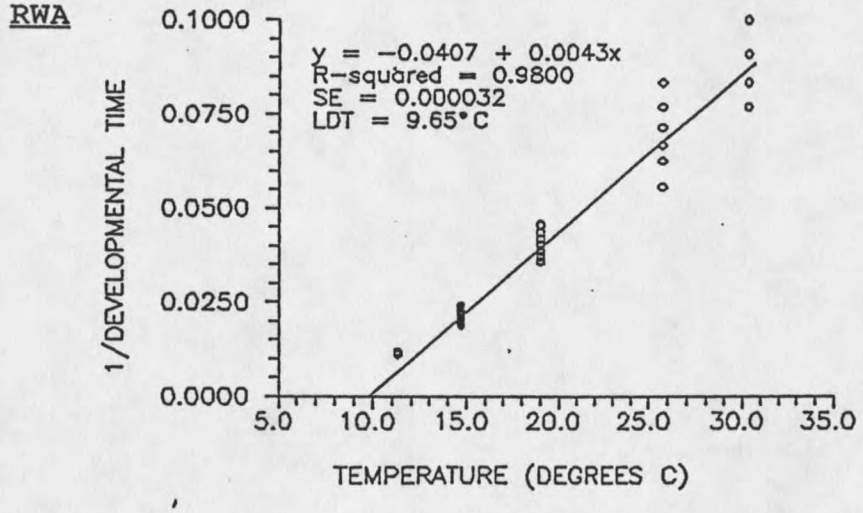
Table 1. Mean development time (±S.E.) data for A. sp. nr. varipes in Russian and western wheat aphids.

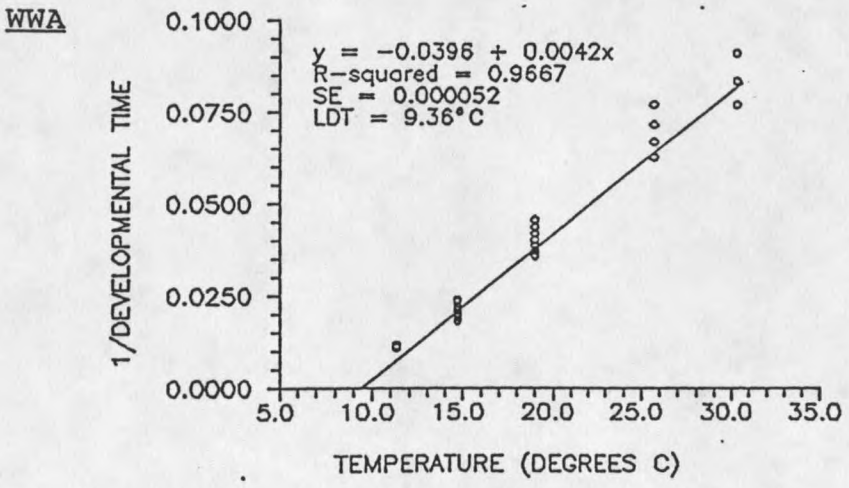
	Temp	N[a]	MTA[b] (±S.E.)
RWA	30.3°C	121	11.3 (±0.07)
	25.7°	134	13.9 (±0.07)
	19.0°	32	24.3 (±0.33)
	14.7°	88	46.8 (±0.26)
	11.3°	7	88.0 (±0.87)
	Total	= 382	
WWA	30.3°C	79	11.6 (±0.08)
	25.7°	73	13.9 (±0.10)
	19.0°	38	24.9 (±0.38)
	14.7°	34	48.6 (±0.57)
	11.3°	3	88.7 (±1.67)
	Total	= 227	

[a] N = no. adult wasps.
[b] MTA = mean time to adult (days).

Developmental threshold for the wasp is approximately 9.65°C (95% C.I. 8.6°,10.7°C) in RWA and approximately 9.36°C (95% C.I. 8.0°,10.7°C) in WWA (Fig. 1.). Confidence intervals for development in RWA and in WWA overlap, showing there is no significant difference in developmental time.

Figure 1. Developmental thresholds of A. sp. nr. varipes in Russian wheat aphid and western wheat aphid.





Because there were multiple observations at each point, it was possible to test the adequacy of the models. One estimate of σ^2 was obtained by adding the deviations within temperatures and another from the regression model. The two estimates were then compared; significant differences did not occur at $P<0.05$ in either model. Both models were thus tested for lack of fit. The analysis did show larger residuals (up to 3.832 in one instance) for several observations at the higher temperatures, possibly indicating the upper thermal limit of the wasp was being approached.

Of the 1,250 CLA exposed to the parasitoids in the developmental study only eight were parasitized, so a wasp developmental threshold was not calculated in this host. However, mean developmental time of the wasps in the eight CLA mummies was comparable to that of wasps developing in RWA and WWA; 12 days at 30.3°C (N = 1), 14.3 days at 25.7°C (N = 4), 48 days at 14.7°C (N = 2), and 87 days at 11.3°C (N = 1). Wasps eclosed from all eight mummies.

Host Selection Study

Among the three species of aphids tested RWA and WWA were attacked with equal frequency (Table 2); equal numbers of RWA and WWA mummies were produced, more adult wasps eclosed from WWA mummies than from RWA mummies in the host selection study. An adult wasp eclosed from the single CLA mummy.

Table 2. Host selection by A. sp. nr. varipes among three species of grain aphid.

Aphid Species	Aphids exposed	Mummies formed	Adults eclosed	LSD (mummies)
RWA	300	93	63	A
WWA	300	93	76	A
CLA	300	1	1	B

F-value = 30.83 comparing mummy formation in all three aphid species.
F-value = 0 comparing mummy formation in RWA and WWA.

Three hundred aphids of both species were exposed to the wasps in the host selection study. Only one CLA mummy was produced from 300 aphids exposed. Greenbug was used in preliminary studies, and like CLA, was seldom attacked, even in no-choice situations. In one preliminary study, three aphid species, greenbug, RWA, and WWA were exposed to a mated female parasitoid singly and in all possible combinations for the lifespan of the parasitoid. A total of 70 aphids per species were used. Number of mummies formed in each aphid species was, greenbug = 1, RWA = 19, WWA = 19. The same host selection among these four species of aphids was seen in the field.

There were differences in sizes of adult wasps produced in RWA compared to those produced in WWA, with those produced in RWA being consistently larger. The maximum head widths of 60 haphazardly chosen female wasps were measured; 30 wasps had developed in RWA and 30 in WWA. Sample means were 0.33 mm for wasps developing in RWA and 0.29 mm for

those in WWA. Standard error for the difference was 0.0042, $t = 9.454$ ($P < 0.0001$). This difference in size of wasps is not surprising because body size of RWA is usually larger than WWA; however, it is possible that the resulting larger wasps that are now produced from this new host source, RWA, will show increased fecundity and vigor compared to that exhibited by wasps produced in WWA, what is assumed to be the original primary host.

Host-feeding by the females also accounts for a substantial amount of RWA and WWA mortality. In a preliminary study, 20 RWA were placed in a petri dish, five cm in diameter, on excised leaf sections. A single female parasitoid was released into the dish. The dish was then placed in a growth chamber at a constant temperature of 23°C, photoperiod 16L:8D, for 24 hours. Ten pseudoreplicates were done. Number of aphids killed by host-feeding per dish were as follows: dish no. 1 = 4, no. 2 (wasp died), no. 3 = 3, no. 4 = 3, no. 5 = 1, no. 6 = 2, no. 7 = 2, no. 8 = 2, no. 9 = 1, no. 10 = 3. This is a mean of 2.3 aphids per wasp per 24-hour period (SE = 0.333). Only RWA and WWA were observed to be fed upon in the course of this research. This source of aphid mortality became an important consideration during experiments and in the rearing of both wasp and aphid stock colonies.

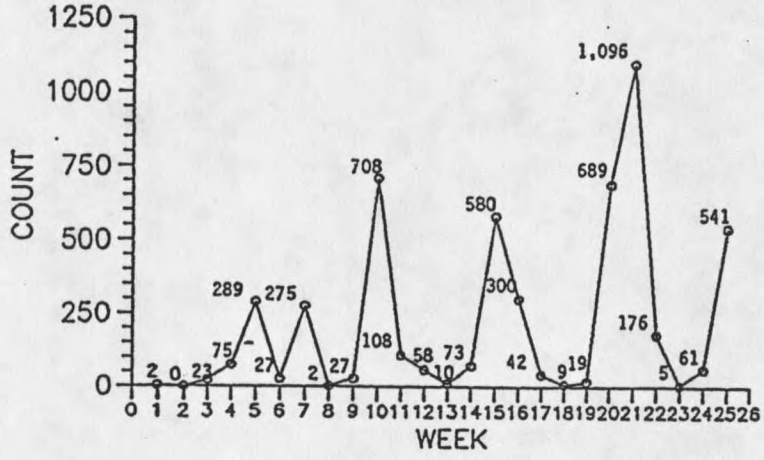
More adult wasps eclosed from WWA mummies than from RWA mummies in the host selection study, 76 and 63 respectively.

However, in other instances (e.g. in the developmental study), more adult wasps eclosed from RWA mummies than from WWA mummies, 382 from RWA mummies and 227 from WWA mummies.

Continuous Rate of Increase

Results of the weekly wasp counts are given in Figure 2. The wasp population increased rapidly, reaching its first peak in five weeks. By the next week the population had 'crashed' dramatically. Thereafter, the population peaked and then crashed approximately every three to four weeks.

Figure 2. Weekly wasp counts- continuous rate of increase study.



The method of estimating the number of wasps collected over the fan opening was discontinued after week seven, when the number of wasps grouped on the circular area was so high (1,500 to 2,500) that accurate estimates became impossible. Counts obtained by sticky traps appeared to give most

consistent results, so those are the figures used to chart population trends in Figure 2.

The sex ratio of the wasps varied from 1:15, at high population levels, to 3:1, at very low population levels in both the stock wasp colony and in the rate of increase study cage. Wasp counts in Figure 2 did not reflect the total number of wasps inside the cage; given the cryptic nature and small size of the wasps no method was developed to take actual counts of the total population.

Data collection was terminated on week 25 because of problems observed in the wasp colony which appeared to be limiting the population growth above a certain level. Also, problems in providing the wasps with conditions necessary for unrestricted growth had become apparent; it was impossible, using these methods, to supply the wasps with enough RWA to serve as both food and hosts. Analyses of the data were not done as planned due to these restrictions on the increase of the wasp population.

DISCUSSION

Developmental Study

The developmental threshold of RWA, the target pest, has been determined to be 4.1°C in north-central United States (Kieckhefer and Elliott 1989). With LDT of 9.7°C for A. sp. nr. varipes this indicates a difference of approximately 5.6°C between LDT of the wasp and LDT of RWA. Kieckhefer and Elliott (1989) estimated that RWA apterae require 139.3 degree-days for development from birth to onset of reproduction; A. sp. nr. varipes was estimated in this study to require 231.8 day-degrees from egg to onset of reproduction. Temperature requirements for RWA for development and reproduction appear to be substantially lower than those for A. sp. nr. varipes. Force and Messenger (1968) found differences of 4.0°-6.5°C between LDT for three species of parasitoids and that of the aphid host, spotted alfalfa aphid, Therioaphis trifolii (Monell). Campbell et al. (1974) and Cohen and Mackauer (1987) found differences of less than 2.8°C between LDT for a number of aphid parasites and those of the aphid hosts. Although predicting interactions in the field from data collected in the laboratory is usually not very reliable, it is generally felt that differences of more than a few degrees between the lower developmental thresholds of a pest and an associated parasitoid limit the early and late season effectiveness of

the parasitoid as a biological control agent (Messenger and Force 1963, Campbell et al. 1974, Cohen and Mackauer 1987). The difference between thresholds of A. sp. nr. varipes and RWA appears to be relatively large. It is not known at this time if this difference may be mediated by a 'greenhouse' effect of the rolled leaf microenvironment. In the harsh climate of the north-central Great Plains, the relatively high LDT of the wasp will be an advantage in surviving late-occurring frosts, but it will possibly limit the effectiveness of the parasitoid in early-season crop protection.

The differences between thresholds of hosts and parasitoids can sometimes be offset to some extent by differences in reproductive capacity, rates of increase, and mean generation times, among other factors (Messenger and Force 1963). It is not known how these other variables will affect interactions between A. sp. nr. varipes and RWA. Kriel et al. (1984), Du Toit and Walters (1984) and Michaels and Behle (1989), and Aalbersberg et al. (1989) found that population growth of RWA is slow initially, with numbers beginning to increase at the time of tillering and stem elongation. Aalbersberg et al. (1989) found that the initial rapid increase in population began when the wheat plants were at growth stages 30 to 45 (Zadoks Scale), which correspond to the later stages of tillering to "boot" stage. This initial lag may give aphelinid numbers time to

increase, helping to compensate for differences in LDT between the parasitoid and its host.

Even if wasp numbers are able to increase before economic thresholds are reached by RWA, observations since 1988 indicate that the aphelinid does not migrate into grain fields very fast or very far. This would be in agreement with other observations on aphelinid movement (Hartley 1922, Hagen and van den Bosch 1968). It would also agree with the observations of Price (1976) that the movement of beneficial insects into a crop is in many cases too slow to prevent pest populations from reaching the economic injury level. Thus, with the higher developmental threshold of A. sp. nr. varipes and slow observed rate of migration into the crops, it might not be realistic to expect an impact by the wasp on RWA populations in the crops unless augmentative-type releases are made. If wasp populations increase over time in response to the new host/food source (RWA), it is possible that within-field densities of the wasp could increase also. At the present time, however, within-field populations seem to be relatively low.

The main impact of the wasp on RWA might actually occur on over-summering alternate hosts. When grain crops mature, RWA moves onto a number of alternate grass hosts including intermediate wheatgrass, Agropyron intermedium (Host) Beauv., crested wheatgrass, Agropyron cristatum (L.) Gaertner, slender wheatgrass Agropyron trachycaulum (Link)

Malte, and onto volunteer small grain plants (Hewitt et al. 1982, Kindler and Springer 1989, Clements et al. 1990, Lajeunesse and Johnson unpub. data). When RWA populations are concentrated in the less favorable habitat of these areas they might be more subject to attack by the aphelinid. More A. sp. nr. varipes were found attacking aphids in this relatively undisturbed habitat (and on volunteer plants) than in crops. Thus, the aphelinid wasp might be of most value in long-term regulation of RWA populations, rather than in short-term (within season) protection of the crop. This type of long-term impact by natural enemies on pest insect populations has been noted by Altieri (1984, 1989) and others, and is compatible with sustainable agriculture practices.

Host Selection Study

Aphelinus sp. nr. varipes in Montana appears to be quite host specific among the aphid species tested. In laboratory tests, RWA and WWA were attacked equally; developmental data suggest that both are suitable hosts. Corn leaf aphid was seldom attacked. Because WWA is a pest in the same small grains as RWA and causes the same type of damage, it would seem to be an advantage that the wasp attacks both aphid species; this should benefit the parasitoid and increase its effectiveness in pest management.

A difference between other A. varipes populations and the A. sp. nr. varipes population in central Montana is indicated in the host selection study; the literature cites the aphid hosts most commonly selected by A. varipes as greenbug and CLA (Howard 1908, Webster and Phillips 1912, Hartley 1922, Wood 1958, Jackson et al. 1970, Langston, Rogers et al. 1972, Archer et al. 1974, Gilstrap and McKinnon 1988). In this study, it was found that A. sp. nr. varipes in central Montana seldom attacked these aphid species, in either the laboratory or the field.

It has been suggested by Hokkanen and Pimentel (1984, 1989) that when potential biological control agents become established on a new host, many times the result is increased potential for suppression of the pest. They suggest this can occur when defense mechanisms that have evolved over long periods of time are bypassed or overcome in the new relationship. It may be that the aphelinid wasp will be more effective in some respects (e.g. larger individuals produced) in the new host species, RWA, if indeed this is a new host-parasitoid association.

The larger size of the parasitoids developing in RWA could also have adaptive advantages. It has been noted by Charnov and Skinner (1984), O'Neill and Skinner (1990), and others that, in some cases, larger body size in parasitoids seems to confer increased fecundity. If this is the case with A. sp. nr. varipes attacking RWA, the result could be

particularly beneficial; WWA infestations are usually small and spotty and do not seem to spread far or rapidly (Parker 1916). With a new host source that is more plentiful and uniformly distributed, it is possible that an increased level of fecundity could quickly manifest itself in this wasp. The larger wasps also might be able to successfully attack larger aphid instars more frequently; when the wasp was observed to attack larger aphids, it appeared to have difficulty if the aphid struggled or attempted to move away.

Sex ratio differences between A. varipes populations elsewhere and that of A. sp. nr. varipes in Montana also became apparent in this study. Sex ratio of A. varipes (= nigritus) was reported by Langston to be male biased, 1.5:1 to 3.1:1 at temperatures ranging from 24°C to 32°C. The sex ratio of A. sp. nr. varipes in our laboratory colonies is usually female biased approximately 1:9. The sex ratio varies from 1:15, female biased at high population levels, to 3:1, male biased at very low population levels. The norm in this research, however, in both RWA and WWA, seemed to be heavily female biased.

Continuous Rate of Increase Study

Although, in many cases, insect populations in nature cycle in peaks and 'crashes', the nature of the crashes in this study soon became a matter of concern. It became apparent that some of the reasons were due to density-

dependent factors that were a function of the rearing procedure. Shifts in sex ratios, mortality resulting from limited food supply, and insufficient numbers of hosts available were three important variables which appeared density-dependent. These variables severely restricted wasp population growth periodically in the study.

Theoretically, intraspecific density-dependent factors should not restrict A. sp. nr. varipes populations in the field for quite some time, except on a limited scale in localized situations. This is due to the low endemic levels of WWA, the original primary host. It seems reasonable to believe that wasp populations in Montana have historically remained low in response to WWA. If this is true, with a more plentiful and uniformly distributed host now available (RWA), wasp populations theoretically would be free to increase exponentially, with minimum occurrence of intraspecific density-dependent restrictions for quite some time. Due to the artificial restrictions on the rate of increase of the wasp population inside the study cage, I feel that this study does not accurately reflect the rate of increase of the wasp.

Limitations due to available food/hosts probably were already affecting population increase early in the study, but were not recognized. After the effects became apparent, an estimate was made, for a particular point in time, of the requirements needed for unrestricted wasp population

increase and it was found that many more aphids were required than were being provided, among other things. A conservative estimate of total number of wasps present in the cage might be five times the number captured on the sticky trap each week. If this estimate is used, the number of wasps present in the cage on sampling day of Week 21, for example, would have been 5,500. If the sex ratio was 1:7, 4,800 of these would have been females. Two to three aphids/day were consumed by the wasps in preliminary tests, so on sampling day of Week 21 a minimum of 9,600 RWA would have been required for food. If an average of six aphids/day are parasitized (up to 13 aphids/day were parasitized in preliminary tests), this means an additional 28,800 aphids/day would be required as hosts for unrestricted increase in the wasp population. This is a total of 38,400 RWA per day required on sampling day in week 21 to provide the wasp colony with ample food and hosts. It was not possible, using the methods in this study, to provide ample numbers of aphids because of the large amount of plant material involved.

The shifts in sex ratio appeared to be another serious result of overcrowding. These shifts coincided with the population 'crashes' which occurred every three to four weeks. As the population began to build again, it became female biased once more. At population peaks, it was female biased approximately 1:15. This is in agreement with

current sex ratio allocation models which predict a lower male:female ratio at higher host densities (Schmidt and Smith 1987), as would be the case in this study when the wasp population was recovering from a crash. It seems safe to assume that without containment in the laboratory, these density-dependent shifts in sex ratio would be less likely to occur. The specific affects of overcrowding on competition, superparasitism, oviposition decisions, and fecundity of the individual in this study are unknown, but we would expect that, in a study of this kind, the affects would be detrimental to unrestricted population increase (Peters and Barbosa 1977, Singh and Moore 1985).

The continuous rate of increase study did produce information about time required to reach given population levels when the wasps are reared using these methods. So, while the assumptions necessary for applying the stochastic exponential growth model to the data were invalid (i.e. density independent growth), it is possible that analyzing the increasing periods only might yield information which could be useful, perhaps in the context of mass rearing of the parasitoid.

Observations of length of cycles, increase in numbers in each cycle, and numbers of RWA required to sustain an increase in the wasp population would seem to indicate that A. sp. nr. varipes has the potential to impact RWA

populations. Further studies on the rate of increase of the parasitoid would be interesting.

Overview of Potential of the Wasp

Aphelinus sp. nr. varipes appears to have the potential to be an effective control agent assisting in long-term regulation of RWA populations in Montana because it 1) enters the protective leaf roll of RWA, 2) is quite host specific among the aphid species tested, 3) functions both as a predator and parasite, and 4) is adapted to the climate of the north-central Great Plains. It appears unrealistic, however, to expect protection from RWA already present on a crop, because it has a higher developmental threshold than RWA and does not appear to migrate into the field very quickly or very far. Differences in reproductive rates between the wasp and RWA might compensate for the differences in developmental thresholds to some extent. Augmentative or inundative releases of the wasp will possibly be the only way to achieve crop protection due to A. sp. nr. varipes. Natural populations of the wasp might impact RWA most when the aphids are concentrated on oversummering alternate hosts. Although it is not possible to compute a maximum rate of increase from this study, the wasp does increase from small to relatively large population levels in two to three weeks, and kills substantial numbers of aphids by both parasitization and host-feeding. Long-

term regulation of pest populations is an important part of pest management. In this context, Aphelinus sp. nr. varipes appears to have the potential to be an effective member of the natural enemy complex of RWA.

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