HOST SELECTION AND SWITCHING BY HYMENOPTEROUS PARASITOIDS (APHIDIIDAE) OF ALFALFA AND PEA APHID (APHIDIDAE)

by

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Host selection and switching by Hymenopterous parasitoids (Aphididiidae)

of alfalfa and pea aphid (Aphididae)

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ABSTRACT

The alfalfa aphid, Macrosiphum creelii, is a relative newcomer to the southern interior of British Columbia. In a survey of the principal alfalfa-growing districts, it was found only in a 70 km strip between Cache Creek and Kamloops, where it was less common than the pea aphid, Acyrthosiphon pisum. Three primary hymenopterous parasitoids were found attacking both aphids at Kamloops, viz. Aphidius ervi, A. pisivorus, and Praon pequodorum. A. ervi was the most common parasitoid of both aphids on alfalfa at Kamloops, but A. pisivorus and P. pequodorum were more common on alfalfa aphids than was A. ervi.

In laboratory choice and switching tests, these three species and Aphidius smithi, formerly the most common parasitoid of the pea aphid in the province, all appeared to prefer second-instar pea aphids and did not switch when the relative abundances of second-instar pea and alfalfa aphids were systematically varied. The preferences for the pea aphid by A. pisivorus and A. smithi were the weakest and strongest, respectively, among the parasitoids. Prior experience with alfalfa aphids did not change the preference of A. pisivorus, A. ervi, and P. pequodorum for the pea aphid. Both aphid species showed similar abilities to evade attack, and the preferences of the parasitoids for pea aphids were apparently innate.

Oviposition and emergence success of the parasitoids did not differ between pea and alfalfa aphids. However, A.

pisivorus developed into a larger wasp when it was reared in the pea aphid, but no differences were found in sex ratio when it was reared in either aphid. *A. ervi*'s host selection, sex allocation, and adult size were not significantly affected by the host in which it was reared. Differences, still to be established, between the acceptability of these two aphids are the only factors that determine the preferences shown by the parasitoids.

Conclusions are drawn concerning the potential of these parasitoids as biological control agents of the alfalfa aphid and its importance as a pest of alfalfa in British Columbia.

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SECTION 1: INTRODUCTION

Host selection and host switching have received considerable attention in biological control because of their importance to the understanding of the following: the role of alternative hosts for enhancing parasitoid activity in crops (Powell 1986); the regulation of several pest species on the same crop by polyphagous parasitoids (Gardner and Dixon 1985); and the ability of indigenous parasitoids to regulate introduced species of pests (Lawton 1986). The ability to predict switching and host range would also be of value in comparing different parasitoids for a biological control programme.

The processes that lead to host selection in the entomophagous Hymenoptera include locating the habitats of hosts, locating the hosts, and accepting the hosts (Salt 1935, Doutt 1959, Mackauer 1973). The combination of these three processes result in the selection of a host insect by the elimination of other species for ecological and behavioral reasons. A theoretical approach that is applicable to host selection by parasitoids is "switching".

The tendency of predators or parasitoids to concentrate on the most abundant species of prey or hosts has been called "switching" by Murdoch (1969). "Prey switching" has been of interest to ecologists because of its relevance to the understanding of both population stability and species diversity in communities (Murdoch and Oaten 1975).

Predatory insects are often the principal subjects of studies on "switching" (Holmberg and Turnbull 1982, Bergelson 1985, Cothran and Thorp 1985, Provencher and Coderre 1987), but polyphagous parasitoids of insects may also be used to study "switching" behavior. In fact, the functional responses of cereal-aphid parasitoids to both habitual and supplementary hosts were determined by Dransfield (1979) in order to investigate the possibility of grass-land aphids acting as a reservoir for these insects. Although Dransfield's studies may be useful in understanding parasitoid behavior in situations when more than one host is available, the information from his studies is restricted to a somewhat artificial situation. The two species of aphids used in his studies are usually not found coexisting in the same plant communities. Consequently, the parasitoids would rarely encounter a host population that consisted of both species being equally accessible in the same habitat. By contrast, studies on the aphids of alfalfa in southern BC and their associated parasitoids should provide a better understanding of host switching and host selection by parasitoids where different host species share the same habitat.

Alfalfa, Medicago sativa L., is one of the most important forage crops grown in North America and many other parts of the world. It is adapted to a wide range of growing conditions and produces forage with excellent nutritional qualities. In British Columbia, alfalfa is the most popular forage legume grown. It accounts for about 40 % (286,000 acres) of the province's total hay acreage of which an estimated 150,000 acres was grown in the southern interior in 1984 (Anon.).

The pea aphid, *Acyrthosiphon pisum* Harris, is a globally common pest of alfalfa. The aphid is believed to have been accidentally introduced into North America from Europe during the second half of the 19th century (Mackauer 1971). Important natural enemies of this aphid are wasps belonging to the family Aphidiidae. These are solitary endophagous parasitoids of aphids. The family has been reviewed in detail by Mackauer and Stary (1967) and Stary (1970). The aphidiids, *Aphidius smithi* Sharma and Subba Rao, *A. ervi* Haliday, *A. pisivorus* Smith (= *pulcher auctt. nec* Baker), and *Praon pequodorum* Viereck are the four primary parasitoids of pea aphids on alfalfa in BC (Campbell 1974, Mackauer and Kambhampati 1986). *A. ervi* and *A. smithi* were imported into North America from Europe and India respectively as biological control agents against the pea aphid, but *A. pisivorus* and *P. pequodorum* are native to North America. *A. ervi* and *A. smithi* have contributed significantly to the successful control of the pea aphid in North America (Hagen and van den Bosch 1968; Mackauer 1971). In BC, natural enemies of the pea aphid are abundant in alfalfa and the need to use insecticides for control has been low in recent years.

The pea aphid was the only aphid pest of alfalfa in BC until *Macrosiphum creelii* Davis was found on alfalfa at Kamloops in 1984. *M. creelii* is commonly referred to as "the alfalfa aphid" in the literature. It is indigenous to North America and appears to occur nowhere else. Prior to 1984, the aphid was reported on alfalfa in Utah, Idaho, Nevada, Oregon, and Washington (Halfhill 1982). Although the alfalfa aphid was found on alfalfa as early as 1909 in the US Pacific Northwest, it was not considered an economic pest until it became increasingly abundant after 1963 (Halfhill 1982). In recent years, the alfalfa aphid has been a major, but sporadic, pest primarily in Washington. Johansen and Eves (1973) quote Halfhill (unpublished) as suggesting that the displacement of the native parasitoids of the alfalfa aphid by _A_. _ervi_ and _A_. _smithi_ may have contributed to the rise in the abundance of this aphid.

At present, little is known of the alfalfa aphid's distribution, abundance, or importance as a pest on the crop in BC; moreover it is not known if established parasitoids of the pea aphid in BC attack the alfalfa aphid. However, studies on host selection and host switching can be used to assess the potential of these wasps as biological control agents of the alfalfa aphid. The following research should help us to gain a better understanding of parasitoid foraging behavior and parasitoid-host interactions. Moreover, it will provide important data on the alfalfa aphid that would be helpful in determining its potential as a pest on alfalfa in BC.

SECTION 1a: OBJECTIVES

The objectives of this study were:

1. To determine the distribution of the alfalfa aphid and its associated parasitoids on alfalfa in the southern interior of BC.

2. To investigate the prevalence of switching behavior among the four primary hymenopterous parasitoids of aphids on alfalfa in BC.

3. To investigate the causes of host selection by these parasitoids.

4. To assess the potential of these parasitoids as biological control agents of the alfalfa aphid.

SECTION 1b: GENERAL MATERIALS AND METHODS

Stock colonies of the pea and the alfalfa aphid were established from viviparous females collected on alfalfa at Kamloops, British Columbia. The colonies were started from individuals collected in 1972 and 1984 respectively. For all experiments, colonies were maintained in the laboratory at 20 ± 1 ^{o}C, 50 ± 5 % RH, with continuous lighting on potted broad-bean plants, (*Vicia faba* L. "Broad Windsor"), grown in garden-mix soil.

To obtain aphids of known age, reproducing adults were transferred to fresh bean plants for 8 h; any offspring produced during the 8-h period were kept and reared as a synchronous colony. Second-instar aphids were 72 ± 4 h old when caged with parasitoids in experiments.

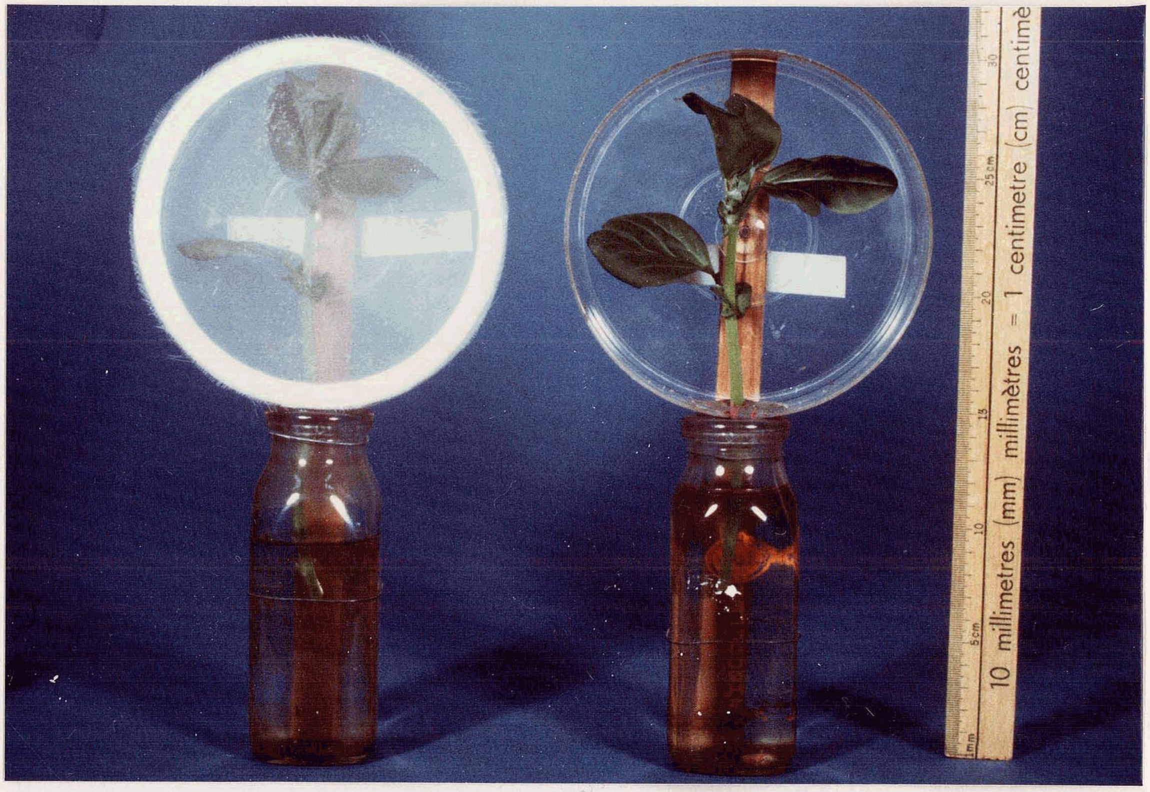
Colonies of four aphidiid hymenopterans were established in the laboratory from individuals that had emerged from parasitized pea aphids collected from alfalfa-growing districts of British Columbia. Colonies of *A. pisivorus* and *P. pequodorum* were started from material collected at Kamloops in July, 1984. Colonies of *A. smithi* and *A. ervi* were started from material collected at Chilliwack BC in July, 1982 and 1984 respectively.

For all experiments, the parasitoids were reared under the same conditions as the stock aphid colonies, on second- and third-instar pea aphids. Mummified aphids were collected and kept at 20 ± 1 ^{o}C with continuous lighting, until the adult parasitoids emerged. Adult parasitoids for stock colonies were allowed to mate freely for 24 to 48 h after emergence, after which they were held at approximately 10 ^{o}C to extend their longevity. However, females intended for experiments, were removed from the colonies and kept at approximately 20 ^{o}C until needed. All the parasitoids were fed a solution of honey and water.

Plastic petri-dish cages (Mackauer and Bisdee 1965) were used for rearing field-collected material and for laboratory experiments. Two sizes were used: 3.5 x 8.5 cm diam., and 4.0 x 15.5 cm diam. The cages had mesh covers, and a 1.5 cm hole in the side wall. Through this hole, a broad-bean shoot was inserted, and held in place with plasticine (Figure 1). All shoots were cut from 9- to 12-day old plants and maintained in bottles full of water during the experiments. Unless otherwise stated, laboratory experiments were conducted at 22 ± 1 ^{o}C, 55 ± 5 % RH, with fluorescent lighting in controlled environmental chambers.

Figure 1. Plastic cages, 4.0 x 15.5 cm diam., used for rearing field-collected material and for laboratory experiments.

8b



SECTION 2: DISTRIBUTION OF THE ALFALFA APHID AND ITS ASSOCIATED PARASITOIDS IN THE SOUTHERN INTERIOR OF BRITISH COLUMBIA

Introduction

In July 1984, S. Kambhampati collected pink aphids on alfalfa at Walachin, BC (personal communication in 1985 from Srinivas Kambhampati, Dept. of Biological Sciences, University of Notre Dame, Notre Dame, Ind.). These aphids were subsequently identified by Forbes and Chan (1986) as *Macrosiphum creelii* Davis, the alfalfa aphid. This species has been a pest on alfalfa from as early as 1909 in Nevada and the U.S. Pacific Northwest (Halfhill 1982), but its presence in Canada had not been confirmed before 1986. A. Campbell had found pink aphids on alfalfa at Kamloops in 1972 (personal communication in 1986 from Manfred Mackauer, Dept. of Biological Sciences, Simon Fraser University), but the identity of these aphids is uncertain.

Not much has been published on the parasitoid community of the alfalfa aphid in the U.S. Pacific Northwest. Both *Aphidius pisivorus* Smith and *Praon pequodorum* Viereck have been reported to parasitize the alfalfa aphid in the region (Anon. 1979), although *A pisivorus* is the only known parasitoid of this aphid in Central Washington (Halfhill 1982).

This section reports the results of surveys for the alfalfa aphid and its associated parasitoids in the principal alfalfa-growing districts of the southern interior of BC.

Materials and Methods

During late May to early July of 1985 and 1986, the distribution and relative abundance of the alfalfa aphid in the southern interior of BC were surveyed in cultivated alfalfa grown for fodder. Alfalfa fields were traversed and sweep net samples were taken at two- to three-meter intervals. The contents of the sweep nets were emptied onto trays and examined after every 100-200 sweeps. If both pea and alfalfa aphids were found, the abundances of both aphids were estimated from the numbers of both species found.

To determine the identity and abundance of parasitoid species, both living alfalfa aphids and field samples of alfalfa and pea aphids in alcohol were brought back to the Burnaby laboratory from Kamloops in July 1986. Approximately 1100 living alfalfa aphids were reared on cut alfalfa shoots in 15.5-cm-diam. plastic cages at 20 °C for two weeks. Aphids that mummified in these cages were removed, placed singly inside transparent gelatin capsules, and kept at 20 °C. Emerged parasitoids were identified as to sex and species according to criteria given by Mackauer and Campbell (1972) and Mackauer and Finlayson (1967). Totals of 300 pea and 300 alfalfa aphids were brought back in alcohol to the laboratory for dissection, and their parasitoid larvae identified as either *Aphidius* or *Praon* according to criteria given by Chorney and Mackauer (1979) for *Aphidius* and Chow and Sullivan (1984) for *Praon*.

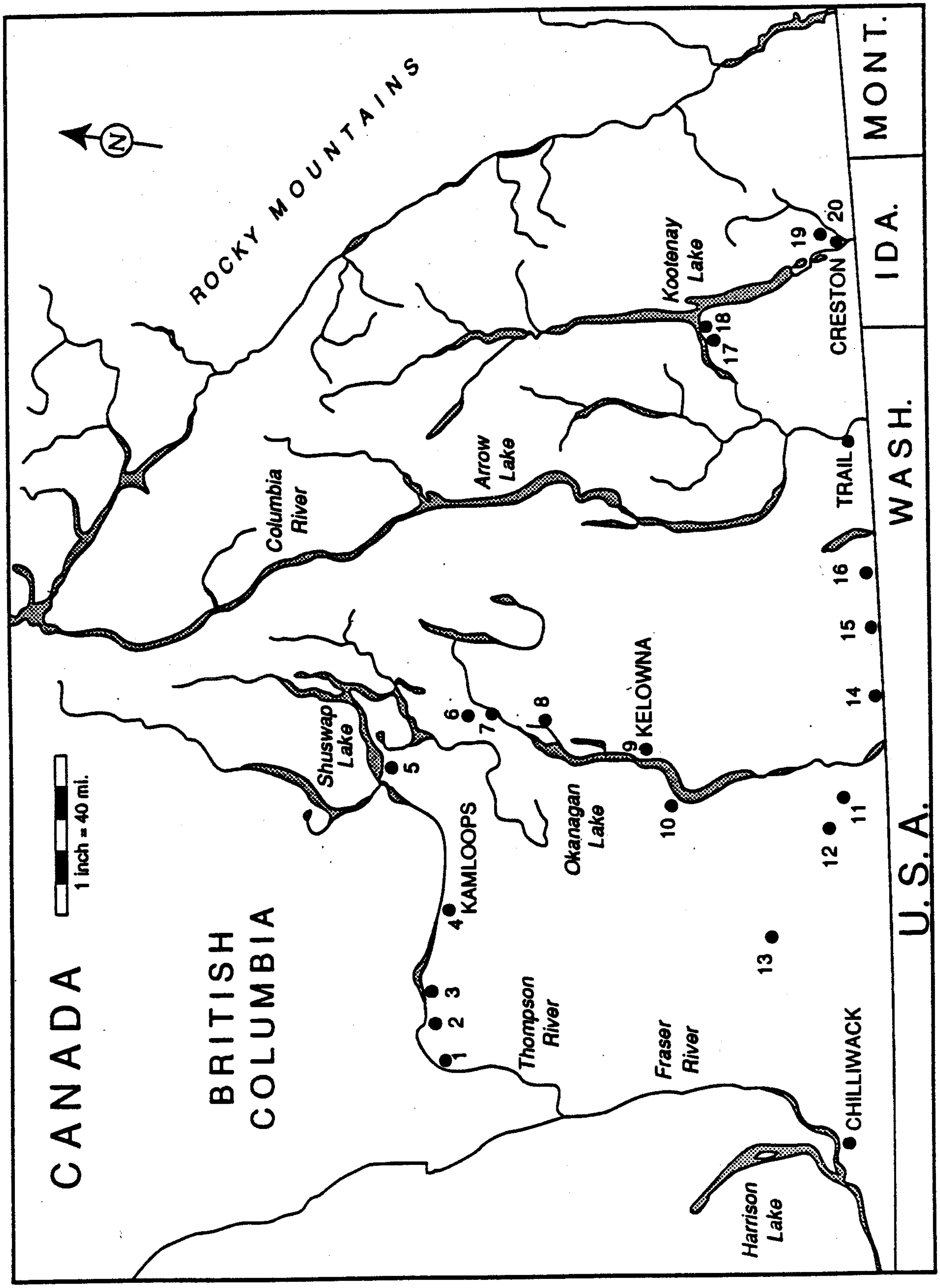
On July 3, 1986, approximately 1000 mummified pea and alfalfa aphids, indistinguishable in the field, were collected from alfalfa fields at Kamloops. The mummies were brought back to the laboratory and placed in covered wax-paper cups. The cups were held at room temperature and when all the parasitoids had emerged, the primary parasitoids were identified as described earlier. The numbers of hyperparasitoids that emerged were also recorded, but they were not formally identified. Additional surveys were made of alfalfa fields from Ashcroft to Kamloops in early August of 1985 and 1986.

Results

Cultivated alfalfa fields at 20 survey sites were examined for the alfalfa aphid (Fig. 2, Table 1). The aphid was found at only three sites, all of which were near Kamloops or between Cache Creek and Kamloops (Fig. 2, Table 1). Pea aphids were found in the alfalfa fields at all 20 sites. Where both aphids were found, pea aphids were from 50 to 100 times more abundant than alfalfa aphids.

Three hymenopterous parasitoid species, belonging to the family Aphidiidae, were identified from specimens which emerged in the laboratory from parasitized alfalfa aphids collected at

Figure 2. Alfalfa sites in the southern interior of British Columbia sampled for the alfalfa (*Macrosiphum creelii*) and the pea aphid (*Acyrthosiphon pisum*) 1985-1986. Collection sites (●) are listed in Table 1.


CANADA
BRITISH COLUMBIA
ROCKY MOUNTAINS
N
1 inch = 40 mi.
Shuswap Lake
KAMLOOPS
Thompson River
Fraser River
CHILLIWACK
Harrison Lake
Okanagan Lake
KELOWNA
Columbia River
Arrow Lake
Kootenay Lake
CRESTON
TRAIL
U.S.A.
WASH.
IDA.
MONT.
1
2
3
4
5
6
7
8
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10
11
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18
19
20

Table 1. Collections of the alfalfa (*Macrosiphum creelii*) and the pea aphid (*Acyrthosiphon pisum*) in the southern interior of British Columbia, 1985-1986.[1]

Region of survey	Map site	Location	Aphid species[2]
Thompson Country	1	Ashcroft	P
	2	Walachin	P,A
	3	Savona	P,A
	4	Kamloops	P,A
	5	Sorrento	P
Okanagan/ Similkameen	6	Enderby	P
	7	Armstrong	P
	8	Vernon	P
	9	Kelowna	P
	10	Peachland	P
	11	Cawston	P
	12	Keremeos	P
	13	Princeton	P
	14	Bridesville	P
Kootenay Boundary	15	Midway	P
	16	Grand Forks	P
	17	Harrop	P
	18	Procter	P
	19	Erikson	P
	20	Creston	P

[1] Sites 5 and 17-20 were surveyed only during 1986.

[2] P=*Acyrthosiphon pisum*, A=*Macrosiphum creelii*

Kamloops: *Aphididus ervi*, *A. pisivorus*, and *Praon pequodorum*. Dissection and emergence studies of alfalfa aphid and dissection studies of pea aphid showed that parasitism in field samples, from Kamloops during July 1986, was 6-7% for the alfalfa aphid and 27% for the pea aphid. Of 82 parasitoid larvae dissected from 300 pea aphids in alcohol from Kamloops, 99% were *Aphidius* and 1% *Praon*, whereas 22 parasitoid larvae dissected from 300 alfalfa aphids from Kamloops were 73% *Aphidius* and 27% *Praon*. In addition, the composition of 57 parasitoids that emerged from 1100 alfalfa aphids, collected in several samples at Kamloops in July 1986 and reared in the laboratory for two weeks, was: *P. pequodorum* (48%), *A. pisivorus* (34%), and *A. ervi* (18%).

A total of 996 parasitoids emerged from about 1000 mummified pea and alfalfa aphids collected near Kamloops on July 3, 1986. Aphidiid species made up 47% of this total, and the remainder were hyperparasitoids. The composition of aphidiids that emerged from these mummies was: *A. ervi* (96%), *P. pequodorum* (3%), and *A. pisivorus* (1%).

The attempts to sample alfalfa fields from Ashcroft to Kamloops in August of 1985 and 1986 were unsuccessful because hot and dry weather had reduced aphid and parasitoid populations to extremely low levels.

Discussion

A. ervi is commonly found in the alfalfa-growing districts of the U.S. Pacific Northwest (Anon. 1979), but it had not previously been reported from there as a parasitoid of the alfalfa aphid. It is possible that *A. ervi* does parasitize the alfalfa aphid in the region, but previous workers might have missed it by chance or incorrectly identified it as *A. pisivorus*. However, these two explanations are unlikely if *A. ervi* was as abundant in the Pacific Northwest during the time of these studies as it was in the southern interior of British Columbia during my survey.

It is also possible that populations of *A. ervi* in the Cache Creek-Kamloops area consist of or include a biotype that parasitizes both pea and alfalfa aphids, whereas their counterparts in the U.S. Pacific Northwest consist of biotypes that parasitize only the pea aphid. This hypothesis could be tested by comparing the host range of *A. ervi* from samples of both aphid species collected from the Pacific Northwest and the Cache Creek-Kamloops area. Cameron *et al*. (1984) proposed that *A. ervi* forms separate races differing in host range and genotype on certain aphid species. Similarly, Pungerl (1984) found that different populations of *A. ervi* had markedly different host ranges, but suggested that this behavior was probably conditioned and not inherited.

The predominance of *A. ervi* at Kamloops was not reflected in the composition of parasitoids that emerged from alfalfa aphids collected from the area. I have observed in the laboratory that when the probability of encountering either pea or alfalfa aphid was equal, alfalfa aphids were more often rejected as hosts by *A. ervi* than by either *A. pisivorus* or *P. pequodorum*, (Section 4b). Therefore, parasitism of the alfalfa aphid by *A. ervi* is not correlated with its abundance relative to other parasitoid species, if *A. ervi* seldom attacks the alfalfa aphid when the pea aphid is abundant.

The absence of *Aphidius smithi* from alfalfa fields at Kamloops was not unexpected. In 1972, this parasitoid was found to be widespread in the southern interior of British Columbia (Campbell 1973). However, by 1984 *A. smithi* had almost disappeared from the region (Mackauer and Kambhampati 1986). The pea aphid is the only host species at present known for *A. smithi* (Mackauer and Finlayson 1967) and therefore it is unlikely that this parasitoid would have parasitized the alfalfa aphid at Kamloops. Except for the absence of *A. smithi* and a decrease in *A. pisivorus*, the proportions of hymenopterous parasitoids in samples of mummified aphids collected at Kamloops during 1986 was similar to those generally found in the southern interior during 1983-1984 (Mackauer and Kambhampati 1986).

The distribution of the alfalfa aphid in the region is interesting because it is so restricted. Its recent discovery in the province indicates that the aphid is probably not native.

It might have been established in the Cache Creek-Kamloops area by wind-dispersed alates from the U.S. Pacific Northwest.

An estimated 100,000-150,000 tons of alfalfa hay is imported annually from eastern Washington into British Columbia (Anon. 1984). The alfalfa aphid is found there (Halfhill 1982), so that it is conceivable that infested forage was exported from Washington to the Cache Creek-Kamloops area.

Aphid alates can also disperse considerable distances by wind or air streams (Wellington 1983). Medler (1962) has found that air movement often transports grain aphids to the northern United States and Canada from overwintering sites several hundred kilometers to the south. Under the right weather conditions, alfalfa-aphid alates may have been transported from the US Pacific Northwest to the Cache Creek-Kamloops area.

Two factors that alone or in combination could restrict both the establishment and dispersal of the alfalfa aphid in the southern interior are topography and air movement patterns.

Mountains are often barriers to weak-flying insects that depend on air movement for dispersal. Aphids and other insects are sometimes dropped with precipitation in rain-shadow belts of mountain ranges (Wellington 1983). Thus the mountains surrounding many alfalfa-growing districts in the southern interior may hinder the introduction of the aphid. Finally, the air masses in the region tend to move from west to east rather than from south to north, and this could also restrict the dispersal of the aphid.

In summary, the alfalfa aphid was found in a single 70 km strip of the southern interior of British Columbia, an alfalfa-growing district between Cache Creek and Kamloops. The three most common parasitoids of the pea aphid in southern British Columbia were found to parasitize the alfalfa aphid in the Kamloops area. However, to the best of my knowledge, *A. ervi* has not been found to parasitize the alfalfa aphid in any other area in North America.

SECTION 3: HOST SELECTION BY FOUR PARASITOIDS

Introduction

Switching is a theoretical concept applicable to host selection by parasitoids. The tendency of predators or parasitoids to concentrate on the most abundant host species was called "switching" by Murdoch (1969). Switching results from the temporary preference of a parasitoid for one of the hosts. 33eference can be measured as a deviation in the proportion of the host parasitized from the proportion available. The causes and mechanisms of switching have been extensively investigated and discussed in the literature (Murdoch and Oaten 1975, Visser 1981, Greenwood 1984). Most of the work has been on switching by predators.

However, switching has also been studied in hymenopterous parasitoids of insects (Cornell and Pimentel 1978, Dransfield 1979, Heong 1981, Gardner and Dixon 1985). Cornell (1976) suggested that an increase in searching efficiency is one of the adaptive values of switching by parasitoids. Reluctance to switch between hosts can limit the usefulness of polyphagous parasitoids in pest management (Powell 1986).

The objectives in this study were: (1) To determine if female *Aphidius ervi*, *A. smithi*, *A. pisivorus*, and *Praon pequodorum* show preference when given a choice between pea and alfalfa aphids; and (2) if preference occurs, to determine if it follows the theory of switching.

Methods

About 30 females each of A. ervi, A. smithi, A. pisivorus, and P. pequodorum were taken from stock colonies. Three- to 4-day old females were placed singly for 6 h in plastic cages of 15.5 cm diam., each containing the apical portion of a broad-bean shoot and 40 second-instar aphids in one of the following respective combinations of pea (AP) to alfalfa aphids (MC): 0:40, 10:30, 20:20, 30:10, 40:0. From 4 to 5 days later, half of the pea and half of the alfalfa aphids in each combination were dissected. The numbers of living aphids in each cage, the dissected aphids containing parasitoid larvae, and parasitoid larvae in each aphid were recorded. Twenty replications of each treatment were completed for each of the parasitoid species. The experiments were conducted in standard conditions.

The means and standard errors were determined for the proportions of pea and alfalfa aphids parasitized in the 40:0 treatments of each parasitoid species. Duncan's multiple range test (DMRT) was used to compare the proportions of pea and alfalfa aphids parasitized by the four parasitoids. The numbers of pea and alfalfa aphids parasitized by the same parasitoid species, were compared by paired-difference t-tests in the 20:20 treatments. In addition, the proportions of parasitized aphids that contained more than one parasitoid larva (superparasitized) were compared within and between the five treatments for each parasitoid species by ANOVA and DMRT. Measurement of the frequency of superparasitism could reveal additional information on the degree of preference shown by parasitoids. For example, if superparasitism is high among pea aphids and parasitism is low among alfalfa aphids, it may indicate that unparasitized alfalfa aphids are less preferred hosts than parasitized pea aphids.

All proportions, for each species of aphid in each replication, were transformed using the following arcsine transformation (Zar 1974):

$$Y = \tfrac{1}{2}\left(\arcsin\sqrt{x/(n + 1)} + \arcsin\sqrt{(x + 1)/(n + 1)}\right) \qquad (1)$$

where "n" is the total number of dissected or parasitized aphids of both or a single species, and "x" is the total number of parasitized or superparasitized aphids of one species.

Host switching was tested by a modification of the method described by Murdoch (1969). In brief, Murdoch proposed that "... the number of attacks (by a predator) upon a (prey) species is disproportionately small when the species is rare". This concept can easily be applied to parasitoids; and the null or "no switch" model for two host species can be written as:

$$P_1 = C*F_1 \;/\; (1-F_1 + C*F_1) \qquad (2)$$

where "P_1" is the proportion of host species 1 among all parasitized hosts, "F_1" is the proportion of host species 1 in the environment, and "C" is the index of parasitoid preference for host species 1. Murdoch suggested that "C" can be expressed as:

$$C = (N_1 / N_2) / (H_2 / H_1) \qquad (3)$$

where "N_1 / N_2" is the ratio of the two host species actually found among all parasitized hosts, and "H_2 / H_1" is the ratio of the two host species in a given environment. In short, "C" is the number of times the parasitoid will select one host species over the other at any given relative frequency of the two hosts. When switching does not occur, "C" is a constant that can be determined at any ratio of "H_2 / H_1". If "C" is known, we can compare the observed proportions of a host species that were parasitized to predicted proportions as its availability changes.

The switching hypothesis is that "C" is in fact not constant, but increases as "H_2 / H_1" decreases. If switching occurs, the observed proportion of host species 1 among all parasitized hosts will be higher than predicted when that species is abundant, and correspondingly lower when rare.

The method used to test for host switching in this study differed from that of Murdoch (1969) in three ways: (1) The "C" values determined for each of the 20 replications of the 20:20

treatments were used to estimate 20 values of "P_1"; (2) The 20 P_1 values were used to estimate the number of host species 1 found among all parasitized aphids in each replication of the 30:10 and 10:30 treatments; (3) The means of these 20 estimates were compared with the actual number of host type 1 found among all parasitized aphids in each replication.

Murdoch (1969) used the mean of the "C" values (C_M) to estimate a P_1 value that would be compared with the proportions of host type 1 parasitized in the different treatments. However, when "C" is variable among replications, C_M may not accurately represent preference. David Eaves (personal communication, July 1987, Dept. of Mathematics and Statistics, Simon Fraser University) suggested that the arithmetic mean of a set of P_1 values, estimated from all the "C" values from an experiment, would be a better estimate of the expected parasitism of host type 1 at any given ratio of hosts than the use of C_M as suggested by Murdoch.

In this study, "C" was estimated for each parasitoid species from the 20:20 treatments. Species 1 in these experiments was the pea aphid and the predicted numbers and actual numbers of pea aphids parasitized at different combinations of hosts were compared by Wilcoxon signed-rank tests.

Results

Superparasitism of the alfalfa aphid by A. smithi and A. ervi did not vary significantly between treatments and fewer than 5 % of the alfalfa aphids parasitized by these wasps were superparasitized. Similarly, superparasitism of the pea and alfalfa aphid by A. pisivorus did not vary between treatments and was also quite low. It occurred in only 4.8 ± 8.9 % of the pea aphids and 8.7 ± 17.3 % of the alfalfa aphids parasitized by A. pisivorus.

Superparasitism of the pea aphid by A. smithi did not differ significantly between treatments. It occurred in 36 ± 8 % of the pea aphids parasitized by A. smithi. In comparison, superparasitism of the pea aphid by A. ervi seemed to increase as the number of pea aphids in the treatments decreased (Table 2). P. pequodorum did not superparasitize either aphid in this study.

All four wasp species parasitized more pea than alfalfa aphids in the 20:20 combination, but parasitism of the alfalfa aphid was highest with A. pisivorus (Table 3). In the 40:0 combinations, the proportions of alfalfa aphids parasitized by A. ervi, A. smithi, and P. pequodorum were only about one third of the proportions of pea aphids parasitized by comparable parasitoids (Table 4). In both 40:0 combinations, proportions of pea and alfalfa aphids parasitized by A. pisivorus were significantly different but close; A. smithi parasitized the

Table 2. Superparasitism of Acyrthosiphon pisum (AP) by Aphidius ervi. Parasitoid females were singly caged for 6 h with A. pisum and Macrosiphum creelii (MC), in different ratios, at 22 ± 1 °C, 51 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Treatment[1] (AP : MC)	n[2]	Total AP parasitized	Total eggs laid[3]	Percentage superparasitized[4]
40 : 0	400	212	234	8.4 ± 7.8[b]
30 : 10	300	206	254	15.8 ± 19.8[b]
20 : 20	200	139	163	17.9 ± 15.3[b]
10 : 30	100	79	115	32.3 ± 35.5[a]

[1] Each treatment group comprised n = 20 parasitoids that were confined with 40 aphids in the given ratio.

[2] One-half of the total numbers of A. pisum in each of 20 replications were dissected to show parasitism.

[3] Into A. pisum by each treatment group.

[4] The mean (± 1 SEM) percentages of parasitized A. pisum that contained more than one parasitoid larva. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

Table 3. Parasitism of *Acyrthosiphon pisum* and *Macrosiphum creelii* by four species of parasitoids. Parasitoid females were singly caged with 20 aphids of each species simultaneously for 6 h at 22 ± 1 °C, 51 ± 5 % RH, with continuous lighting.[1] All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Mean aphids parasitized[2] (± 1 SEM)		Percentage total parasitism[3] (± 1 SEM)	
	A. pisum	*M. creelii*	*A. pisum*	*M. creelii*
Aphidius ervi	6.9 ± 2.5**	1.7 ± 1.6	80.1 ± 16.2^{a,b}	19.9 ± 16.2
A. pisivorus	7.5 ± 2.0**	4.9 ± 2.3	61.6 ± 12.2^{c}	39.4 ± 12.2
A. smithi	8.3 ± 2.2**	1.2 ± 0.9	88.3 ± 7.5^{a}	11.7 ± 7.5
Praon pequodorum	6.8 ± 2.2**	3.0 ± 2.5	73.3 ± 17.0^{b}	26.7 ± 17.0

[1] Ten of 20 aphids of each species in each of 20 replications were dissected to show parasitism.

[2] Statistical significance of differences between means within rows (by paired-difference t-test, two-tailed): **, $P \leq 0.01$.

[3] Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

Table 4. Parasitism of Acyrthosiphon pisum (AP) and Macrosiphum creelii (MC) by four species of parasitoids. Parasitoid females were singly caged for 6 h with 40 aphids of one species at 22 ± 1 °C, 51 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Total parasitized[1]		Percentage parasitized[2] ($\bar{X} \pm 1$ SEM)	
	AP	MC	AP	MC
Aphidius ervi	212	80	53.0 ± 23.5^{c}	20.0 ± 13.3^{b}
A. pisivorus	266	210	66.5 ± 12.5^{b}	52.5 ± 16.0^{a}
A. smithi	340	34	85.0 ± 10.0^{a}	8.5 ± 11.5^{c}
Praon pequodorum	211	75	52.8 ± 18.5^{c}	18.8 ± 12.0^{b}

[1] Twenty of 40 aphids in each of 20 replications were dissected to show parasitism.

[2] Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

largest proportion of pea aphids and the smallest proportion of alfalfa aphids; and P. pequodorum and A. ervi parasitized similar proportions of both aphids.

Switching, as defined by Murdoch (1969), was not observed among the parasitoids examined in this study. Fewer pea aphids than predicted were parasitized by A. ervi and P. pequodorum in the 10 AP:30 MC combination (Table 5). However, the differences between observed and predicted numbers of pea aphids parasitized by the same wasps in the 30 AP:10 MC combination were not significant (Table 5). Differences between the predicted and observed numbers of pea aphids parasitized by A. pisivorus and A. smithi were not significant.

Discussion

Preference is usually measured as a deviation in the proportion of the hosts parasitized from the proportion of the hosts available. However, this definition of preference does not distinguish between the different factors that may cause certain hosts to be disproportionately attacked. In this study, disproportionately large proportions of the pea aphids contained parasitoid larvae. This may have resulted from different rejection of the aphids by the wasps, from different abilities of the aphids to escape the wasps, or from different survival of parasitoid eggs in the aphids. By investigating these interactions, we may find behavioral and physiological

Table 5. Predicted and observed numbers of *Acyrthosiphon pisum* (AP) parasitized by four species of parasitoids. Parasitoid females were singly caged for 6 h with 40 *A. pisum* and *Macrosiphum creelii* (MC), in different ratios, at 23 ± 1 °C, 30 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Treatment (AP : MC)	Mean parasitized *A. pisum*[1]	
		Observed[2] (± 1 SEM)	Predicted[3] (± 1 SEM)
Aphidius ervi	10 : 30	4.0 ± 1.1**	5.0 ± 2.1
	30 : 10	10.3 ± 3.1	9.9 ± 3.3
A. pisivorus	10 : 30	3.7 ± 1.3	3.9 ± 1.3
	30 : 10	10.2 ± 2.6	10.4 ± 2.6
A. smithi	10 : 30	3.8 ± 1.1	4.0 ± 2.2
	30 : 10	12.8 ± 1.6	12.6 ± 1.7
Praon pequodorum	10 : 30	3.7 ± 1.0**	4.7 ± 1.6
	30 : 10	9.1 ± 3.3	8.9 ± 3.2

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[1] Statistical significance of differences between means within rows (by Wilcoxon signed-rank test): **, $P \leq 0.01$.

[2] One-half of the total numbers of *A. pisum* in each of 20 replications were dissected to show parasitism.

[3] Predicted values were determined by Murdoch's proportionality constant "C" (Murdoch 1969) as described in Section 3.

explanations for the different parasitism of pea and alfalfa aphids by these wasps.

Host discrimination, the ability to distinguish between parasitized and unparasitized hosts and to limit oviposition to the latter, has been found in *A. smithi* and *P. pequodorum* (Chow and Mackauer 1984), and other aphidiids (Chow and Mackauer 1986; Collins and Dixon 1986; Cloutier *et al*. 1984). Yet, superparasitism is common among the Aphidiidae under laboratory conditions (Mackauer 1983; Cloutier 1984; Kambhampati *et al*. 1987). The frequency of superparasitism by these wasps may depend upon their egg load and the availability of hosts (Cloutier 1984; Collins and Dixon 1986; Kambhampati *et al*. 1987). Collins and Dixon (1986) suggested that egg load, the numbers of mature eggs in the gonads, could affect the motivation of parasitoids to oviposit. When their egg-load is high and unparasitized hosts become rare, wasps may intentionally oviposit into hosts already parasitized.

Superparasitism of pea aphids by *A. ervi* increased when the availability of these aphids decreased. This may indicate that alfalfa aphids are less acceptable to *A. ervi* than to *A. pisivorus* or *P. pequodorum*. Similarly, the high proportions of pea aphids superparasitized by *A. smithi* in all the two-host treatments may reflect this parasitoid's strong reluctance to parasitize alfalfa aphids. Kambhampati (1987) found that age-specific fecundity was higher in 3- to 4-day-old female *A. smithi* than in comparable females of the other three aphidiids.

This may also explain why superparasitisim was often more frequent among pea aphids confined with A. smithi than among pea aphids confined with the other parasitoid species.

Murdoch's definition of switching (1969) implied a numerical result, rather than any particular mechanism. Predators may concentrate on a particular host for many reasons. Murdoch et al. (1975) suggested four mechanisms for switching in predators: variable rejection of prey; variable discovery or recognition of prey; variable time spent in different parts of a habitat searching for different prey; and different rates of capture for prey with different escape strategies. Cornell (1976) showed that conditions which favor switching include: patchy distribution of prey; nonsessile searching by the predator; and sensory detection systems of the predator that work at a distance. It is apparent that these conditions and mechanisms are also applicable to many parasitoid systems, but switching has not been extensively studied in parasitoids.

To the best of my knowledge, host switching has been examined only in hymenopterous parasitoids of insects. Heong (1981) studied host selection in Anisopteromalus calandrae given access to mixed third and fourth instars and to pupae of Callosobruchus maculatus, a stored products beetle. In choice tests where two stages of the host were available, the parasitoid respectively showed preference for the fourth instar followed by the pupa and the third instar. There was, however, no evidence of switching when the relative abundance of the host types was varied.

Dransfield (1979) studied host selection in *Aphidius uzbekistanicus* given different ratios of a cereal aphid, *Metopolophium dirhodum*, and a grassland aphid, *Hyalopteroides humilus*. The wasp showed a clear preference for *M. dirhodum* and switching did not occur. In comparison, Gardner and Dixon (1985) found that *Aphidius rhopalosiphi* showed no preference between the cereal aphids, *Metopolophium dirhodum* and *Sitobion avenae*, and did not concentrate its attacks on the more abundant of the aphids in switching experiments.

Cornell and Pimentel (1978) found switching in *Nasonia vitripennis*, a wasp that feeds on and oviposits in fly pupae, using as hosts *Musca domestica*, *Phormia regina*, and *Lucilia sericata*. *N. vitripennis* always preferred *P. regina* when this host and one of the other two were equally available. But in the switching tests, the wasp concentrated its attacks on the most abundant host and the authors suggested that the alternative host was rejected.

In the present study, I found that none of the four parasitoids switched when the relative abundance of pea and alfalfa aphids was varied. It may be suggested that *A. ervi* and *P. pequodorum* showed partial switching because they parasitized fewer pea aphids than predicted in the 10 AP:30 MC ratio. However, these deviations from the null models were small and they probably indicated no more than a slight increase in the parasitoids' acceptance of alfalfa aphids when pea aphids were relatively rare. *A. ervi* and *P. pequodorum* preferred the pea aphid under all circumstances .

Murdoch and Oaten (1975) suggested that the absolute density of prey and the experience of the predator may affect switching. Moreover, there is more than one mechanism that can lead to switching (Murdoch _et al_. 1975) and the absence or presence of switching will depend on the mechanism that is tested. It is possible that the aphidiids, tested in these laboratory experiments, switch under different conditions and with different hosts.

Switching seems to occur less often in parasitoids than in predators, and this may be due to their difference in goals. It is commonly assumed that both predators and parasitoids attempt to maximize their total genetic contributions to future generations, in the case of predators this is done by maximizing the rate of energy intake during foraging (MacArthur and Pianka 1966; Charnov 1976; Krebs et al. 1977). However, when the egg supply of a parasitoid is limited, maximization of the oviposition rate may not be the best strategy to achieve this goal (Iwasa et al. 1984). By sampling what is available, predators can learn to switch to different kinds of prey (Holling 1965). In comparison, parasitism is more directly related to fitness than predation and it is therefore not surprising that the host ranges of parasitoids are often more restrictive than the diets of predators.

Parasitoids can show preference for the host in which they were reared (Vinson 1976). Innate preference may hinder switching, but switching is possible if parasitoids can be conditioned to prefer certain hosts. Cornell and Pimentel (1978) suggested that N. vitripennis showed switching when the wasp became conditioned to attacking the host on which it previously fed. Murdoch and Oaten (1975) showed that conditioning was often required before predators would switch. It is possible that the aphidiids, tested in these laboratory experiments, did not switch because they were not sufficiently conditioned to the more abundant aphid in their treatments.

In summary, all four parasitoid species in this study showed preference for the pea aphid and did not switch when the relative abundance of pea and alfalfa aphids were systematically varied from equality. The following section will examine behavioral explanations for the parasitoids' preference.

SECTION 4: BEHAVIORAL ASPECTS OF HOST SELECTION BY PARASITOIDS

Introduction

Many factors can influence the selection of hosts by parasitoids. In Section 3, the four aphidiid species showed different degrees of preference for pea over alfalfa aphids, which may have resulted from different abilities of the aphids to escape the parasitoids, different rejection of the aphids by the parasitoids, or different survival of the parasitoid's eggs in the aphids. In the four sub-parts of this section, I examine behavioral explanations for the apparent preferences of the parasitoids for pea aphids and the absence of switching among these wasps.

The ability of different hosts to escape from parasitoids may account for the observed variations in parasitism. A common escape behavior of aphids is to drop from their plant hosts. I compared the dropping responses of pea and alfalfa aphids to determine if they varied (Section 4a).

Preference may also result from frequent rejection of the alfalfa aphid by parasitoids following encounter, or from different encounter rates with the two aphid species, or from different abilities of the aphids to avoid parasitism after encounter. I examined the contribution of these factors to differences between the parasitism of pea and alfalfa aphids by the four wasps (Section 4b).

Finally, preference could also be affected by recent or prior experiences of parasitoids with hosts. I tested the hypothesis that parasitoids can learn to show absolute preference for the pea aphid (Section 4c). The effect of conditioning parasitoids on a single host and its implications for switching, was examined in Section 4d.

SECTION 4a: ESCAPE BEHAVIOR OF PEA AND ALFALFA APHIDS

The escape responses of aphids may vary with different species and instars of the same species. They escape from natural enemies by walking away, kicking, using passive avoidance, or dropping from the plant (Hajek and Dahlsten 1987), a common behavior among aphids (Dixon 1958). For example, pea aphids readily fall from plants when disturbed (Dixon 1958), but first-instar nymphs are less likely to drop than adults (Roitberg and Myers 1978). Hajek and Dahlsten (1987) also found the dropping response to be more highly developed in old than in young *Euceraphis betulae* Koch.

During colony rearing of both pea and alfalfa aphids, I noted that alfalfa aphids appeared to drop more frequently than pea aphids when the host plants were disturbed. Aphids that drop readily when disturbed, avoid enemies more successfully than those that do not (Roitberg *et al*. 1979; Hajek and Dahlsten 1987). Host selection by aphid parasitoids is influenced by the ability of the available hosts to escape or avoid parasitism (Gardner and Dixon 1985). Evaluation of the escape responses of aphids may improve our understanding of host selection by aphid-parasitoids.

This study examined the dropping response of different instars of pea and alfalfa aphid to potential danger as signaled by plant vibration.

Materials and Methods

Ten pea and ten alfalfa aphids, all of the same ages and instars, were placed in two separate 15.5-cm-diam. plastic cages containing the apical portion of a cut broad-bean shoot. The cages were kept under continuous lighting at 20 ± 1 °C.

After the aphids had settled on the plants for 5-6 h, the stalk of each bean shoot was gently struck three times with a pencil, and the numbers of aphids that fell were recorded. The tests were made with first-, second-, third-, and fourth-instar nymphs, and apterous adults. The adults were 216 ± 4 h old. (9 days) Five replications of each test were completed.

Results

The results are shown in Table 6. No statistical comparisons were used because the data were highly uniform and the differences were apparent. Third- and fourth-instar and adult alfalfa aphids dropped in much higher numbers than their pea-aphid counterparts. First- and second-instar alfalfa aphids dropped in lower numbers than the older aphids, but not in higher numbers than their pea-aphid counterparts. Second-, third-, and fourth-instar and adult pea aphids did not drop in different numbers, and no first-instar pea aphids dropped.

Table 6. Numbers of pea (*Acyrthosiphon pisum*) and alfalfa aphids (*Macrosiphum creelii*) that fell from broad-bean shoots tapped three times with a pencil ($\overline{X}$ ± 1 SEM)[1].

Instar	Pea aphid	Alfalfa aphid
I	0.0 ± 0.0	0.2 ± 0.4
II	1.8 ± 0.4	2.4 ± 0.5
III	1.8 ± 0.8	9.6 ± 0.5
IV	2.0 ± 0.7	10.0 ± 0.0
Adult	1.6 ± 0.9	10.0 ± 0.0

[1] The mean of 10 aphids in five trials.

Discussion

Like Roitberg and Myers (1978), I found that young instars were less likely to drop than their older counterparts, possibly because the risks associated with leaving a host plant are high for the small nymphs. According to Roitberg et al. (1979), "young instars are less successful at finding new plants and more susceptible to high ground temperatures than adults, so (young instars) may require a stronger stimulus to drop than older instars". In addition, Roitberg and Myers suggested (1978) that withdrawing the stylets is more difficult for young than for old aphids. Therefore, young instars may drop only when the potential danger of remaining on a plant is high.

High mortality of aphids that drop onto the ground may select against dropping behaviour as a first line of defense against enemies (Roitberg and Myers 1978). The rapid dropping-response of third-instar and older alfalfa aphids implies that dropping is less risky for these individuals than for their pea-aphid counterparts. Alfalfa aphids may suffer lower mortality on the ground, than pea aphids. Aphids that fall to the ground are attacked by ground-zone predators (Scheller 1984) and become paralyzed when ground temperatures are high (Roitberg and Myers 1979). It is therefore advantageous for aphids to quickly locate a host plant and spend as little time as possible on the ground. During this study, I observed that alfalfa aphids of the third instar and older, seemed to have a greater tendency to disperse after dropping, than their pea aphid counterparts. These alfalfa aphids may locate a host plant in less time than comparable pea aphids. Heat tolerance and dispersal studies, similar to those conducted by Roitberg and Myers (1979), could be used to test this hypothesis.

Alternatively, it is conceivable that nondropping escape-behavior is less successful among alfalfa aphids than pea aphids. When danger is detected, remaining on a plant can potentially be more risky for third-instar and older alfalfa aphids than for their pea-aphid counterparts. Therefore, even when the risks of leaving a plant are the same for both aphid species, these alfalfa aphids may drop more readily than pea aphids. Direct observations, on the behavioral interactions between these two species and their natural enemies, could be used to examine this hypothesis.

Finally, Roitberg and Myers (1978) found dropping to be the only effective escape-behavior for young pea aphids. First- and second-instar alfalfa aphids did not drop more readily than their pea-aphid counterparts. Consequently, young aphids of both species may be equally susceptible to either predation or parasitism.

In summary, this study provides information on the dropping responses of different instars of both aphid species to potential danger. Future studies should evaluate this behavior using living parasitoids. In Section 4b of this thesis, I did so, using second-instars of both aphid species and four parasitoid species.

SECTION 4b: INTERACTIONS BETWEEN THE PARASITOIDS AND APHIDS

Host preference can be defined as the innate or learned attributes of a parasitoid that predispose it to locate and parasitize certain hosts more than others. However, it is difficult to assess preference directly because selective parasitism is often affected by the availability and the susceptibility of the hosts in the habitat. Some hosts may be attacked more frequently than others, not because they are preferred, but simply because they are more accessible (Gardner and Dixon 1985), more vulnerable (Luck et al. 1982), or require less time to handle (Gardner and Dixon 1985, Ankersmit et al. 1986).

In Section 3, I found that female Aphidius ervi, A. smithi, A. pisivorus, and Praon pequodorum appeared always to prefer the pea aphid when they were given different combinations of second-instar pea and alfalfa aphids. In these studies, preference was measured as a deviation in the proportion of the host parasitized from the proportion of the host in the environment. The problem with this measurement is that it combines all of the possible reasons why the pea aphid was disproportionately parasitized. Preference for the pea aphid may have resulted from different encounter rates between the pea and alfalfa aphid, from frequent rejection of the alfalfa aphid following encounter, from different abilities of the aphids to escape after encounter, or from different survival of parasitoid eggs in the aphids.

For better understanding of host preference and selection by these four parasitoid species, it is necessary to determine the relative importance of the different behavioral components and the suitability of the two aphid species. The observational studies in this section examine the behavioral explanations for the parasitoids' preference for the pea aphid.

Methods

About 30 females each of *A. ervi*, *A. smithi*, *A. pisivorus*, and *P. pequodorum* were taken from stock colonies, at less than 24 h-old, and placed singly for 24 to 30 h in 15.5-cm-diam. plastic cages, with 50 second-instar pea aphids, 50 second-instar alfalfa aphids, and the apical portion of a broad-bean stalk. The parasitoids were then kept in empty cups and fed a honey and water solution for 30 to 60 min, after which they were put singly in 15.5-cm-diam. plastic cages, each containing 30 second-instar pea aphids, 30 second-instar alfalfa aphids, and the apical portion of a broad-bean stalk. The mesh covers of the cages were replaced with transparent cellophane covers for direct observations of the interactions between parasitoids and aphids.

The observations recorded the following: the species of aphid encountered by the parasitoid; and whether the parasitoid attempted to strike the aphid with its ovipositor (attack); successfully struck the aphid; allowed the aphid to escape before it was struck; or rejected it. A "rejection" was recorded when a parasitoid came into contact with and had the opportunity to strike and parasitize an aphid, but failed to do so. In addition, aphids that escaped parasitism were categorized as having escaped either before or after the parasitoids had an opportunity to examine or attempt to parasitize them.

Aphids struck by parasitoids were removed from the cages and replaced with an unparasitized second-instar aphid of the same species. If struck aphids were not removed, parasitoids would have encountered four types of hosts: unparasitized pea aphids, unparasitized alfalfa aphids, parasitized pea aphids, and parasitized alfalfa aphids. Therefore, struck aphids were removed because I was primarily interested in the response of parasitoids to unparasitized pea and alfalfa aphids. It would have been interesting to determine the effect of encounters with parasitized aphids on the foraging behavior of these parasitoids, but I was unable to distinguish newly parasitized aphids from their unparasitized counterparts.

The observations were ended after a parasitoid had encountered 20 aphids, and a total of 10 replications had been completed for each of the four parasitoid species during April and June, 1987. An additional 10 replications were completed for _A_. _smithi_ and _A_. _ervi_ during November, 1987. The observations were made at 23 ± 1^{o}C, 30 ± 5 % RH, with continuous lighting.

The data were analyzed by fully randomized ANOVA. Separate ANOVAs were run for each of the following dependent variables: the proportion of encountered aphids that were struck, rejected, or allowed to escape; and the proportion of attacks that were successful. The factors examined were species of parasitoids and aphids. One-way ANOVAs were used to analyze the data for each of the four parasitoid species, and two-way ANOVAs were used to compare the four parasitoid species. When significant main effects or interactions were found, Duncan's multiple range tests were used to compare the dependent variables. All proportions were transformed into their arcsine values by equation (1) (Section 3) and analyzed by ANOVA. The numbers of pea and alfalfa aphids encountered by each parasitoid species were compared by paired-difference t-tests.

I also made general observations on the searching and host-handling behavior of the parasitoids and the escape behavior of the aphids.

Results

I. Studies completed during April, May, and June, 1987

Female parasitoids encountered equal numbers of pea and alfalfa aphids (Table 7), but they attacked more pea than alfalfa aphids (Tables 8). _A_. _pisivorus_ and _P_. _pequodorum_ attacked pea and alfalfa aphids with equal success (Table 8) but attacked more alfalfa aphids than _A_. _smithi_ or _A_. _ervi_. In

Table 7. Numbers of *Acyrthosiphon pisum* and *Macrosiphum creelii* among 20 aphids consecutively encountered by four species of parasitoids. Parasitoid females were singly caged with 30 aphids of each species simultaneously at 23 ± 1 °C, 30 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Months in 1987[1]	Encountered aphids[2] ($\bar{X}$ ± 1 SEM)[3]	
		A. pisum	*M. creelii*
Aphidius ervi	3 - 6	9.9 ± 1.2	10.1 ± 1.2
	11 - 11	11.3 ± 1.9**	8.7 ± 1.9
A. pisivorus	3 - 6	9.9 ± 1.2	10.1 ± 1.2
A. smithi	3 - 6	9.9 ± 1.2	10.1 ± 1.2
	11 - 11	11.1 ± 0.9	9.1 ± 0.9
Praon pequodorum	3 - 6	10.6 ± 1.5	9.4 ± 1.5

[1] The studies were completed during these months in 1987.

[2] Statistical significance of differences between means within rows (by paired-difference t-test, two-tailed): **, $P \leq 0.01$.

[3] Means are based on a total of 10 replications.

Table 8. Attempted and successful strikes on *Acyrthosiphon pisum* and *Macrosiphum creelii* by four species of parasitoids. Parasitoid females were singly caged with 30 aphids of each species at 23 ± 1 °C, 30 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C. All observations were made during April-June 1987.

Parasitoid species	Encountered aphids attacked[1,2] (%)		Successful strikes[2] (%)	
	A. pisum	*M. creelii*	*A. pisum*	*M. creelii*
Aphidius ervi	$89 \pm 12^{a**}$	37 ± 12^{b}	92 ± 10^{a}	78 ± 20^{a}
A. pisivorus	$90 \pm 9^{a*}$	80 ± 12^{a}	$82 \pm 13^{a*}$	75 ± 14^{a}
A. smithi	$88 \pm 8^{a**}$	33 ± 18^{b}	77 ± 18^{a}	43 ± 40^{b}
Praon pequodorum	$93 \pm 8^{a**}$	51 ± 14^{c}	90 ± 11^{a}	78 ± 20^{a}

[1] Each female encountered 20 aphids in each of 10 replications.

[2] The mean (± 1 SEM) percentages of encountered aphids that were attacked and the mean (± 1 SEM) percentages of successful strikes were compared separately for statistical significance. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test. Statistical significance of differences between means within rows (by ANOVA): *, $P \leq 0.05$; **, $P \leq 0.01$.

comparison, *A. ervi* also attacked both aphids with equal success, but *A. smithi* attacked pea aphids with greater success than alfalfa aphids (Table 8). Attacks by *A. smithi* on the alfalfa aphid were less successful than attacks by other parasitoids on either aphid.

All of the four parasitoids struck a greater proportion of encountered pea than alfalfa aphids (Table 9). The proportions of pea aphids struck by *A. pisivorus*, *P. pequodorum*, *A. ervi*, and *A. smithi* were respectively 1.3, two, three, and five times greater than the proportions of alfalfa aphids struck by comparable parasitoids. The proportions of pea and alfalfa aphids struck by *A. smithi* were the lowest among the four parasitoids examined in these studies.

Pea aphids were rarely rejected, but close to half of the alfalfa aphids encountered by *A. ervi*, *A. smithi*, and *P. pequodorum* were rejected (Table 9). *A. pisivorus* did not reject more than 13 % of the alfalfa aphids that were encountered.

Both aphid species escaped more frequently from *A. smithi* and *A. pisivorus* than from *A. ervi* and *P. pequodorum* (Table 9). However, alfalfa aphids did not escape more frequently than pea aphids. Some aphids dropped from the plants before parasitoids could reject or attack them, but most of them dropped only after they were attacked.

II. Studies completed during November, 1987

A. smithi encountered equal numbers of both aphids, but *A.*

Table 9. Percentages of encountered *Acyrthosiphon pisum* and *Macrosiphum creelii* that were struck by, rejected by, or escaped from four species of parasitoids. Parasitoid females were singly caged with 30 aphids of each species at 23 ± 1 °C, 30 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C. All observations were made during April-June 1987.

Parasitoid species	Struck[1,2] (%)		Rejected[1,2] (%)		Escaped[1,2] (%)	
	A. pisum	*M. creelii*	*A. pisum*	*M. creelii*	*A. pisum*	*M. creelii*
Aphidius ervi	$81 \pm 11^{a**}$	28 ± 9^{c}	$1 \pm 4^{a**}$	54 ± 14^{a}	17 ± 11^{c}	18 ± 14^{c}
A. pisivorus	$75 \pm 16^{b*}$	59 ± 12^{a}	$0 \pm 0^{a*}$	4 ± 5^{c}	25 ± 16^{b}	37 ± 12^{a}
A. smithi	$68 \pm 18^{c**}$	13 ± 12^{d}	$0 \pm 0^{a**}$	58 ± 17^{a}	32 ± 18^{a}	29 ± 15^{b}
Praon pequodorum	$84 \pm 14^{a**}$	40 ± 14^{b}	$2 \pm 5^{a**}$	43 ± 14^{b}	15 ± 11^{c}	17 ± 6^{c}

[1] Each female encountered 20 aphids in each of 10 replications.

[2] The mean (± 1 SEM) percentages of encountered aphids that were struck by, rejected by, or escaped from parasitoids were compared separately for statistical significance. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test. Statistical significance of differences between means within rows (by ANOVA): *, $P \leq 0.05$; **, $P \leq 0.01$.

ervi encountered more pea than alfalfa aphids (Table 9). Both parasitoids struck more pea aphids than alfalfa aphids and *A. ervi* struck a greater proportion of encountered pea and alfalfa aphids than *A. smithi* (Table 10). *A. ervi* and *A. smithi* always attacked the pea aphid, but *A. smithi* rejected a greater proportion of encountered alfalfa aphids than *A. ervi* (Table 10). Pea aphids were more successful at escaping from *A. smithi* than from *A. ervi* (Table 10). Moreover, pea aphids were also more successful at escaping from *A. smithi* than were alfalfa aphids.

III. Behavior of aphids

Second-instar pea and alfalfa aphids escaped most frequently by dropping from the plants when encountered by a parasitoid but fewer than 10 % escaped by moving away from the parasitoids. Aphids struck by a parasitoid's ovipositor usually produced cornicle secretions and dropped from the plants or moved away from the parasitoid. Some aphids did not drop or move away when struck, but these aphids did produce cornicle secretions and kicked for several seconds with their hind legs. Parasitoids would often stop searching for aphids to clean cornicle secretion from their appendages or bodies, but the aphids did not seem intentionally to use the secretions as a deterrent to attack.

Pea and alfalfa aphids appeared to intermingle readily on the plant and both species settled mostly on the undersides of

Table 10. Percentages of encountered *Acyrthosiphon pisum* and *Macrosiphum creelii* that were struck by, rejected by, or escaped from *Aphidius ervi* and *Aphidius smithi*. Parasitoid females were singly caged with 30 aphids of each species at 23 ± 1 °C, 30 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C. All observations were made during Nov. 1987.

Parasitoid species	Struck[1,2] (%)		Rejected[1,2] (%)		Escaped[1,2] (%)	
	A. pisum	*M. creelii*	*A. pisum*	*M. creelii*	*A. pisum*	*M. creelii*
Aphidius ervi	$62 \pm 11^{a**}$	38 ± 15^{a}	$0 \pm 0^{a**}$	33 ± 14^{b}	37 ± 11^{b}	29 ± 10^{a}
A. smithi	$44 \pm 14^{b**}$	11 ± 9^{b}	$0 \pm 0^{a**}$	57 ± 14^{a}	$56 \pm 14^{a**}$	33 ± 13^{a}

[1] Each female encountered 20 aphids in each of 10 replications.

[2] The mean (± 1 SEM) percentages of encountered aphids that were struck by, rejected by, or escaped from parasitoids were compared separately for statistical significance. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test. Statistical significance of differences between means within rows (by ANOVA): **, $P \leq 0.01$.

leaves. Aphids that dropped were able to find their way back onto the shoots within a few seconds or minutes.

IV. Behavior of parasitoids

Female parasitoids seemed to alternate between slow and fast searching rates. Parasitoids would search the plants slowly when they were first introduced to a cage or if encounters with aphids were infrequent. However, they appeared to search faster when aphids were frequently encountered. When the parasitoids searched slowly, they seemed to disturb fewer aphids before striking them, but those that searched quickly often collided with aphids and caused them to drop or run away before the parasitoids had a chance to examine or strike them.

The parasitoids spent most of their time searching for aphids on the leaves of the broad-bean shoots, but they would also search the surface of the cages if encounters with aphids on the shoots became infrequent. Rejection of the alfalfa aphid seemed to decrease with low encounter rates or with unsuccessful attacks on both aphids or the pea aphid alone.

Parasitoids initially used their antennae to tap rapidly on the aphids encountered before rejecting or striking them. However, after several encounters, the parasitoids would often reject or strike an aphid without prior physical contact. Some parasitoids were able to hold onto and strike aphids that attempted to drop off the plants. These parasitoids appeared to use the tarsal claws of their front legs to grasp an aphid by the leg and prevent it from falling to the floor of the cage before it had been struck. Females of all the parasitoid species were observed to grasp and strike aphids that attempted to fall from the plants, but _P_. _pequodorum_ seemed to accomplish this act more frequently than the other wasps.

Finally, all the parasitoids often stopped searching for hosts for periods that varied from several seconds to several minutes. Parasitoids would stop searching if the intervals between encounters were longer than several minutes. When they paused from searching, they either cleaned their appendages and body parts or remained motionless except for occasional movements of their antennae. When the antennae or ovipositor of the wasps came into contact with the cornicle secretion of aphids, the wasps would often stop and clean the parts.

Discussion

Host selection is affected by the availability and susceptibility of hosts. Even though the parasitoids may not show preferences, some hosts are more accessible, more vulnerable, or need less time to deal with than others, so that the rates of parasitism may vary. For example, Gardner and Dixon (1985) found that _Aphidius_ _rhopalosiphi_ showed no real preference between two cereal aphids, _Metopolophium_ _dirhodum_ and _Sitobion_ _avenae_. However, _A_. _rhopalosiphi_ encounters and parasitizes _M_. _dirhodum_, which feeds on the leaves, more frequently than *S. avenae*, which feeds on the ear. The parasitoid prefers to search the leaves and it has less success parasitizing aphids that feed on the ears than those that feed on the leaves. Moreover, even when both aphids were feeding on the leaves of young plants without ears, *A. rhopalosiphi* took longer to handle *S. avenae* than *M. dirhodum*.

Similarly, Ankersmit *et al*. (1986) found that *A. rhopalosiphi* parasitized the green form of *S avenae* more often than the brown form. The higher parasitism resulted not only from greater acceptance, but also from shorter handling times and lower mortality of the developing parasitoids in the green than the brown form. It follows that deviations in the proportions of the host parasitized from the proportions of the host available are clearly inappropriate measures of preference.

In Section 4a, I found that the dropping responses of second-instar pea and alfalfa aphids were similar and I suggested that these instars would be equally susceptible to parasitism or predation. From the results of the present study, it is apparent that second-instar pea and alfalfa aphids actually were equally open to attack by all of the four parasitoids tested, but *A. smithi* was markedly less successful than the other three in striking alfalfa aphids. I suggest that *A. smithi* had a low acceptance of alfalfa aphids which allowed them to escape more often than pea aphids. *A. smithi* often hesitated before it attempted to strike alfalfa aphids, but it rarely paused before striking pea aphids. Alfalfa aphids often escaped while the wasp hesitated.

Differences between the proportions of pea aphids that escaped from A. smithi and A. ervi were unexpected because the pea aphid was apparently an acceptable host, and the two wasps had similar searching and host-handling behavior. But A. ervi allowed fewer pea aphids to escape than A. smithi and this may indicate that A. ervi was the more efficient of the two. Nevertheless, A. smithi parasitized more pea aphids in single-host treatments than did A. ervi (Section 3). It may be that, when pea aphids are abundant, A. smithi compensates for its lower efficiency by spending more time foraging than A. ervi.

Alternatively, parasitism of the pea aphid by A. smithi may be lower when alfalfa aphids are present. If A. smithi encounters both aphids, the parasitoid may require more time to confirm the identity of potential hosts than when only pea aphids are encountered. Consequently, pea aphids may have a better chance of escaping when alfalfa aphids are present. When the costs of incorrectly taking the less preferred host or prey are high, animals may benefit by reducing their foraging rate and taking only the preferred prey or host (Greenwood 1984).

Pea aphids were clearly preferred over alfalfa aphids by the four parasitoids. The wasps always accepted pea aphids but showed variable acceptance of alfalfa aphids. Variable acceptance or "partial preference" may result from parasitoids making errors of discrimination (Krebs et al. 1977), having imperfect knowledge of the availability of hosts (Krebs and

McCleery 1984, McNamara and Houston 1987), encountering more than one host simultaneously (Waddington 1982), or encountering clumped hosts (Lucas 1983).

Such factors as the experience of the parasitoid (Greenwood 1984, McNamara and Houston 1987), its egg load or oviposition pressure (Collins and Dixon 1986), and the absolute density of the preferred host (Hubbard *et al*. 1982, Greenwood 1984) may also influence oviposition decisions. Simbolotti *et al*. (1987) predicted host selection by *Lariophagus distinguendus*, a wasp parasitic on weevils, with a model that based oviposition decisions on the parasitoid's egg load, its previous encounters with hosts, and the quality of the present host. Another model, by Roitberg and Mangel (1989), showed how the physiological and informational state of the apple maggot, *Rhagoletis pomonella*, and host quality could influence a parasite's oviposition decisions. Similar models could be constructed to predict host selection by the parasitoids in this study.

It is interesting that *A*. *ervi* and *A*. *smithi* do not readily accept the alfalfa aphid, but that *A*. *pisivorus* does. The three *Aphidius* species are morphologically and biologically similar in many respects (Mackauer and Finlayson 1967) and yet they clearly differ in their acceptance of the alfalfa aphid. Moreover, it is also curious that *A*. *pisivorus* and *P*. *pequodorum*, which are native to the North American fauna, show greater acceptance of the alfalfa aphid than *A*. *ervi* and *A*. *smithi* which were respectively introduced from Europe and India.

Of the four wasps, *A. pisivorus* seems to be the best control agent for the pea and alfalfa aphid because it readily attacks both species. However, *A. ervi* is the dominant parasitoid of the pea aphid in the main regions of alfalfa cultivation in British Columbia (Section 2). *A. ervi*'s reluctance to attack the alfalfa aphid may limit its ability to regulate populations of the aphid in the field. From samples of alfalfa aphids collected at Kamloops it was clear that *A. ervi* parasitized the aphid less frequently than *A. pisivorus* or *P. pequodorum* (Section 5).

In summary, preference for the pea aphid is apparently innate in the parasitoids. *A. smithi* had less success in attacking alfalfa than pea aphids and this may have been due to the parasitoid's low acceptance of the alfalfa aphid. Preference for the pea aphid was absolute, but preference for the alfalfa aphid was partial and seemed to depend on the parasitoids' sequence and rate of encounters with the two aphids. Learning and the experience of the parasitoids may affect host preference and the importance of these factors will be examined in Sections 4c and 4d.

SECTION 4c: PARTIAL AND ABSOLUTE PREFERENCES BY PARASITOIDS

Iwasa _et_ _al_. (1984) suggested that optimal choice of hosts by parasitoids can be analyzed by models similar to those used to determine prey selection by predators, which attempt to maximize their mean rate of energy gain (Pulliam 1974, Charnov 1976, Krebs _et_ _al_. 1977, Houston _et_ _al_. 1980). If female parasitoids behave so as to maximize their genetic contribution to future generations, the optimal strategy would be to select host types which maximize the parasitoids' rate of increase in reproductive success or fitness. Iwasa _et_ _al_. showed (1984) that the host-range problem of a parasitoid is identical to the optimal diet problem for predators, when reproductive success of an egg laid in a host is substituted for energy gained by the consumption of prey.

Theories of optimal diets predict (MacArthur and Pianka 1966; Pulliam 1974; Charnov 1976), that hosts within particular categories should always be accepted or rejected (= absolute preference). Partial preference means that in given circumstances a host is sometimes taken and sometimes rejected. Absolute preferences are usually the exception rather than the rule in many laboratory studies on host selection by insect parasitoids (Cornell and Pimentel 1978, van Alphen and Janssen 1982, Sequeira and Mackauer 1986). Many explanations for partial preference have been suggested in the literature and they have been recently reviewed by McNamara and Houston (1987).

Krebs and McCleery (1984) suggest that some partial preference may result from a short training period. Animals cannot be expected to know the exact availability of prey or hosts in the habitat. They may have learning processes that gradually approach optimal policies during which simple rules of thumb and reinforcement may result in the maximization of their rate of energy gain or of their total genetic contribution to future generations (Shettleworth 1984; McNamara and Houston 1987).

When the availability of hosts is unknown, parasitoids may initially accept many types of hosts; however, by sampling they may learn to accept only the most preferred hosts (van Alphen and Janssen 1982). In Section 3, I showed that *Aphidius ervi*, *A. smithi*, and *Praon pequodorum* did not readily accept the alfalfa aphid even when the pea aphid was not available. It was therefore surprising that the parasitoids showed partial preferences for the alfalfa aphid when the two aphid species were equally available (Section 4b). However, these parasitoids may have shown partial preferences because they did not have enough time to assess the relative availability or quality of the two host species.

In this study, I tested this hypothesis by comparing the host selection of *A. ervi*, *A. smithi*, *A. pisivorus*, and *P. pequodorum* after different periods of confinement with equal numbers of pea and alfalfa aphids. In particular, I will test if these parasitoids show absolute or partial preference for the two aphids.

Methods

About 30 to 60 3- to 4-day old females of A. ervi, A. smithi, A. pisivorus, and P. pequodorum were taken from stock colonies and placed singly in 15.5-cm-diam cages, each containing 20 second-instar pea aphids, 20 second-instar alfalfa aphids, and the apical portion of a broad-bean shoot. A. ervi and P. pequodorum were confined in the cages for 2, 5, or 8 h. A. pisivorus were confined for 2, 4, or 6 h and A. smithi were confined for 2 or 4 h. Ten of the pea aphids and 10 of the alfalfa aphids in each cage were dissected 4 to 5 days later. The numbers of living aphids in each cage, dissected aphids containing parasitoid larvae, and parasitoid larvae in each aphid were recorded.

Ten replications of each confinement treatment were completed for A. smithi and A. pisivorus. Fifteen and 17 replications of each confinement treatment respectively were completed for P. pequodorum and A. ervi. Experiments for each parasitoid species were conducted on different dates but the confinement treatments and their replications were made on the same day. The experiments were conducted in standard conditions.

The data from each experiment were analyzed by fully randomized ANOVA. The dependent variable was the proportion of aphids that were parasitized in each cage and the factors used were the host species and the confinement period. When significant main effects or interactions were found, Duncan's multiple range tests were used to compare the parasitism of pea and alfalfa aphids within each confinement treatment. All proportions, for both aphids in each replication, were transformed into their arcsine values by equation (1) (Section 3).

Results

In this study, superparasitism of pea and alfalfa aphids was very low in the three Aphidius species and did not occur in P. pequodorum (Table 11). Significant aphid species effects were found in which the proportions of dissected aphids containing parasitoid larvae were always greater among pea than alfalfa aphids in the same study (Tables 12, 13). However, the progression of host selection differed between the four parasitoids. Two-way interactions for the period of confinement and the species of aphid were highly significant in P. pequodorum and significant in A. smithi. No significant interactions were found in A. pisivorus and A. ervi.

The differences between the proportions of alfalfa aphids parasitized by P. pequodorum in 2 h and 5 h were one-third of those found between pea aphids in comparable treatments (Table 13). In comparison, the proportions of alfalfa aphids parasitized by A. smithi in 2 h and 4 h were not significantly different, but the proportions of pea aphids parasitized in 4 h were almost double those parasitized in 2 h (Table 12).

Table 11. Numbers of *Acyrthosiphon pisum* (AP) and *Macrosiphum creelii* (MC) parasitized by four species of parasitoids. Parasitoid females were singly caged with 20 aphids of each species simultaneously, for different periods, at 22 ± 1 °C, 55 ± 5 % RH, with continuous lighting.[1] All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Confinement period (h)	Total parasitized		Total eggs laid	
		AP	MC	AP	MC
Aphidius smithi	2	38	1	39	1
	4	64	3	67	3
A. pisivorus	2	43	20	45	21
	4	57	29	58	30
	6	61	45	66	46
A. ervi	2	69	33	71	34
	5	132	65	139	65
	8	147	69	172	74
Praon pequodorum	2	30	19	30	19
	5	76	23	76	23
	8	108	56	108	56

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[1] Ten of 20 aphids of each species were dissected to show parasitism in each of 10 replications for *A. smithi* and *A. pisivorus*, 17 replications for *A. ervi*, and 15 replications for *P. pequodorum*.

Table 12. Percentages of *Acyrthosiphon pisum* and *Macrosiphum creelii* parasitized by *Aphidius smithi* and *A. pisivorus*. Parasitoid females were singly caged with 20 aphids of each species simultaneously, for different periods, at 22 ± 1 °C, 55 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Confinement period (h)	Percentage parasitized[1,2]	
		A. pisum	*M. creelii*
Aphidius smithi	2	$38 \pm 26^{b**}$	1 ± 3^{a}
	4	$64 \pm 16^{a**}$	3 ± 7^{a}
A. pisivorus	2	$43 \pm 19^{b**}$	20 ± 14^{b}
	4	$57 \pm 16^{a**}$	29 ± 14^{b}
	6	$61 \pm 15^{a**}$	45 ± 12^{a}

[1] Ten of 20 aphids of each species were dissected to show parasitism in each of 10 replications

[2] The mean (± 1 SEM) percentages of aphids that were parasitized by *A. smithi* and *A. pisivorus* were compared separately for statistical differences. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test. Statistical significance of differences between means within rows (by ANOVA): **, $P \leq 0.01$.

Table 13. Percentages of *Acyrthosiphon pisum* and *Macrosiphum creelii* parasitized by *Aphidius ervi* and *Praon pequodorum*. Parasitoid females were singly caged with 20 aphids of each species simultaneously, for different periods, at 22 ± 1 °C, 55 ± 5 % RH, with continuous lighting. All the aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Confinement period (h)	Percentage parasitized[1,2]	
		A. pisum	*M. creelii*
Aphidius ervi	2	$41 \pm 19^{c**}$	19 ± 17^{b}
	5	$75 \pm 23^{b**}$	38 ± 18^{a}
	8	$86 \pm 19^{a**}$	41 ± 21^{a}
Praon pequodorum	2	$20 \pm 8^{c**}$	13 ± 8^{b}
	5	$51 \pm 26^{b**}$	19 ± 13^{b}
	8	$72 \pm 26^{a**}$	37 ± 17^{a}

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[1] Ten of 20 aphids of each species were dissected to show parasitism in each of 17 replications for *A. ervi* and 15 replications for *P. pequodorum*.

[2] The mean (± 1 SEM) percentages of aphids that were parasitized by *A. ervi* and *P. pequodorum* were compared separately for statistical differences. Means, within columns, showing the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test. Statistical significance of differences between means within rows (by ANOVA): **, $P \leq 0.01$.

The proportions of pea aphids parasitized by A. *ervi* in 2 h, 5 h, and 8 h were significantly different (Table 13), but the differences between the actual numbers in 5 h and 8 h were small. The proportions of alfalfa aphids parasitized by A. *ervi* at 2 h, 5 h, and 8 h were one half of the proportions of pea aphids parasitized in the same treatments. The values for 5 h and 8 h did not differ significantly.

Similarly, the proportions of pea aphids parasitized by A. *pisivorus* in 4 h and 6 h were not significantly different, but those of alfalfa aphids parasitized in 4 h and 6 h were (Table 12).

Discussion

Understanding the adaptive significance of observed behavior is as important as determining how behavior is caused. Because of the correlation between the selection of hosts and the production of offspring, host preference should be strongly influenced by natural selection. Therefore, host selection by parasitoids is ideal for testing optimization hypotheses based on evolutionary theory.

In parasitoid foraging studies, it is generally assumed that females employ strategies which maximize their oviposition rates and the fitness of their offspring. According to theories of optimal diet (MacArthur and Pianka 1966; Pulliam 1974; Charnov 1976), prey or hosts should always be accepted or rejected. There is an encounter rate for the best hosts above which the parasitoid maximizes its foraging efficiency by accepting only those hosts. Below this rate, it becomes optimal for the parasitoid to accept also less profitable hosts. However, parasitoids are not omniscient and all-or-none selection may not occur until they gain experience.

I have found that A.ervi, A. smithi, A. pisivorus, and P. pequodorum females prefer to parasitize pea aphids when second-instar pea and alfalfa aphids are equally available (Section 3, 4b). There is no evidence that pea aphids are more suitable hosts for the eggs of these parasitoids than alfalfa aphids. Consequently, parasitoid females may not have been selecting hosts in a manner that maximized reproductive success. However, assuming that parasitoid females "perceive" alfalfa aphids as being of lower quality than pea aphids, I suggest that models of optimal diets could provide a good description of host selection by these wasps.

In the present study, A. smithi almost completely rejected the alfalfa aphid at the start of the experiments. Apparently, this parasitoid species has a strong preference for the pea aphid and does not need to estimate the relative abundance of the two aphid species before showing absolute preference. When differences between the perceived benefits of different hosts are large and quickly apparent, parasitoids may not need to sample.

By contrast, P. pequodorum, A. ervi, and A. pisivorus seemed to require a period of sampling before they would parasitize the pea aphid only. But A. pisivorus and P. pequodorum also went back to parasitizing both aphids when a large proportion of the pea aphids had been parasitzed; however, this was probably due to the inability of the parasitoids to leave the cages when unparasitzed pea aphids became scarce.

Under the conditions of these studies, parasitoids encountered pea and alfalfa aphids that were parasitized or unparasitized. Host discrimination, the ability to distinguish between parasitized and unparasitized hosts and to limit oviposition to the latter, is common among the Aphidiidae (Chow and Mackauer 1984, 1986). Failure to discriminate can result in super- or multiple parasitism and possible wastage of offspring (Chow and Mackauer 1986). I suggest that the acceptability of the four host types, from most to least acceptable, is as follows: unparasitized pea aphid, unparasitized alfalfa aphid, parasitized pea aphid, and parasitized alfalfa aphid. It is also likely that parasitized pea and alfalfa aphids are equally distinguishable from their unparasitized counterparts.

Given these assumptions, changes in the numbers of these four host types, during the course of the experiments, will affect the parasitoids' perception of the availability of the most preferred host type. If parasitoids "perceive" that unparasitized pea aphids are relatively rare in comparison to parasitized pea aphids and unparasitized alfalfa aphids, the wasps will accept unparasitized alfalfa aphids as hosts.

Therefore, parasitism of pea aphids will seem to decrease or stop, while parasitism of alfalfa aphids will seem to increase as unparasitized pea aphids become rare in the longer treatment periods. The results indicate that these parasitoids can show absolute preference when unparasitized pea aphids are available in sufficient numbers and the parasitoids are given enough time to assess the fact.

Van Alphen and Janssen (1982) found that Asobara tabida, a hymenopteran parasitoid of Drosophilia species, also required a period of sampling before it accepted only the most profitable hosts in the habitat. Sampling is also used by predators to achieve optimal diets (Holmberg and Turnbull 1982, Krebs *et al*. 1977).

As suggested by Krebs and McCleery (1984), an animal that does not know the parameters of the experiment may have a learning process that gradually approaches an optimal policy. They may learn by constantly reassessing the rate of encounter with the preferred host (Pulliam 1974, McNamara and Houston 1987). However, oviposition decisions may depend on several factors such as the parasitoid's egg load, its past experience with hosts, and the quality of its current host (Simbolotti *et al*. 1987, Roitberg and Mangel 1989).

In summary, parasitoids may show partial preferences when they do not know the quality or availability of the hosts in their habitat. However, when these parameters have been assessed, the parasitoids may show absolute preferences and accept only the preferred host. In the field, the availability of pea and alfalfa aphids probably varies in space and time. It thus apppears adaptive that the willingness of *A. ervi*, *A. pisivorus*, and *P. pequodorum* to accept alfalfa aphids is influenced by the recent experience of the wasps.

SECTION 4d: EFFECT OF PRIOR EXPERIENCE ON SELECTION OF HOSTS

Doutt (1959) suggested that host selection by insect parasitoids consists of three stages: location of the host's habitat, location of the host, and acceptance of the host. At all these stages, host selection may be affected by the previous experience of the parasitoids (van Alphen and Vet 1986). Chemical and physical stimuli are frequently used by parasitoids to locate potential hosts and make ovipostion decisions (Vinson 1976, 1984). Parasitoids usually have innate responses to these stimuli, but experience can alter their responses (Vinson 1976). Cornell (1976) suggested that some parasitoids increase their searching efficiency by using sensory cues to form "search images" of the dominant host species in a habitat.

The effects of conditioning on acceptance of hosts, through previous oviposition or feeding experience, is important to understanding the parasitoid's preference for and selection of hosts. Parasitoids with previous experience on certain host species may show greater preference than inexperienced parasitoids for the same host species in choice tests (Cornell and Pimentel 1978). Moreover, parasitoids may initially accept all the potential hosts in a habitat but learn to reject the less profitable species following a period of sampling (van Alphen and Janssen 1982). Krebs and McCleery (1984) suggest that partial preference may be the result of animals undergoing a "training" or "learning" process in unfamiliar habitats before their selection of prey or host becomes optimal.

"Learning" has been broadly defined as any change in behavior caused by experience (Shettleworth 1984). But in the literature of predation it is often used to imply that the predator has "learned how to do something" (Murdoch and Oaten 1975). Predators may learn to reject unpalatable prey and accept palatable prey after eating a certain number of each type. Similarly, some parasitoids apparently "remember" the first suitable host-type that they encounter and prefer it even when other suitable host-types are available (Cornell 1976).

In Section 5, I found that unconditioned female *Aphidius ervi*, *A. smithi*, *A. pisivorus*, and *Praon pequodorum* did not show switching as defined by Murdoch (1969). Murdoch and Oaten (1975) suggested that switching may not occur if there is no opportunity for the animal to become conditioned to the more abundant prey or host. It is possible that these parasitoids may have shown switching, had they been previously conditioned on the more abundant host species in the experiments.

In the following study, I examined the effects of conditioning on host selection by *A. ervi*, *A. pisivorus*, and *P. pequodorum* using pea or alfalfa aphids. *A. smithi* was not tested because the results of previous studies and preliminary trials clearly indicated that its preference for the alfalfa aphid could not be significantly altered by the conditioning treatments used here.

Methods

Thirty females each of A. ervi, A. pisivorus, and P. pequodorum, less than 24-h old, were taken from stock colonies and separated into two groups. From each species group ten were put into a covered wax-paper cup and fed a solution of honey and water; the remaining 20 were separated into pairs each of which was kept for 24 h in a 15.5-cm-diam plastic cage containing 150 second-instar aphids of one species and the apical portion of a broad-bean shoot. Five pairs were confined with pea aphids, the other five with alfalfa aphids. These parastoids were then transferred to empty cups and fed the honey and water solution. At the same time, the 10 parasitoids being held without aphids were also fed. Twenty minutes later, the 30 parasitoids from each of the three groups were placed singly in 15.5-cm-diam. cages, which contained 20 second-instar pea aphids, 20 second-instar alfalfa aphids, and the apical portion of a broad-bean shoot.

A. ervi and A. pisivorus females were confined in the cages for 4 h and P. pequodorum females were confined for 6 h. P. pequodorum females were confined for 6 h because I found in preliminary trials that these wasps parasitized only a small proportion of the available hosts at 4 h. Ten of the pea aphids and 10 of the alfalfa aphids in each cage were dissected 4 to 5 days later. I recorded the numbers of living aphids in each cage, the number of dissected aphids containing parasitoid larvae, and the number of parasitoid larvae in each aphid. The experiments with each parasitoid species were conducted in standard conditions on different dates.

The data were analyzed by ANOVA or paired-difference t-tests. The proportions of pea aphids among all aphids parasitized by females of the same species were compared by ANOVA. The ANOVAs used one factor, the experience of the wasps. All proportions were transformed using equation (1) (Section 3) where "n" is the total number of dissected aphids that contained parasitoid larvae, and "x" is the total number of dissected pea aphids that contained parasitoid larvae. The numbers of pea and alfalfa aphids parasitized by wasp females, of the same species and with similar experience, were compared by paired-difference t-tests. Females were categorized as pea-aphid experienced, alfalfa-aphid experienced, or inexperienced.

Results

Superparasitism of pea and alfalfa aphids by _A_. _ervi_ and _A_. _pisivorus_ was very low. Only _P_. _pequodorum_ did not superparasitize any of the aphids that I dissected (Table 14). Parasitoid females, confined without aphids prior to the experiment, parasitised more aphids than comparable females previously confined with pea or alfalfa aphids (Table 14).

Females of _A_. _ervi_ and _P_. _pequodorum_ always parasitised more pea aphids than alfalfa aphids (Table 15), but parasitism

Table 14. Total numbers of *Acyrthosiphon pisum* (AP) and *Macrosiphum creelii* (MC) parasitized by three species of parasitoids. Parasitoid females were confined without aphids or with aphids of one species for 24 h before they were singly caged with 20 aphids of each species simultaneously for 4 h or 6 h at 22 ± 1 °C, 55 ± 5 % RH, with continuous lighting.[1] All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Previous experience	Total parasitized		Total eggs laid	
		AP	MC	AP	MC
Aphidius ervi	AP	51	9	57	10
(4 h)	MC	58	17	66	17
	None	78	28	91	30
A. pisivorus	AP	34	18	34	18
(4 h)	MC	30	32	30	32
	None	57	48	62	52
Praon pequodorum	AP	58	21	58	21
(6 h)	MC	62	35	62	35
	None	72	37	72	37

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[1] Ten of 20 aphids of each species were dissected to show parasitism in each of 10 replications.

Table 15. Mean numbers of _Acyrthosiphon pisum_ (AP) and _Macrosiphum creelii_ (MC) parasitized by three species of parasitoids. Parasitoid females were confined without aphids or with aphids of one species for 24 h before they were singly caged with 20 aphids of each species simultaneously for 4 h or 6 h at 22 ± 1 °C, 55 ± 5 % RH, with continuous lighting.[1] All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Previous experience	Aphids parasitized[2] ($\bar{X}$ ± 1 SEM)	
		A. pisum	_M. creelii_
Aphidius ervi	AP	5.1 ± 2.3**	0.9 ± 0.7
(4 h)	MC	5.8 ± 2.0**	1.7 ± 1.2
	None	7.8 ± 1.5**	2.8 ± 1.8
A. pisivorus	AP	3.4 ± 1.4*	1.8 ± 1.2
(4 h)	MC	3.0 ± 3.2	3.2 ± 1.3
	None	5.7 ± 1.9	4.8 ± 2.1
Praon pequodorum	AP	5.8 ± 1.4**	2.1 ± 1.1
(6 h)	MC	6.2 + 1.0**	3.5 ± 1.4
	None	7.2 + 1.4**	3.7 ± 1.5

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[1] Ten of 20 aphids of each species were dissected to show parasitism in each of 10 replications.

[2] Statistical significance of differences between means within rows (by paired-difference t-test, two-tailed): *, $P \leq 0.05$; **, $P \leq 0.01$.

of pea and alfalfa aphids did not significantly differ between A. pisivorus previously confined with alfalfa aphids or without aphids (Table 15). A. pisivorus, previously confined with pea aphids, parasitized more pea aphids than alfalfa aphids (Table 15). No significant statistical differences were found in the proportions of pea aphids parasitized between females of the same species that differed in their previous experience.

Discussion

Parasitoids often have innate preferences for hosts, but preference may be influenced by experience. Cornell and Pimentel (1978) studied switching in Nasonia vitripennis, a hymenopterous parasitoid that feeds and oviposits on the pupal stage of sarcophagous flies, using three hosts: Musca domestica, Phormia regina, and Phaenicia sericata. N. vitripennis had a strong innate preference for P. regina but concentrated its attacks on the most abundant host. Moreover, N. vitripennis' acceptance of a host was increased if the wasp had previous feeding experience on that host. From these results, the authors suggested that learning influenced host selection and contributed to switching in this parasitoid.

Similarly, van Alphen and van Harsel (cited by van Alphen and Vet 1986) found that previous experience influenced host selection in Asobara tabida, a hymenopterous parasitoid of Drosophila larvae. When A. tabida was given different ratios of D. melanogaster and D. subobscura larvae, the wasp always preferred *D. subobscura*. However, *A. tabida* conditioned on *D. melanogaster* accepted more *D. melanogaster* than did wasps conditioned on mixtures of the two hosts. It was apparent that oviposition was influenced by the previous experience of the wasps.

Host selection in *A. ervi* and *P. pequodorum* was not significantly affected by conditioning, but *A. pisivorus* conditioned on pea aphids had lower acceptance for alfalfa aphids than did comparable parasitoids that were unconditioned or conditioned on alfalfa aphids. *A. ervi* and *P. pequodorum* have strong innate preferences for pea aphids, but *A. pisivorus* has a weak innate preference for pea aphids. These results suggest that parasitoids with weak preference for pea aphids will accept few alfalfa aphids if they have previously been conditioned on pea aphids.

Studies on the foraging behavior of parasitoids have often assumed that egg supply is not limiting (Waage 1979, Cook and Hubbard 1977). But once a parasitoid's complement of eggs is depleted it should not continue to forage for hosts; in effect, the egg load of parasitoids may operate similarly to hunger in predators. Collins and Dixon (1986) suggested that a parasitoid's selectivity for hosts increases if egg load decreases. Therefore, the behavior of parasitoids in choice tests could be affected by the number of eggs that they released prior to these tests.

Parasitoids that release most of their eggs during conditioning may differ in their acceptance of hosts from parasitoids that release fewer or no eggs. In the present study, it was not possible to separate the effects of experience and depletion of egg load on host selection. It could, therefore, be argued that conditioning _A_. _pisivorus_ females on pea aphids reduced the parasitoids' acceptance of alfalfa aphids by decreasing the egg load of these wasps.

However, I found in previous studies (Section 3) that _A_. _pisivorus_ females parasitized approximately the same numbers of pea and alfalfa aphids if the wasps were given only one of these aphid species. I suggest that the decrease in egg load was similar for _A_. _pisivorus_ females conditioned on pea or alfalfa aphids in this study. It is unlikely that depletion of egg load was the only factor that decreased the acceptance of pea-aphid conditioned females for alfalfa aphids.

Conditioning _A_. _pisivorus_ on pea aphids may have increased the parastoid's expectation of encountering pea aphids in the choice tests and consequently, reduced the wasp's acceptance for alfalfa aphids. Optimal diet models (Charnov 1976, Pulliam 1974, Krebs _et al_. 1977) predict that acceptance of alfalfa aphids is dependent on the parasitoid's expectation of encountering pea aphids. If the parasitoid uses previous experience to estimate the availability of pea aphids in a current patch, conditioning on pea aphids would result in a high expectation for this aphid. The parasitoid may initially accept few alfalfa aphids because its expectation of encountering pea aphids is higher than that of an unconditioned parasitoid.

A. pisivorus, conditioned on alfalfa aphids, probably accepted alfalfa aphids according to encounter rates with pea aphids after the wasps "realized" that pea aphids were also available. It is possible that A. ervi and P. pequodorum could not be conditioned to reduce their acceptance of alfalfa aphids. When innate acceptance for alfalfa aphids is already low, conditioning on pea aphids may not significantly decrease the parasitoids' acceptance of alfalfa aphids.

In summary, I have shown that conditioning A. pisivorus on pea aphids reduced this parasitoid's acceptance of alfalfa aphids. These results show that foraging decisions by this wasp may have been affected by previous experience. It is possible that when expectations for preferred hosts are high, less preferred hosts are rejected more often. However, conditioning on pea aphids was noticeable only when preference for pea aphids was weak. A. ervi and P. pequodorum had strong preferences for pea aphids and conditioning did not affect their host selection; the parasitoids could not be conditioned to increase their acceptance of alfalfa aphids. It is conceivable that longer periods of conditioning would affect the selectivity of these wasps. Moreover, selectivity could also vary with the age of the parasitoids. It is apparent that further studies are required to separate the effects of experience, egg load, and age on host selection by these wasps. But from the results of this study, I suggest that conditioning would not have affected the trends found in the switching studies of Section 3.

SECTION 5: CONSEQUENCES OF HOST SELECTION ON PARASITOID COMPONENTS OF FITNESS

Introduction

For parasitoids there is a direct correlation between host choice and the production of offspring. Parasitoid females should be efficient in selecting suitable hosts and rejecting others. Recognition of hosts that are suitable may be genetically fixed and, under such conditions, parasitoids will show innate preference for these hosts. In the three sub-parts of this section, I will test the hypothesis that the alfalfa aphid is a less suitable host for the four wasps than the pea aphid.

In Section 5a, I compare the oviposition and emergence success of the four wasps on pea and alfalfa aphids. In Sections 5b, I compared the sex ratio and size of the offspring of _A_. _pisivorus_ that developed in pea and alfalfa aphids, and made the same comparisons for _A_. _ervi_ in Section 5c. _A_. _pisivorus_ and _A_. _ervi_ differed in their preference for pea aphids (Section 3, 4b), but they are similar in morphology and biology (Mackauer and Finlayson 1967). Therefore, it would be interesting to determine if their differences in host preference are reflected in measurements of fitness.

Finally, it has been suggested that parasitoid females may prefer the same species that served as their larval hosts (Hopkins 1917, Vinson 1976). It seems possible that the preferences of these parasitoids for pea aphids could be reversed by rearing them in alfalfa aphids. This hypothesis was also tested also in Section 5c by comparing the host selection and sex ratio of _A. ervi_ reared in alfalfa aphids with those reared in pea aphids.

SECTION 5a: OVIPOSITION AND EMERGENCE SUCCESS OF PARASITOIDS ON PEA AND ALFALFA APHIDS

Host acceptance and suitability are essential for successful parasitism (Doutt 1959). Piercing and probing of potential hosts by parasitoids with their ovipositors can be stimulated by the shape, size, movement, sound, and odor of the hosts (Vinson 1976). However, the mere insertion of the ovipositor is an unreliable indicator of oviposition if egg release needs other stimuli, such as specific compounds in the host's hemolymph (Hegdekar and Arthur 1973).

Suitability is an important aspect of host selection (Vinson 1976); when they are given a choice of hosts, certain hymenopterous parasitoids appear to prefer some over others (Mackauer 1973; Dransfield 1979; Sequeira and Mackauer 1986). Vinson (1984) has suggested that host suitability includes both constraints and regulation. Constraints can be defined as characteristics of a host that hinder the successful development of a parasitoid such as the host's internal defensive system or its nutritional inadequacy. The ability of a parasitoid to survie within a host may depend on its capability to regulate the development and physiology of the host.

In the work described in Section 4b, I found that females of _A_. _ervi_, _A_. _smithi_, _A_. _pisivorus_, and _P_. _pequodorum_ attacked fewer second-instar alfalfa than second-instar pea aphids when both aphids were equally available and susceptible. From the results of these studies, I suggest that probing with the ovipositor is not required for host discrimination. However, if pea aphids struck with ovipositors are parasitized more frequently than their alfalfa-aphid counterparts, it could indicate either that the parasitoids discriminate and withhold their eggs after the insertion of their ovipositors, or that the alfalfa aphid is less suitable for the development of parasitoid eggs than the pea aphid, and the eggs die undeveloped (*i.e.* undetected).

Furthermore, it is possible that alfalfa aphids are more difficult to oviposit into than pea aphids. I have observed second-instar pea and alfalfa aphids kicking parasitoids when the aphids were struck by ovipositors; parasitoids that are kicked may withdraw their ovipositors without laying an egg in the host. The responses of pea and alfalfa aphids to being struck may contribute to differences between the ovipositon success of parasitoids on these aphids. This hypothesis could be tested by comparing the oviposition success of parasitoids on active and anesthetized aphids.

The following studies examined both oviposition and emergence success of the four parasitoids on anesthetized and active pea and alfalfa aphids.

Methods

Second-instar aphids and female parasitoids were reared as described in Section 1. In studies with active aphids, 20 second-instars of the same species were placed in a 60 x 151mm plastic petri-dish with a single female parasitoid. The parasitoid was allowed to strike 15 aphids, which were immediately removed after being struck once. These aphids were separated into groups of five, according to the order in which they were struck, and reared on cut broad-bean shoots in separate 8.5-cm-diam. cages. The first two groups were dissected 5 days after being struck, and the numbers of aphids containing parasitoid larvae were recorded. The remaining group was reared for 10 days, and the aphids that did not mummify were dissected to determine the reason. Mummified aphids were placed singly into clear gelatin capsules, for the emergence of parasitoids. A. ervi, A. pisivorus, and P. pequodorum were tested on both aphids, and five replications of each test were completed. A. smithi was tested on both aphids in 10 replications, but the females used in the first five replications were not from the same generation as the females used in the last five. A different female was used for each replication; and with the exception of the A. smithi study, all the females belonged to a single generation.

Oviposition success was determined by the number of parasitized aphids among the 1st to 5th and the 6th to 10th aphids struck in each combination of parasitoids and aphids. The proportion of 1st to 5th and 6th to 10th aphids struck were compared to determine if oviposition success increased after the parasitoids had struck several aphids of the same species. Emergence success was determined by comparing the number of parasitoids that emerged with the number of mummies found in each combination. Data from the replications of each combination were combined to obtain totals for parasitism, mummification, and parasitoid emergence.

For the study with anesthetized pea and alfalfa aphids, only females of parasitoid species that had greater oviposition success on active pea aphids than active alfalfa aphids were used. Second-instars were anesthetized with 4-5 min exposures to CO_2. Parasitoids were allowed to strike 15 aphids, of a single species, and the aphids were immediately removed after being struck once.

It was assumed that development and survival of parasitoid larvae in aphids treated with CO_2 did not differ significantly from those of larvae in untreated aphids. Anesthetized aphids needed from 10-15 minutes to recover from treatment with CO_2 and no side effects were observed. These aphids were separated into the first five and the following ten struck, then reared in separate 8.5-cm-diam. cages. They were dissected 4-5 days after being struck, and five replications were made for each combination of parasitoid and aphids. The number of parasitized aphids among the 1st to 5th and the 6th to 15th struck were converted into a proportion of the number of dissected aphids in each replication. The means and standard deviations of these proportions were determined and compared within each combination.

All studies of active and anesthetized aphids were conducted at 21 ± 1 °C and 40 ± 10 % RH, and struck or mummified aphids were kept under continuous light at 20 ± 1 °C and 60 ± 10 % RH. The parasitoids were 3-4 days old and had not had previous contact with aphids.

Results

It is clear that there were no differences between the percentages of pea and alfalfa aphids parasitized by A. ervi, A. pisivorus, and P. pequodorum (Table 16). Larvae were found in 84 and 92% of the dissected pea aphids struck by A. smithi, but none in any of the dissected alfalfa aphids struck by A. smithi (Table 16). I observed that pea aphids were usually struck in their initial encounters with parasitoids, but alfalfa aphids were often rejected and re-encountered several times before being struck. Rejection counts were not recorded, but I observed that A. pisivorus rejected alfalfa aphids less often than the other three wasps. However, there were clearly no differences in parasitism among the 1st to 5th and 6th to 10th aphids struck by the parasitoids (Table 16).

Table 16. Oviposition and emergence success of four species of parasitoids on *Acyrthosiphon pisum* (AP) and *Macrosiphum creelii* (MC) at 21 ± 1 °C, 40 ± 10 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Parasitoid species	Dissected aphids parasitized (%)[1]				Struck aphids mummified (%)[1]		Emergence from mummies (%)	
	AP		MC		AP	MC	AP	MC
	a[2]	b[3]	a[2]	b[3]				
Aphidius ervi	80	84	88	84	80	84	90	95
A. pisivorus	84	80	88	84	88	80	100	95
A. smithi	88	86	0	0	90	0	98	—
Praon pequodorum	88	84	76	84	84	72	100	100

[1] Percentages were obtained from 25 aphids struck by five different parasitoids, except those for *A. smithi* which were obtained from 50 aphids struck by 10 different parasitoids. Each parasitoid was used to strike five different aphids.

[2] 1st-5th aphids struck in sequence of 10.

[3] 6th-10th aphids struck in sequence of 10.

It is also clear that there were no differences between the percentages of pea and alfalfa aphid mummies that formed from aphids struck by *A. ervi*, *A. pisivorus*, and *P. pequodorum* (Table 16). No mummies formed from alfalfa aphids struck by *A. smithi*, but 92 and 88% of the pea aphids struck by *A. smithi* mummified (Table 16). There were no differences between the percentages of mummified aphids and the percentages of parasitoids that emerged (Table 16). Unsuccessful emergence ranged from 1 to 10% of the mummies that formed in each test, and no parasitoid larvae were found among the unmummifed aphids that were dissected.

A. smithi females were used in the study with anesthetized aphids because this parasitoid species had greater oviposition success on active pea aphids than active alfalfa aphids. Parasitoid larvae were not found in anesthetized alfalfa aphids struck by *A. smithi*. By contrast, parasitoid larvae were found in 92 ± 11% of the first five and 98 ± 5% of the following ten anesthetized pea aphids struck by *A. smithi*. Mortality of anesthetized pea and alfalfa aphids was respectively 10 ± 8% and 6 ± 6%.

Discussion

Experiments that provide only one host type at a time do not permit inferences about parasitoid preference, but they may reveal which hosts are susceptible to attack and suitable for parasitoid development. For better understanding of parasitoid-host relationships, it is important to distinguish between susceptibility to attack and suitability for parasitoid development. According to Mackauer (1973), susceptibility includes any interactions between the host and the adult parasitoid that may prevent attack or oviposition, whereas suitability refers only to the interactions between the host and the immature stages of the parasitoid. A successful attack requires that the parasitoid avoids or overcomes the host's physical, chemical, or behavioral defences. In comparison, successful development is dependent upon the host's nutritional suitability, and the parasitoid's ability to evade or overcome the host's internal defensive system (Vinson and Iwantsch 1980). Therefore, a potential host can obviate successful parasitism if it is unacceptable or unsuitable.

Under the conditions of these studies, second-instar pea and alfalfa aphids were equally susceptible to attack and oviposition by *A. ervi*, *A. pisivorus*, and *P. pequodorum*. Both aphids were suitable hosts for the parasitoids, but additional studies might reveal differences in suitability for these parasitoids. Criteria that could be used to assess the suitability of pea and alfalfa aphids for the development of parasitoids include: average developmental time of the parasitoids, their sex ratio, dry weight of the adults, and fecundity.

The absence of larvae of *A. smithi* in both active and anesthetized alfalfa aphids does not indicate that the eggs of *A. smithi* cannot develop in the alfalfa aphid. I have found the larvae of *A. smithi* in alfalfa aphids during previous studies (Sections 3, 4c) and have reared *A. smithi* male and female adults from alfalfa aphids. It is, therefore, most likely that the *A. smithi* females did not release eggs into the alfalfa aphids that they struck in the present study, probably because of insufficient oviposition pressure. Oviposition pressure, defined here as the parasitoid's motivation or desire to oviposit, may depend on factors such as the number of mature eggs in the parasitoid's gonads or "egg load" (Collins and Dixon 1986), and the age of the parasitoid (Kambhampati *et al*. 1987). It is possible that oviposition pressure was lower in the *A. smithi* females of this study than in their counterparts in previous studies.

On the basis of these results, I suggest that oviposition and developmental success of these parasitoids do not markedly differ between pea and alfalfa aphid. However, differences between the acceptibilty of these two aphids are significant and may be the only factors that determine the preferences shown by these parasitoids.

SECTION 5b: SEX RATIO AND ADULT SIZE OF <u>APHIDIUS</u> <u>PISIVORUS</u> REARED IN PEA AND ALFALFA APHIDS

The successful production of offspring by parasitoids is dependent upon correlation between host selection and suitability (Mackauer 1973). Thus, it is not surprising that parasitoids oviposit in certain hosts rather than in others. Aphid parasitoids of the genus <u>Aphidius</u> often fail to oviposit into hosts that appear suitable for larval development (Cameron <u>et</u> <u>al</u>. 1984, Pungerl 1984). Conditioning (Pungerl 1984) or the development of parasitoid biotypes (Cameron <u>et</u> <u>al</u>. 1984) may explain this behavior, but we must assume that these parasitoids select hosts of optimal suitability for their offspring.

In Section 3, I showed that <u>A</u>. <u>pisivorus</u> parasitized more second-instar pea than second-instar alfalfa aphids when both hosts were equally available and abundant, but the two aphid species were parasitized with equal frequency when offered separately. In Section 4b I showed that although second-instar pea and alfalfa aphids were equally susceptible to being struck, alfalfa aphid were rejected more frequently than pea aphids. From these results, I suggested that the alfalfa aphid may be less acceptable than the pea aphid.

To understand better the apparent preference of <u>A</u>. <u>pisivorus</u> for the pea aphid, it was important to know whether the pea aphid really was the most suitable host. Progeny of parasitoids have been found to reach abnormally small adult-size

(Zohdy 1976), to consist mostly of males (Jackson _et al_. 1974; Zohdy 1976), and to have high pre-emergence mortality (Calvert 1973) if reared on certain hosts. Therefore, these three criteria were used to compare the suitablity of pea and alfalfa aphids for _A_. _pisivorus_.

In addition, Charnov (1982) suggested that the sex ratio of progeny from a given host type may vary if sex allocation by the parasitoid is dependent on its experience with hosts in the environment. Parasitoids that prefer to overproduce daughters in hosts of high suitability might "learn" the range of available host types and treat some as hosts for only sons and others as hosts for only daughters. I have found that _A_. _pisivorus_ females, when conditioned on the alfalfa aphid, showed no apparent preference for pea or alfalfa aphids (Section 4d). It is conceivable that sex allocation by _A_. _pisivorus_ is similarly affected by conditioning, and this factor should also be examined.

The following studies had two objectives: (1) To compare the emergence sex-ratio, pre-emergence mortality, and dry weight of adult _A_. _pisivorus_ reared in the pea aphid with those reared identically in the alfalfa aphid, and (2) to examine the effect of conditioning on sex allocation by _A_. _pisivorus_.

Methods

Second-instar pea aphids were held for 3 h in wax paper cups with *A. pisivorus* females from stock colonies. The aphids were then put on potted broad-bean plants at 23 °C, and those that mummified within 8 days were placed singly inside transparent gelatin capsules. Female parasitoids that emerged from these mummies were put singly into capsules with a single male. Females that mated were kept at 20 °C and fed a solution of water and honey until they were needed.

Thirty two 3- to 4-day-old mated females were separated into eight groups of four, and each group was kept for 4 h in a covered wax-paper cup with 100 second-instar aphids of one species. Sixteen of the females were confined with pea aphids and the other 16 with alfalfa aphids. The parasitoids were then kept in empty cups and fed the honey and water solution. Twenty four h later, the 32 parasitoids were placed singly for 6 h in 15.5-cm-diam. cages, each containing 20 second-instar pea aphids, 20 second-instar alfalfa aphids, and the apical portion of a broad-bean shoot. On the following day, the alfalfa aphids were separated into cages containing broad-bean shoots. Both aphids were reared at 20 ± 1 °C and 50 ± 5 % RH and those that mummified were placed in covered wax-paper cups. Each cup was checked daily for parasitoids, and those that emerged were separated by gender and allowed to expire in the cups. Mummies from which no parasitoids emerged were counted two weeks after the last mummy was placed into its cup.

All parasitoids were placed in one of four groups according to the host in which they had developed and the host on which their mothers had been conditioned. The four groups were: pea-aphid host and pea-aphid conditioned mother, pea-aphid host and alfalfa-aphid conditioned mother, alfalfa-aphid host and alfalfa-aphid conditioned mother, alfalfa-aphid host and pea-aphid conditioned mother. Forty males and 40 females were selected from each group and dried in an oven at 80°C for 120 h. The dried parasitoids were kept in a desiccator at room temperature for 30 min before being weighed.

This experiment was repeated twice, and the second two weeks after the first. Both experiments were carried out at 24 ± 1 °C and 53 ± 3 % RH, and all mummies were kept under continuous lighting at 20 ± 1 °C and 50 ± 5 % RH. During the second experiment, 30 second-instars of each aphid were taken from the synchronous colonies used for the experiment. These aphids were 72 ± 4 h old when they were killed with CO_2. The dry weights were determined with the same procedure used for the parasitoids.

Data from both experiments were pooled and analyzed by randomized block-design ANOVA. Separate ANOVAs were run for each of the following dependent variables: proportion of females among all parasitoids that emerged (emergence sex-ratio); proportion of mummies from which parasitoids emerged (survivorship); and dry weight of parasitoids. The ANOVAs for emergence sex-ratio used three factors: the host species; the conditioning of the parasitoid; and the experiment. The ANOVA for dry weight used the host species from which the parasitoid was reared and the sex of the parasitoid. The ANOVA for survivorship used the host species and the experiment. If a significant experiment-block effect was found, then separate ANOVAs were run for each experiment and the dependent variable that was affected.

All proportions, for each host species in each replication, were transformed using equation (1) (Section 3) where "n" is the total number of parasitoids, mummies, or aphids of one species, and "x" is the total number of female parasitoids, mummies from which parasitoids emerged, or mummified aphids of one species.

Differences between the dry weight of second-instar pea and alfalfa aphids were tested by fully randomized ANOVA. The numbers of pea and alfalfa aphid mummies produced by parasitoids, conditioned on the same host species, were compared by paired-difference t-tests.

Results

Host conditioning did not significantly affect host selection by A. pisivorus in this study (Table 17). Both pea- and alfalfa-conditioned females parasitized significantly more pea aphids than alfalfa aphids in both experiments.

The emergence sex-ratio and mortality of parasitoids did

Table 17. Mummies of *Acyrthosiphon pisum* and *Macrosiphum creelii* produced by *Aphidius pisivorus*. Parasitoid females were confined with aphids of one species for 4 h and, 24 h later, singly caged with 20 aphids of each species simultaneously for 6 h at 20 ± 1 °C, 50 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Treatment[1]	Experiment	Mummies produced[2] ($\bar{X} \pm 1$ SEM)[3]	
		A. pisum	*M. creelii*
Confined with	Exp. 1	$13.5 \pm 2.8^{**}$	8.6 ± 2.5
A. pisum	Exp. 2	$11.6 \pm 2.8^{**}$	8.7 ± 3.7
Confined with	Exp. 1	$13.6 \pm 2.8^{**}$	10.3 ± 2.8
M. creelii	Exp. 2	$14.6 \pm 3.3^{**}$	9.7 ± 3.2

[1] Each treatment group comprised n = 16 parasitoids that were confined with a single species of aphid for 4 h prior to confinement with both species of aphid.

[2] Statistical significance of differences between the mean numbers of *A. pisum* and *M. creelii* mummies produced in each treatment group (by paired-difference t-test, two-tailed): **, $P \leq 0.01$.

[3] Means are based on a sample size of n = 20 aphids in 16 replications.

not differ significantly with host type, experiment, or the conditioning of the mother. Survivorship was 95 ± 8 % on the pea aphid and 95 ± 7 % on the alfalfa aphid. The emergence sex-ratio of parasitoids from both aphids was 0.6 ± 0.2.

Parasitoids from the first experiment were significantly heavier than comparable parasitoids from the second (Table 18). Male and female parasitoids that developed in pea aphids were significantly heavier than their counterparts from alfalfa aphids. Females were significantly heavier than males which had developed from the same host type; however, the interaction between gender and host type was not significant.

No significant differences were found between the dry weight of second-instar pea and alfalfa aphids. Mean dry-weight was 0.056 ± 0.012 mg for the pea aphid and 0.055 ± 0.012 mg for the alfalfa aphid.

Discussion

In this study I have shown that A. pisivorus develops into a larger adult in a second-instar pea aphid than in a comparable alfalfa aphid. However, it was not shown that the smaller parasitoids from the alfalfa aphid had lower lifetime fitness than their larger pea aphid counterparts. Mackauer suggested (1986) that the parasitoid larva needs to grow only to the minimal size required for functioning effectively as an adult, after which size becomes less important for successful

Table 18. Mean dry weights of male and female *Aphidius pisivorus* reared in *Acyrthosiphon pisum* and *Macrosiphum creelii*, at 20 ± 1 °C, 50 ± 5 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Sex	Experiment	Dry weights[1,2] ($\bar{X}$ ± 1 SEM) 10^{-1} mg	
		Reared in *A. pisum*	Reared in *M. creelii*
Females	Exp. 1	1.86 ± 0.23**	1.61 ± 0.23
	Exp. 2	1.45 ± 0.23**	1.28 ± 0.21
Males	Exp. 1	1.63 ± 0.26**	1.35 ± 0.24
	Exp. 2	1.18 ± 0.26**	1.03 ± 0.19

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[1] Means are based on samples of n = 80 for male and female parasitoids.

[2] Statistical significance of differences between means within rows (by ANOVA): **, P ≤ 0.01.

parasitism than the developmental rate. Adult fitness components that could be compared include: age-specific fecundity, longevity, mating success, and ability to deal with hosts.

Vinson and Iwantsch (1980) reviewed many studies which found that nutritional insufficiency during larval development in the host may lead to reduced adult size, longevity and fecundity. Liu (1985) found that the size and fecundity of *Aphidius sonchi* were greater when reared on large than small aphids. Moreover, Calvert (1973) found that *Monoctonus paulensis* reared on the unsuitable hosts, *Therioaphis trifolii* and *Rhopalosiphum maidis* were short-lived and had deformed wings.

Furthermore, I have observed disadvantages for small *A. pisivorus*. Firstly, small males often have difficulties mating with larger females when the differences in size are great. Secondly, third-instar and larger aphids can more easily fend off or escape from small than large females.

In this study, I found that parasitoids that developed in the first experiment were larger than their counterparts in the second experiment. Differences in the quality of the plants on which the parasitized aphids were reared could well have resulted in the differences between the quality of the host aphids in the two experiments. Variables such as temperature (Campbell *et al.* 1974), stage or size of the host (Liu 1985), and the plant (Vinson and Iwantsch 1980) possibly also affect suitability and should be taken into account in comparisons between different host types.

Parasitoids have been found to develop more slowly in relatively small than in large hosts (Fox _et al_. 1967; Mackauer 1973), and this may be the result of the parasitoid's development being arrested until the host has reached a certain size or stage (Corbet 1968). In addition, the parasitoid's rate of development may vary with that of the host (Mackauer and Kambhampati 1984) and with the host's nutritional suitability (Vinson and Iwantsch 1980). I did not measure the developmental time of _A_. _pisivorus_ in the present study, but I observed that many of the parasitoids reared from the alfalfa aphid required from 24 to 48 h longer to emerge than their counterparts from the pea aphid. Second-instar pea aphids were not heavier than comparable alfalfa aphids in the present study, but parasitoid growth and development may be dependent on not only the initial size of the host but also on its potential for growth (Mackauer 1986). I suggest that the growth of parasitized pea and alfalfa aphids be compared in future studies.

Pre-emergence mortality may result from a number of factors, including the immunity, nutritional unsuitability, and possible toxicity of the host (Vinson and Iwantsch 1980). In this study, I found no differences between the emergence of parasitoids from mummified pea or alfalfa aphids, but I did not compare pre-emergence mortality before mummification. High proportions of dead larvae (Calvert 1973) and encapsulated eggs or degenerated embryos (Griffiths 1960) have been found in studies of aphidiids that oviposit into unsuitable hosts. However, I suggest that the pre-emergence mortality of A. pisivorus does not differ materially between the two aphids because of the high proportions of both aphids that were successfully parasitized.

Emergence sex-ratio could be a useful indicator of differences in host suitability if the female parasitoid has the ability to ascertain host quality and then selectively deposit fertilized or unfertilized eggs. Most Hymenoptera have haplodiploid sex determination, which gives the female the ability to control the sex of offspring (Charnov 1982). Progeny from sub-suitable hosts may include reduced numbers of females if the parasitoids lay few fertilized eggs into these hosts, or if males survive better on them than females (Flanders 1956, 1965).

A. pisivorus clearly preferred the pea aphid in the present study, but the sex ratios of progeny that emerged from the two aphids were still not significantly different. With other Aphidiidae, Dransfield (1979) also found no consistent differences between the sex ratios of the progeny of Aphidius uzbekistanicus reared from Metopolophium dirhodum, a preferred and suitable aphid host, or Hyalopteroides humilis, one less preferred and less suitable. In contrast, Jackson et al. (1974) found that Ephedrus plagiator produced more females on preferred than on less preferred hosts, and these results apparently resulted from selective oviposition of fertilized eggs.

If parasitoids are able to distinguish between and show preference for hosts of different suitability, it would be advantageous for them to allocate their fertilized eggs accordingly. Natural selection favors a strategy of producing mainly sons in small hosts and mainly daughters in large, when the females gain more than males in terms of lifetime fitness by being large (Charnov 1982). However, this same theory says that a given host type may be large or small, depending upon the other hosts present in the environment. If the distribution of host types varies in time and space, short-term sex ratio shifts can occur for any given host type.

Assuming that this theory is also true for parasitoids given a choice of host types that differ in suitability, I suggest that host selection and sex allocation among the Aphidiidae is dependent on: previous encounters with other hosts; quality of the present host; and the number of ripe eggs in the parasitoid. Under the conditions of the present study, the allocation of fertilized eggs to the alfalfa aphid may have varied in a manner that resulted in similar sex allocations for both aphids. Using a similar set of factors, Simbolotti _et al_. (1987) prepared a model that accurately predicted both host selection and sex allocation by _Lariophagus distinguendus_ when hosts of different sizes were available.

Host conditioning did not affect host selection or sex ratio in this study, but it is possible that the conditioning was ineffective or its effects were lost during the 24 h between the conditioning period and the experiment. However, even if host conditioning did affect selection it is unlikely that it would have had a significant effect on sex ratio. The factors responsible for short-term sex ratio shifts would probably obscure any effect by host conditioning.

In summary, I found that _A_. _pisivorus_ developed into a larger parasitoid when reared in the pea aphid, but no differences were found in the mortality or sex ratio of parasitoids that were reared on pea or alfalfa aphids. In an environment varying in time and space, sex allocation would not be expected to be rigid. Under these conditions, sex ratio may be a poor indicator of host suitability. Comparisons which show meaningful differences between the adult fitness of _A_. _pisivorus_ reared from the two aphids are probably the most appropriate tests for suitability.

SECTION 5c: SEX RATIO, ADULT SIZE, AND HOST SELECTION OF *APHIDIUS ERVI* REARED IN PEA AND ALFALFA APHID

In surveys described in Section 2, I found that *A. ervi* and *A. pisivorus* were parasitoids of both pea and alfalfa aphid on cultivated alfalfa in the southern interior of British Columbia. *A. ervi* adults were more abundant than *A. pisivorus* at Kamloops, but their predominance was not reflected in the composition of the samples of three parasitoids that emerged from the alfalfa aphids that I collected from the area. Moreover, I found in laboratory studies that *A. pisivorus* had a weak preference for the pea aphid, but *A. ervi* had a strong preference for the same aphid (Sections 3, 4b, 4d).

Reviews of host records (Mackauer and Finlayson 1967; Stary 1973) show that *A. ervi* is polyphagous. However, Pungerl (1984) and Cameron *et al*. (1984) found that different populations of *A. ervi* showed markedly different host ranges. Cameron *et al*. (1984) suggested that *A. ervi* forms biotypes or races, on certain aphid species that differ significantly in their esterase-enzyme banding patterns and host ranges. Pungerl (1984) demonstrated that different populations of *A. ervi* and two other *Aphidius* species varied in their host preferences even when the populations of each species were electrophoretically and morphometrically homogeneous.

Most attempts to transfer *A. ervi* to different hosts in the laboratory were unsuccessful; no mummies or female offspring were produced from the new hosts (Pungerl 1984; Cameron et al. 1984). Successful transfers were characterized by low parasitism and by few females being produced in the first generation after transfer, but parasitism and numbers of females increased after several generations on the new host (Pungerl 1984; Cameron et al 1984). Smith and Cornell (1979) explained improved performance in the first generation after transfer as simple conditioning in the larval stage, and subsequent improvement as some form of selection. Pungerl (1984) suggested that conditioning may result in different populations of the same species of *Aphidius* attacking different hosts preferentially.

Hopkins was the first to suggest that female parasites (parasitoids) prefer to oviposit in the same species that served as their larval hosts (Hopkins 1917). It has been demonstrated that a female parasitoid of a species with a wide host range often prefers a host species from which she has been reared (Salt 1935; Thorpe and Jones 1937; Ohgushi 1960; Eijsackers and van Lenteren 1970). Smith and Cornell (1980) have shown that the host preferences of female parasitoids were affected after one generation on a new host.

The objectives of the present study were: To compare the emergence sex-ratio, pre-emergence mortality after mummification, and dry weight of adult *A. ervi* reared in the pea aphid with those reared identically in the alfalfa aphid, and to compare the host selection and sex allocation of *A. ervi* reared for one generation in the alfalfa aphid with those reared continuously in the pea aphid.

Methods

Thirty-two A. ervi females were obtained from stock colonies and separated into eight groups of four. Each group was kept for 4 h in a covered wax-paper cup with approximately 100 second-instar aphids of one species. Sixteen females were confined with pea aphids and the other sixteen with alfalfa aphids. The aphids were removed from the cups and kept on potted broad-bean plants. Aphids that mummified within 8 days were placed singly into gelatin capsules which were kept in covered wax-paper cups. The parasitoids that emerged were mated and fed a solution of water and honey until needed.

Fifteen 3- to 4-day-old mated females were selected from the parasitoids reared in pea aphids and a similar fifteen from those reared in alfalfa aphids. The 30 parasitoids were placed singly for 3 h in 8.5-cm-diam. cages, each containing 12 second-instar pea aphids, 12 second-instar alfalfa aphids, and the apical portion of a broad-bean shoot. On the following day, the alfalfa aphids were removed from each cage and placed singly in separate cages containing broad-bean shoots. Aphids that mummified were placed in covered wax-paper cups. Each cup was checked daily for parasitoids, males and females that emerged were separated by gender into other cups and allowed to expire.

Mummies from which no parasitoids emerged were counted two weeks after the last mummy was put into its cup. All phases of these experiments were carrried out at 22 ± 1 °C, 30 ± 3 % RH, with continuous lighting.

Parasitoids were placed in one of four groups according to the host in which they and their mothers had developed. The four groups were: pea-aphid host and pea-aphid reared mother, pea-aphid host and alfalfa-aphid reared mother, alfalfa-aphid host and alfalfa-aphid reared mother, and alfalfa-aphid host and pea-aphid reared mother. All parasitoids were dried in an oven at 80 °C for 120 h. Dried parasitoids were kept in a desiccator at room temperature for 30 min before being weighed.

The data were analyzed by ANOVA and paired-difference t-tests. Separate ANOVAs were run for each of the following dependent variables: proportion of pea aphids among all parasitized aphids (preference); proportion of females among all the offspring of _A. ervi_ that emerged (emergence sex-ratio); and dry weight of the parasitoids. The ANOVAs for preference used one factor, the host of the wasp that parasitized the aphids. The ANOVAs for emergence sex-ratio used two factors, the aphid species and the parental host. The ANOVA for dry weight used three factors: the aphid species; the parental host; and the sex of the parasitoid.

All proportions, for each aphid species in each replication, were transformed using the equation (1) (Section 3) where "n" is the total number of parasitoids, or mummies of both host species, and "x" is the total number of female parasitoids or mummified aphids of one species. The sex-ratio data were pooled only from the replications that had females that produced both male and female progeny. Four of the parasitoids reared in pea aphids and four reared in alfalfa aphids did not produce any females. The numbers of pea and alfalfa aphid mummies produced by parasitoids, reared in the same host species, were compared by paired-difference t-tests.

Results

A. ervi females reared in pea or alfalfa aphids parasitized significantly more pea than alfalfa aphids (Table 19). There were no significant differences between the proportions of pea aphids among all aphids parasitized by *A. ervi* reared in pea or alfalfa aphids.

Survivorship in both aphid species was above 92% (Table 19), and the emergence sex-ratio did not differ significantly with host or the host of the parasitoid's mother. The emergence sex-ratio was 0.7 ± 0.2 for parasitoids from pea aphids and 0.6 ± 0.2 for those from alfalfa aphids.

A. ervi reared in pea aphids were significantly heavier than their counterparts reared in alfalfa aphids (Table 20) and females were significantly heavier than males from the same host (Table 20); however, interactions between gender, host type, and parental host were not significant.

Table 19. Mummies of *Acyrthosiphon pisum* (AP), and *Macrosiphum creelii* (MC), produced by *Aphidius ervi* reared in *A. pisum* or *M. creelii*. Parasitoid females were singly caged with 12 aphids of each species simultaneously for 3 h at 22 ± 1 °C, 30 ± 3 % RH, with continuous lighting All aphids were 72 ± 4 h old and reared at 20 °C.

Host of origin	Total mummies		Mean mummies[1] ($\bar{X} \pm 1$ SEM)[2]		Total parasitoids emerged	
	AP	MC	AP	MC	AP	MC
A. pisum	130	68	$8.7 \pm 2.7^{**}$	4.5 ± 2.2	120	67
M. creelii	123	73	$8.2 \pm 3.3^{**}$	4.9 ± 1.8	114	69

[1] Statistical significance of differences between means within rows (by paired-difference t-test, two-tailed): **, $P \leq 0.01$.

[2] Means are based on a sample size of n = 12 aphids in 15 replications.

Table 20. Mean dry weights of male and female *Aphidius ervi* reared in *Acyrthosiphon pisum* and *Macrosiphum creelii*, at 22 ± 1 °C, 30 ± 3 % RH, with continuous lighting. All aphids were 72 ± 4 h old and reared at 20 °C.

Host of origin	Dry weights[1,2] ($\bar{X}$ ± 1 SEM) [in mg x 10^{-1}]	
	Females	Males
A. pisum	1.52 ± 0.19*	1.28 + 0.17*
M. creelii	1.46 ± 0.17	1.23 ± 0.14

[1] Means are based on samples of n = 110 for females reared in *A. pisum*, n = 68 for females reared in *M. creelii*, n = 109 for males reared in *A. pisum*, and n = 63 for males reared in *M. creelii*.

[2] Statistical significance of differences between means within columns (by ANOVA): *, $P \le 0.05$.

Discussion

Jermy et al. (1968) suggested that the preference of female parasitoids for certain hosts is developed through preimaginal conditioning. Smith and Cornell (1979) considered preimaginal olfactory conditioning to be the mechanism that was responsible for a shift in the host preference of the parasitoid wasp, Nasonia vitripennis, after it was reared in a different host for a single generation.

In this study, A. ervi was reared in alfalfa aphids for one generation, but the females of that generation did not switch their preference from pea to alfalfa aphids. Moreover, females reared in pea aphids did not parasitize proportionately fewer alfalfa aphids than their counterparts reared in alfalfa aphids. It is therefore unlikely that host selection by females reared for a single generation in alfalfa aphids was different from that by females continuously reared in pea aphids.

Vinson (1976) showed that host specificity is determined by a sequence of chemical and physical cues. Volatile chemicals from the host, the host's food, or a combination of these factors appear to be important in host selection and acceptance by insect parasitoids. Among the Aphidiidae, some species will attack a host only on specific food-plants. For example, Fox et al. (1967) found that A. smithi will attack Myzus persicae reared on broad bean but not those reared on tobacco. But even more interesting is that some investigators have found different populations of the same Aphidius species to respond differently to certain aphid and plant species. Powell and Zhang (1983) demonstrated in olfactometer studies that A. ervi reared in pea aphids showed a significant response to pea aphids but not to English grain aphids, Sitobion avenae, or nettle aphids, Microlophium carnosum. Furthermore, Powell and Zhang showed that male and female A. ervi reared in pea aphids cultured on broad bean plants responded to leaves of bean and wheat but not to leaves of nettle, Urtica dioica.

Pungerl (1984) suggested that conditioning was responsible for the different host ranges that she found in different populations of A. ervi. However, evidence from colour patterns (Stary 1983), enzyme analysis (Nemec and Stary 1983; Cameron et al. 1984), and olfactory studies (Powell and Zhang 1983) indicate that A. ervi appears to form separate biotypes on certain aphid species. In the present study, I did not find any evidence which showed that the form of conditioning proposed by Hopkins (1917) influenced the preference of A. ervi for the alfalfa or pea aphid. Both the pea and alfalfa aphid were reared on broad bean in this study and it is possible that the common host plant may have reduced the effects of preimaginal conditioning, if any.

Smith and Cornell (1979) found that the host preference of N. vitripennis shifted in favor of a new host only when the diet of the new host was very different from the diet of the original one. Continuous rearing of A. ervi on the alfalfa aphid might conceivably result in a significant shift or even a switch in host preference, which would indicate that biotypes of A. ervi can be selected from a more diverse parental genotype with the pea aphid as a host. However, this hypothesis would need to be tested by examining the host range of A. ervi collected from alfalfa and pea aphids from the field and by using electrophoretic and morphometric techniques to compare field populations of this parasitoid from the two aphid species.

In Section 5b I found that female A. pisivorus had a weak preference for pea aphids and their progeny developed into larger adults when reared in second-instar pea aphids than in comparable alfalfa aphids. From the strong preference shown by female A. ervi for pea aphids in previous studies (Sections 4, 4b, 4d), I expected that A. ervi would also develop into larger adults in pea aphids than in alfalfa aphids. However, male and female A. ervi from pea aphids were only slightly heavier than comparable parasitoids from alfalfa aphids and I suggest that A. ervi developed into adults of equivalent size in either aphid species.

If adult size is an accurate measure of host suitability, then second-instar pea and alfalfa aphids may have been equally suitable hosts for A. ervi in this study. Yet, as I discussed in Section 5b, the suitability of a host should be assessed by the potential lifetime fitness of the parasitoids reared in it. In the present study adult A. ervi reared in either aphid did not differ in size, but I suggest that they may have differed in parameters of adult fitness such as longevity or fecundity.

Pungerl (1984) found in transfer studies that a population of *A. ervi*, collected on pea aphid and transferred to *Myzus persicae* produced only six females but 64 males. Other investigators have also found that more males are produced in less preferred than in preferred hosts (Jackson *et al* 1974; Calvert 1973). Factors that influence the sex ratio of emerging parasitoids were reviewed by Vinson and Iwantsch (1980) and discussed in detail by Flanders (1965) and Charnov (1982). The sex ratio of emerging parasitoids did not differ between those reared in the two aphids in the present study and I obtained similar results with *A. pisivorus* (Section 5b). Possible explanations for the absence of detectable sex-allocation, under the conditions of these studies, were discussed in Section 5b.

In summary, *A. ervi*'s host selection, sex allocation, adult size, and pre-emergence mortality were not significantly affected by the host in which it was reared. *A. ervi* attacks a wide range of aphids occurring on a variety of unrelated plants (Stary 1973), but it is possible that this species forms biotypes that are restricted to certain aphid species. Switching between different hosts may be hindered if different parasitoid biotypes become associated with certain hosts (Gonzalez *et al*. 1979). It is possible that the low occurrence of *A. ervi* on the alfalfa aphid at Kamloops is due to the existence of biotypes of the parasitoid that appear to prefer the pea aphid.

SECTION 6: GENERAL DISCUSSION AND CONCLUSIONS

Before this study, little was known of the alfalfa aphid's distribution or importance as a pest of alfalfa in British Columbia, nor was it known if it was attacked by the established parasitoids of the pea aphid in the region. Phytophagous insects may become serious pests of crops when they are not attacked by resident parasitoids or predators. Strong preference for the pea aphid and reluctance to switch hosts may limit the usefulness of parasitoids of the pea aphid against the alfalfa aphid. It was, therefore, important to investigate host selection and switching by these parasitoids. The experiments and field observations recorded here have contributed new information on these topics.

In a survey of the alfalfa-growing districts of the region, the alfalfa aphid was found only in a 70 km strip between Cache Creek and Kamloops (Section 2). The alfalfa aphid was always less common than the pea aphid. The recent discovery and rarity of the alfalfa aphid in the province suggests that the aphid is not native and is a newcomer. It may well have been established in the area by wind-dispersed alates or infested alfalfa hay from the U.S. Pacific Northwest.

The alfalfa aphid appears to be a less important pest of alfalfa in BC than the pea aphid; however, its range in the southern interior could increase through further introductions from the U.S. or dispersal from the Cache Creek-Kamloops area.

It is, therefore, advisable to monitor the spread and abundance of the aphid, and to examine factors that might affect its proliferation.

In Washington, Johansen and Eves (1973) found that prebloom cleanup sprays of dimethoate, carbofuran, propoxur, or aldicarb on alfalfa contributed to outbreaks of the alfalfa aphid. The biotypes of the aphid in Washington were apparently more resistant to these insecticides than their pea aphid counterparts. The effects of different insecticides on biotypes of pea and alfalfa aphids in BC should also be investigated.

Climate may affect the spread and abundance of the alfalfa aphid in the province. Halfhill (1982) studied the effect of some temperatures on its survival and reproduction. He found that it reproduced best on alfalfa at 20 °C, but its reproduction dropped by 65 % at 25 °C and stopped at 30 °C. I measured the intrinsic rate of increase, or "rm", of the Kamloops biotype on broad bean at 20 °C, and found it to be lower than that of its pea aphid counterpart (Appendix). However, accurate models of the population dynamics of the alfalfa aphid and predictions of its potential range might require field data.

Hagen and van den Bosch (1968) considered that parasitoids have been important control agents of aphids of alfalfa in North America. In the southern interior of BC, pea aphids are heavily attacked by a complex of four primary parasitoids (Campbell 1974). However, these are not necessarily effective control agents for alfalfa aphids.

To be effective against both aphid species, the parasitoids should readily attack either, or switch to the more abundant species if preference is shown for one at equality. In addition, the parasitoids should be able to develop in either host to the adult stage. At Kamloops, alfalfa aphids were parasitized by the wasps, *Aphidius ervi*, *A. pisivorus*, and *Praon pequodorum* (Section 2). In the laboratory, I found that the developmental success of these parasitoids did not differ between pea and alfalfa aphids (Sections 5a, 5b, 5c). But I also found that they all preferred the pea aphid (Sections 3, 4b), did not switch (Section 3), and could not be conditioned to increase their acceptance of the alfalfa aphid (Sections 4d, 5c).

In recent surveys, *A. ervi* was the most common of the three wasps at Kamloops (Section 2) and throughout the southern interior of BC (Mackauer and Kambhampati 1986). This wasp currently appears to be the most successful parasitoid of pea aphids in the region, but the findings here indicate that it may be ineffective against alfalfa aphids. The strong preference of *A. ervi* for the pea aphid and its reluctance to switch could, to a large extent, allow populations of the alfalfa aphid to escape parasitism. For the same reasons, I expect *P. pequodorum* to be an ineffective control agent for the alfalfa aphid.

Of the three wasps, *A. pisivorus* seems to be the best control agent for the alfalfa aphid. Although *A. pisivorus* did not switch in this study, it readily oviposited into alfalfa aphids and its preference for the pea aphid was weak (Sections 3, 4b). However, A. pisivorus was the least common of the three wasps at Kamloops (Section 2) and it appears to be consistently uncommon throughout the province (Mackauer and Kambhampati 1986); thus, its impact on populations of alfalfa aphids may be limited.

Prior to 1983, A. smithi was the most common parasitoid of the pea aphid in the southern interior of BC (Mackauer and Kambhampati 1986). For reasons, yet to be determined, this parasitoid has practically disappeared from this region. In the laboratory, its reluctance to parasitize alfalfa aphids was apparently greater than that of the other wasps tested (Sections 3, 4b, 4c, 5a). I would not expect it to parasitize alfalfa aphids in the field.

These predictions are based on experiments that used only second-instar aphids. In the field, parasitoids would encounter aphids in all nymphal instars and as adults. To predict parasitism in the field more accurately, the various tests might be repeated using the different stages of the hosts. However, the present study may still be useful for assessing the potential of the parasitoids as control agents. I suggest that the impact of parasitoids on the alfalfa aphid at Kamloops is not great. Predators and environmental factors undoubtedly play a role in keeping down populations of the aphid.

It is interesting that second-instar alfalfa aphids were consistently less acceptable than similar pea aphids, to all four parasitoids. Second-instar pea and alfalfa aphids were equally vulnerable to attack (Section 4b), and I could not conclusively find that pea aphids were more suitable hosts than alfalfa aphids (Sections 5a, 5b, 5c). Additional studies are needed to determine the criteria used by these parasitoids to select hosts.

Switching, as defined by Murdoch (1969), appears to be a rare phenomenon among parasitoids; to my knowledge only one case (Cornell and Pimentel 1978) has been reported. From the present study, I propose that parasitoids may not switch, when the availability of potential hosts are varied, if all of the following conditions are found: the parasitoids show consistent preference for one host; the hosts are located and handled in the same way, and the hosts are equally vulnerable. As discussed in Section 3, switching might occur less often in parasitoids than in predators because the goals are different. It is possible that some of these four wasps would switch under different conditions; for example, if they had to use a different search mode for each host.

Although these wasps did not switch, they seemed to show absolute preference for the pea aphid and partial preference for the alfalfa aphid (Sections 4b, 4c). It appeared that alfalfa aphids were attacked only when the encounter rates with unparasitized pea aphids were low. I suggest that host selection in these circumstances could be explained by models that base oviposition decisions on the physiological and informational state of the parasitoid, as well as on the quality of the hosts. Models of this type have been used to predict host selection by parasites of fruit (Roitberg and Mangel 1989) and parasitoids of insects (Simbolotti _et_ _al_. 1987).

Finally, for reasons of convenience and practicality, we usually study parasitoid problems in the laboratory, which means they are greatly simplified from those in the field. Consequently, our solutions may well be inconsistent with field observations or reality. The differences between laboratory cultures and their counterparts in the field may confound the results. Although they are much more difficult to conduct, field studies may be needed for the proper examination of host preference and switching.

APPENDIX: RATES OF DEVELOPMENT AND LIFE TABLE CHARACTERISTICS OF PEA AND ALFALFA APHIDS ON BROAD BEAN

Introduction

Considerable differences exist in the rates of development between different aphid species and even between different biotypes of one species (Kilian and Nielson 1971). Campbell (1974) determined the rates of development and life table characteristics for the Kamloops biotype of the pea aphid, on alfalfa, at four different temperatures. Halfhill (1982) determined the survival and development of the alfalfa aphid on different host plants and at different temperatures. However, I have found no comparisons, under identical conditions, between the rates of development and life table characteristics of the pea and the alfalfa aphid. This section reports a study that made these comparisons. From this study, I found that second-instars of both species could be obtained, for parasitoid-aphid studies, by rearing the aphids at 20 °C for 72 ± 4 h.

Materials and Methods

Eighty nymphs of alfalfa aphids and 20 of pea aphids were selected from progeny borne by apterous adults during a 3-h period. Pairs of newly deposited nymphs of the same species were placed in 8.5-cm-diam petri-dish cages with broad bean shoots. The cages were checked every 24 h for cast skins, which indicated edysis. When the aphids had developed into adults, 20 apterous alfalfa aphids and 10 apterous pea aphids were placed singly in 8.5-cm-cages. Each cage contained the apical portion of a broad-bean shoot that was replaced when necessary but not less than every 10 days. The adult aphids were checked every 24 h and their progeny were counted and removed until the adults died. The experiment was run at 20 ± 1 °C, 51 ± 3 % RH, with continuous lighting.

From this experiment, mean values of the following measurements were determined for both apterous pea and alfalfa aphids: duration of each of the four nymphal instars; pre-reproductive period; reproductive period; post-reproductive period; longevity; and total fecundity. Reproductive and demographic characteristics of the apterous aphids were assessed by the construction of life tables from the age-specific fecundity (m_x) and survival (l_x) values for each 24-h age interval (x). From these data the intrinsic rate of increase for the apterous viviparous morph of each species (rm) was calculated by use of a computer program, written by A. Campbell (1974). This program was also used to calculate gross reproductive rate (GRR), net reproductive rate (R_o), finite rate of increase (FRI), generation time (T), and doubling time (DT) for the aphids. ANOVA was used to test for differences between the pre-reproductive period, reproductive period, post-reproductive period, longevity, and total fecundity of the pea and the alfalfa aphid.

Results

Developmental periods of the immature stages of both apterous and alate alfalfa aphids and apterous pea aphids, at 20 ± 1 °C, are given in Table 21. The developmental periods of the first three apteriform instars of both species and of the alatae of the alfalfa aphid were essentially the same. However, the fourth alatiform instar of the alfalfa aphid required an average of 0.63 days longer for its completion than its apterous counterpart, which in turn required an average of 0.86 days longer for its completion than the fourth apteriform of the pea aphid (Table 21).

Reproductive and pre-reproductive periods of the apterae of both species are given in Table 22. Apterous pea aphids averaged significantly shorter pre-reproductive, reproductive, and post-reproductive periods than apterous alfalfa aphids. Reproduction started earlier in apterous pea than in alfalfa aphids (Table 22).

Reproductive and demographic characteristics of apterous pea and alfalfa aphids are given in Table 23. GRR, R_o, rm, and FRI of apterous pea aphids were greater than those of apterous alfalfa aphids. DT and T of apterous pea aphids were less than those of apterous alfalfa aphids.

Table 21. Developmental time of apterous and alate *Macrosiphum creelii* and apterous *Acyrthosiphon pisum* at 20 ± 1 °C, 51 ± 3 % RH, with continuous lighting.[1]

Species	Length of nymphal instar (days)					Time-to-adult (days)	
	I	II	III	IV (apt.)	IV (alat.)	Apt.	Alat.
A. pisum							
Mean	1.50	2.05	2.05	2.00	-	7.60	-
SEM	0.00	0.22	0.09	0.00	-	0.31	-
M. creelii							
Mean	1.59	2.04	2.05	2.87	3.48	8.55	9.16
SEM	0.28	0.05	0.05	0.08	0.10	0.30	0.48

[1] Means are based on samples of n = 20 for apterous *A. pisum*, n = 80 for I- to III-instar *M. creelii*, n = 45 for IV-instar and adult apterous *M. creelii*, and n = 35 for IV-instar and adult alate *M. creelii*.

Table 22. Longevity and mean lengths of pre-reproductive, reproductive, and post-reproductive periods of apterous *Acyrthosiphon pisum* and apterous *Macrosiphum creelii* at 20 ± 1 °C, 51 ± 3 % RH, with continuous lighting.[1,2]

Species		Pre-reprod. period (days)	Reprod. period (days)	Post-reprod. period (days)	Longevity (days)
A. pisum	Mean	8.5**	19.2*	9.0**	36.7**
	SEM	0.5	3.8	3.9	3.7
M. creelii	Mean	10.3	23.6	15.9	49.2
	SEM	0.7	5.4	6.5	6.3

[1] Means are based on samples of n = 10 for *A. pisum* and n = 19 for *M. creelii*.

[2] Statistical significance of differences between means within columns (by ANOVA): *, $P \leq 0.05$; **, $P \leq 0.01$.

Table 23. Reproductive and demographic characteristics of apterous *Acyrthosiphon pisum* and apterous *Macrosiphum creelii* at 20 ± 1 °C, 51 ± 3 % RH, with continuous lighting.[1]

	A. pisum	*M. creelii*
Total fecundity[2]	109.9 ± 11.7	91.8 ± 12.5
GRR	108.9	91.6
R_o	108.9	91.5
rm	0.355	0.289
FRI	1.426	1.335
T	13.212	15.627
DT	1.953	2.398

[1] GRR, gross reproductive rate (in females/female/generation); R_o, net reproductive rate (in females/female/generation); rm, intrinsic rate of natural increase (in females/female/day); FRI, finite rate of natural increase (in females/female/day); T, generation time (in days); DT, doubling time (in days).

[2] Means (± 1 SEM) are based on samples of n = 10 for *A. pisum* and n = 19 for *M. creelii*.

Discussion

Developmental times of the pea and the alfalfa aphid were similar, until the fourth-instar. Alfalfa aphids needed more time to develop from the fourth instar to adults than did pea aphids, and this may help to explain why parasitoids required less time to emerge from pea than from alfalfa aphids (Section 5b). Mackauer and Kambhampati (1984) have shown that the parasitoid of the cabbage-aphid, Diaeretiella rapae, took longer to develop in hosts that grew slowly than in hosts that grew rapidly.

The alfalfa aphid's rate of development on alfalfa (cv. Buffalo) at 20 °C (Halfhill 1982) was similar to its rate of development on broad bean (cv. Windsor) in this study. Halfhill (1982) also found that both survival and reproduction of adult alfalfa aphids did not vary between alfalfa and broad bean. In comparison, the pea aphid's rate of development on alfalfa at 19.7 °C (Campbell and Mackauer 1975) was slower than its rate of development on broad bean in this study at 20 °C. These differences between the pea aphid's rate of development in the two studies may have been due to experimental methods, the pea aphid colonies, or the type of host plant used.

On alfalfa, total reproduction and reproductive rate of the alfalfa aphid were greatest at 20 °C (Halfhill 1982); but in this study, the pea aphid exceeded the alfalfa aphid in both reproductive parameters. The pea aphid continued to reproduce well on alfalfa at temperatures up to 26 °C (Campbell 1974), whereas the reproductive rate of the alfalfa aphid decreased rapidly at temperatures above 20 °C (Halfhill 1982).

Overall, the pea aphid may develop more quickly and produce a larger total number of offspring in less time than the alfalfa aphid, under a wide range of conditions. Consequently, it is not surprising that the pea aphid is more common than the alfalfa aphid in alfalfa-growing districts of BC and the U.S. Pacific Northwest.

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