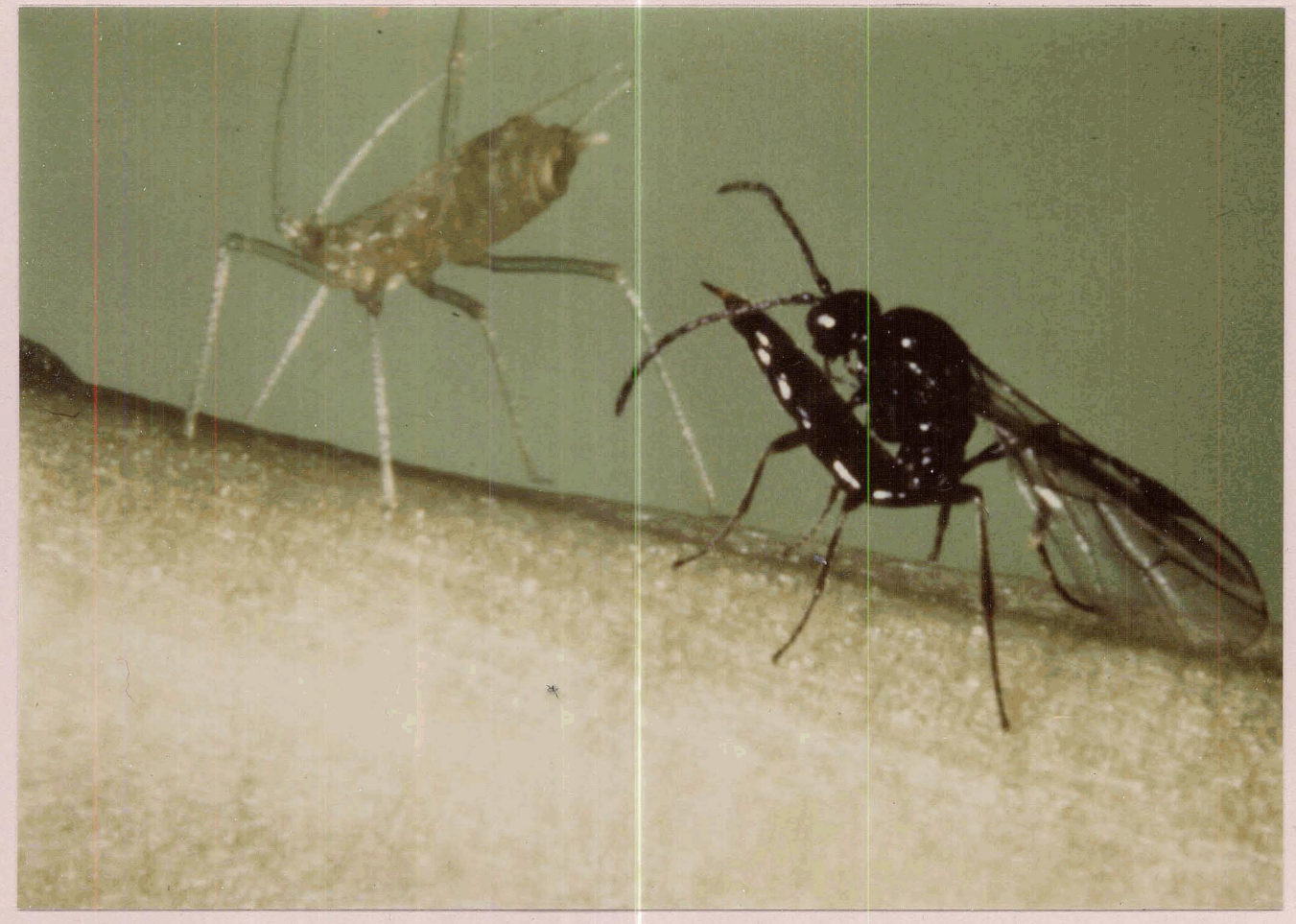

BIOLOGY AND ECOLOGY OF *EPHEDRUS CALIFORNICUS* BAKER (HYMENOPTERA: APHIDIIDAE)

by

Michael Benjamin Cohen
B.A., Colgate University, 1982

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Biology and ecology of Ephedrus californicus Baker (Hymenoptera: Aphidiidae).

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August 6, 1985
(date)

ABSTRACT

Aspects of the biology and ecology of the aphid parasite *Ephedrus californicus* Baker were studied on two host species: the lupine aphid, *Macrosiphum albifrons* Essig, recently introduced from North America to the United Kingdom and a pest of commercial lupines; and the pea aphid, *Acyrthosiphon pisum* (Harris), a globally-distributed pest of alfalfa. In the laboratory, with the pea aphid as host, the parasite had a mean total fecundity of 1193.00±SE 88.41 eggs, the highest recorded fecundity for any species of aphid parasite, and a mean longevity of 13.42±SE 1.13 days. The median time required for the parasite to complete development from oviposition to adult emergence, determined at four constant temperatures, ranged from 21.37 days at 17.6°C to 12.34 days at 26.4°C. A regression equation describing the parasite's rate of development versus temperature was calculated. From this equation, the developmental threshold of the parasite was estimated as 6.84±SE 0.38°C, considerably higher than those of the lupine and pea aphids.

In a choice test, the parasite showed no clear preference for either the lupine or the pea aphid. The sex ratio of offspring emerging from the two host species did not differ significantly, but pre-emergence mortality was higher with the lupine aphid as host because of the formation of "gregarious mummies".

In a survey of southwestern British Columbia, four primary parasites were found attacking the lupine aphid. These were *E. californicus*, *Aphidius lupini* Liu, *Praon* sp. nr. *occidentale* Baker, and *Praon* sp. *A. lupini* was well synchronized with the early spring appearance of the lupine aphid, and was the most abundant and widespread parasite. It appears to be the best choice for biological control of the lupine aphid in the United Kingdom. *E. californicus* was almost as widespread as *A. lupini*, but was only occasionally abundant and, as predicted from its high developmental threshold, did not appear until early summer.

Conclusions are drawn concerning the ecology of *E. californicus* on the lupine aphid, and the absence of this parasite from the pea aphid in North American alfalfa fields.

ACKNOWLEDGEMENTS

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The Aphidiidae are a small but well-studied family of the insect order Hymenoptera. In addition to their importance in controlling aphid pests, these parasites and their hosts provide a convenient laboratory system for studying host-parasite relationships. Information on the family has been reviewed in detail by Mackauer and Stary (1967) and Stary (1970), and only a brief summary will be presented here.

Members of the Aphidiidae are solitary endoparasites of vivi-oviparous aphids (Homoptera: Eriosomatidae, Hormaphididae, Aphididae). As with other parasitic Hymenoptera, the larval stage is parasitic and the adult free-living. The life cycle begins with oviposition, which the female accomplishes by thrusting her abdomen forward between her legs to strike the host. The egg hatches in the aphid haemocoele, and the parasite larva begins to feed selectively on non-vital host tissues. During the fourth and final larval instar, the host is killed as the parasite consumes the remainder of the aphid's internal tissues, leaving only the integument. The fourth instar spins a cocoon inside or beneath the eviscerated host, voids its stored waste or meconium, and pupates. The aphid integument with the

parasite cocoon inside or beneath it is called a "mummy". After pupation, the parasite cuts an emergence hole in the mummy and leaves to begin the free-living adult stage.

The adults are ready to mate shortly after emergence. Females mate only once, while a male can inseminate several females. Sex determination is arrhenotokous. At oviposition, the female may fertilize the egg, producing a female offspring; non-fertilized eggs become males. The life cycle from oviposition to adult emergence requires approximately two weeks at 21°C. Adults generally live less than a week in the field.

In several cases, introduced aphidiids have provided successful control of aphid pests. Notable examples include *Aphidius ervi* Haliday and *Aphidius smithi* Sharma and Subba Rao against the pea aphid in North America, *Praon exsoletum* (Nees) and *Trioxys complanatus* Quilis against the spotted alfalfa aphid in California, and *T. pallidus* (Haliday) against the walnut aphid in California (Hagen and van den Bosch 1968; Clausen 1978).

B. Objectives

The objectives of this study were:

1. to investigate the general biology of *Ephedrus californicus* Baker;
2. to assess the potential of *E. californicus* as a biological control agent of the lupine aphid, *Macrosiphum albifrons*

Essig; and

3. to explain, if possible, the absence of *E. californicus* from the pea aphid, *Acyrthosiphon pisum* (Harris), in alfalfa.

Objective 1

Previous work on *E. californicus* has covered only taxonomy, host range, and brief notes on field biology. The species was described in 1909, from a female colleted in Claremont, California (Baker 1909), and redescribed by Smith (1944) and Mackauer (1963). The reported North American host range includes *Acyrthosiphon pisum* (Smith 1944), *Dactynotus ambrosiae* (Thomas) (Smith 1944; Schlinger and Hall 1960b), *Macrosiphoniella artemiseae* (Boyer de Fonscolombe) (Mackauer and Stary 1967), *Macrosiphum agrimoniellum* (Cockerell) (Mackauer and Stary 1967), *M. euphorbiae* (Thomas) (Stary and Remaudiere 1982; Oatman *et al.* 1983), *M. rosae* (L.) (Smith 1944; Schlinger and Hall 1960b), *Myzus persicae* (Sulzer) (Oatman *et al.* 1983), *Rhopalomyzus grabhami* (Cockerell) (Smith 1944), and *Uroleucon* sp. (Stary and Remaudiere 1982).

Notes on the field biology of *E. californicus* state that it "appears to be an important parasite of *Macrosiphum rosae* in coastal California" and "appears to be somewhat specific to species of *Macrosiphum*" (Schlinger and Hall 1960b). The final instar larva, mummy, and characteristics for field identification of adults were described by Mackauer and Finlayson (1967).

Although *Ephedrus* contains several species of economic importance (Mackauer and Stary 1967), only a few, *E. incompletus* (Provancher) (Withington 1909), *E. persicae* Froggatt (Stary 1962), *E. plagiator* (Nees) (Jackson *et al.* 1974), and *E. cerasicola* Stary (Hofsvang and Hagvar 1975, 1977, 1978, 1983a, 1983b), have been studied in any detail. It is hoped that, by investigating the biology and ecology of a previously unstudied species, information of interest has been obtained concerning *Ephedrus*, the Aphidiidae, and host-parasite relationships in general.

Objective 2

While lupines (*Lupinus*, family Leguminosae) are regarded only as wildflowers and ornamentals in Canada, they are being studied in many parts of the world for a variety of commercial uses. The lupine aphid, *Macrosiphum albifrons* Essig, is a species restricted to *Lupinus* and indigenous to North America (Smith and Parron 1978). It has recently spread to the United Kingdom, where it has become a pest of cultivated lupines (Carter *et al.* 1984). In order to obtain information relevant to biological control of the lupine aphid, a survey of its hymenopterous parasites in southwestern British Columbia was begun in 1983, and *E. californicus* was found to be one such parasite. A major objective of this study was to assess the potential of *E. californicus* as a biological control agent for *M. albifrons*. This objective was approached through laboratory

assessment of the parasite, and study of its field ecology. The identity and importance of other parasites attacking the lupine aphid were also determined.

Objective 3

The pea aphid, *A. pisum*, is a globally distributed pest of alfalfa, *Medicago sativum* L. This aphid has been the subject of numerous biological control efforts. Two exotic parasites have been introduced to North America: *Aphidius smithi* and *A. ervi*. Two common indigenous parasites are *A. pisivorus* Smith and *Praon pequodorum* Viereck (Mackauer and Finlayson 1967). The pea aphid was first recorded as a host of *E. californicus* by Smith (1944), in Oregon and California. However, the parasite is extremely rare on this host. Extensive surveys of pea aphid populations in alfalfa in eastern North America (Mackauer and Finlayson 1967), Iowa (Mertins 1985), and British Columbia (Campbell 1973) found not a single incidence of parasitism by *E. californicus*, while the parasite has only rarely been collected in surveys of alfalfa in Washington, Oregon (Halfhill *et al.* 1972), and California (Gutierrez 1968).

The reasons for the absence of *E. californicus* from the pea aphid are not immediately obvious. The parasite has a wide host range, and *Acyrthosiphon* is related to *Macrosiphum*, which contains several common hosts of *E. californicus*. Both the parasite and the pea aphid are widely distributed in North America. In addition, the pea aphid is a suitable host for *E.*

californicus in the laboratory (Gutierrez 1968, and this study). Much has been published on the field ecology and life table statistics of North American pea aphid parasites (e.g. Campbell 1973, Mackauer 1983). In this study, similar information was obtained on *E. californicus* and used for comparison, providing insight into the absence of this parasite from the pea aphid.

C. General Materials and Methods

Aphid and parasite colonies

The pea aphid colony used in all laboratory experiments was started from aphids collected on alfalfa in the Kamloops, B.C., area, in 1972. The laboratory host plant used was broad bean (*Vicia faba* L. c.v. "Broad Windsor"). Beans were potted in "Garden Mix" soil, with four to six shoots in 12.6 cm diameter pots, and large stock colonies of aphids were maintained on these plants. A portion of the stock colony was transferred to fresh host plants each week.

Specimens used to begin a laboratory colony of *E. californicus* were obtained in July, 1983 by sampling colonies of lupine aphids on *Lupinus polyphyllus* Lindl. in West Vancouver, B.C., and rearing the collected aphids on lupine cuttings until any parasitized aphids had mummified. Adult *E. californicus* which emerged from these mummies were mated and introduced to pea aphids. It was found that the parasites readily atttacked pea aphids and that their progeny completed development on this

host.

New stock colonies of parasites were prepared at least once a week. Fifteen to twenty parasite females were introduced into a plexiglass cage (33x34x44 cm) containing 250-350 third-instar pea aphids distributed on three pots of bean plants. Parasites were removed after two days, and the aphids were reared until mummification. Mummies were collected and placed in wax paper cups (9.5x11.5 or 9.5x6.5 cm) with 9 cm plastic petri dishes used as lids. Upon emergence, the parasites were fed a honey solution streaked across the inside of the lid, and were allowed to mate freely. Stock colonies were often stored in a controlled environment chamber at 15°C, in order to extend parasite longevity.

Rearing cages for experiments

Small plastic rearing cages, as described by Mackauer and Bisdee (1965a), were used throughout this study. These cages provided a convenient technique for rearing field-collected material or for replicating laboratory experiments. Two sizes of cages were used: 8.5 cm diameter x 3.5 cm, and 15.5 cm diameter x 4 cm. The cages were fitted with mesh covers, and had a 1.5 cm hole in the side wall. Through this hole, a bean or lupine shoot was passed, and held in place with plasticine (which also sealed the hole). The cage was placed on a milk bottle or plastic vial, with the cut stem immersed in water.

Controlled environment chambers

Experiments requiring controlled temperature, relative humidity (R.H.), and photoperiod conditions were conducted in one of two types of controlled environment chambers: Conviron Model E 15 (Controlled Environments, Winnipeg, Manitoba) or Percival Model 1-35-LL (Percival Manufacturing Company, Boone, Iowa). The temperature inside cages was determined by use of a Keithly Model 871 digital thermometer with probe (Keithly Instruments Inc., Cleveland, Ohio).

II. Parasite Fecundity and Longevity on the Pea Aphid

A. Introduction

Fecundity, longevity, and rate of development are fundamental parameters of animal populations. When experimentally determined, these parameters can be used to construct a life table and to estimate the intrinsic rate of natural increase, which is defined as the maximum rate of population increase under a given set of conditions (Andrewartha and Birch 1954). Thus, fecundity, longevity, and rate of development are useful for evaluating the potential of biological control agents and for comparing the potential for population increase of natural enemies and of the pests which they attack.

In this thesis, the life table statistics of *Ephedrus californicus* were used in order to interpret data on the ecology of the parasite attacking the lupine aphid (Chapter V), and to consider various hypotheses about the absence of the parasite from the pea aphid in the field (as reviewed in Chapter I). Previous life table studies of aphidiids have been conducted on *Aphidius smithi* attacking the pea aphid (Mackauer 1983), and on *Praon exsoletum* and *Trioxys complanatus* attacking the spotted alfalfa aphid (Force and Messenger 1964; Messenger 1964).

Fecundity is a measure of the reproductive capacity of an organism. In this chapter, it is defined as the total number of eggs actually laid by a female. There is an extensive body of literature on the fecundity of many species of Aphidiidae. However, differences in the experimental methods used to measure fecundity have led to a wide range of published results, which must be interpreted carefully. In the discussion, the literature on aphidiid fecundity is reviewed in order to obtain a meaningful comparison of the fecundity of *E. californicus* to other aphidiids. Of particular interest are the reported fecundities of other pea aphid parasites (Mackauer 1971, 1983), and those of other *Ephedrus* species (Withington 1909; Sorokina 1970; Jackson *et al.* 1974; Hofsvang and Hagvar 1975).

B. Materials and Methods

In order to obtain a cohort of *E. californicus* approximately equal in adult size and age, parasites from the stock colony were introduced to a synchronous colony of third-instar pea aphids. Upon emergence, a sample of 0-10 h-old female parasites was caged with males and honey for 4 h. Thirteen females were then placed singly in 15.5 cm diameter plastic rearing cages (Mackauer and Bisdee 1965a) containing the apical portion of a cut bean shoot and 40 second-instar pea aphids (reared for 48±4 h at 21.5°C). The cages were placed in a controlled environment chamber at 23±1°C, 65±10% R.H., and a 16

L:8 D h photoperiod.

Every 24 h, until dead, each parasite was transferred to a new cage containing 40 unparasitized second-instar aphids. After exposure to parasite attack, the aphids were reared in their cages. Four days after parasite attack, 20 randomly-chosen aphids from each cage were preserved in 70% ethanol for later dissection. The remaining 20 aphids from each cage were reared to mummification, then transferred to wax paper cups for emergence. Preserved aphids were dissected under a dissecting microscope, and the number of parasite eggs and larvae found in each aphid was recorded.

C. Results

One parasite was lost during transfer; the remaining twelve had a mean total fecundity of 1193.00±SE 88.41 eggs and a mean longevity of 13.42±SE 1.13 days. The numbers of eggs laid per day by each female are shown in Appendix A. The data were compiled into a life table (Table 1) where x is the pivotal age (in days); l_x is the age-specific survival rate, i.e., the proportion of individuals alive at time x of an original cohort of identical age; and m_x is the age-specific fecundity rate, i.e., the average number of female offspring produced per female alive during the age interval x (Andrewartha and Birch 1954).

For constructing the life table, the mean developmental time at 23°C was estimated as 14 days from the time of

Table 1. Life table of *Ephedrus californicus* at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod, with fecundity rate calculated according to total eggs and effective eggs, and according to sex ratios of 0.50 and 0.66

Pivotal age (x)	Survival rate(l_x)	Fecundity rate (m_x)			
		Sex ratio=0.50		Sex ratio=0.66	
		Total eggs	Effect. eggs	Total eggs	Effect. eggs
0.5-12.5	1.00	0.00	0.00	0.00	0.00
13.5	1.00	11.75	9.75	15.51	12.87
14.5	1.00	48.08	16.08	63.47	21.23
15.5	1.00	78.58	18.67	103.73	24.64
16.5	1.00	79.67	19.83	105.16	26.18
17.5	1.00	80.50	19.50	106.26	25.74
18.5	1.00	63.08	19.17	83.27	25.30
19.5	1.00	61.58	17.08	81.29	22.55
20.5	0.92	52.73	16.64	69.60	21.96
21.5	0.92	38.64	15.00	51.00	19.80
22.5	0.75	37.11	16.56	48.99	21.85
23.5	0.67	28.13	14.25	37.13	18.81
24.5	0.67	20.25	13.75	26.73	18.15
25.5	0.67	16.38	11.25	21.61	14.85
26.5	0.58	11.86	9.14	15.65	12.07
27.5	0.42	12.00	10.00	15.84	13.20
28.5	0.33	11.00	8.75	14.52	11.55
29.5	0.25	8.33	7.67	11.00	10.12
30.5	0.17	5.00	4.50	6.60	5.94
31.5	0.08	0.00	0.00	0.00	0.00
32.5	0.00	0.00	0.00	0.00	0.00

oviposition to adult emergence. This estimate was derived from the regression equation of developmental time versus temperature, calculated in Chapter III of this study. Larval mortality of the cohort of parasites reared for the fecundity experiment was assumed to be zero.

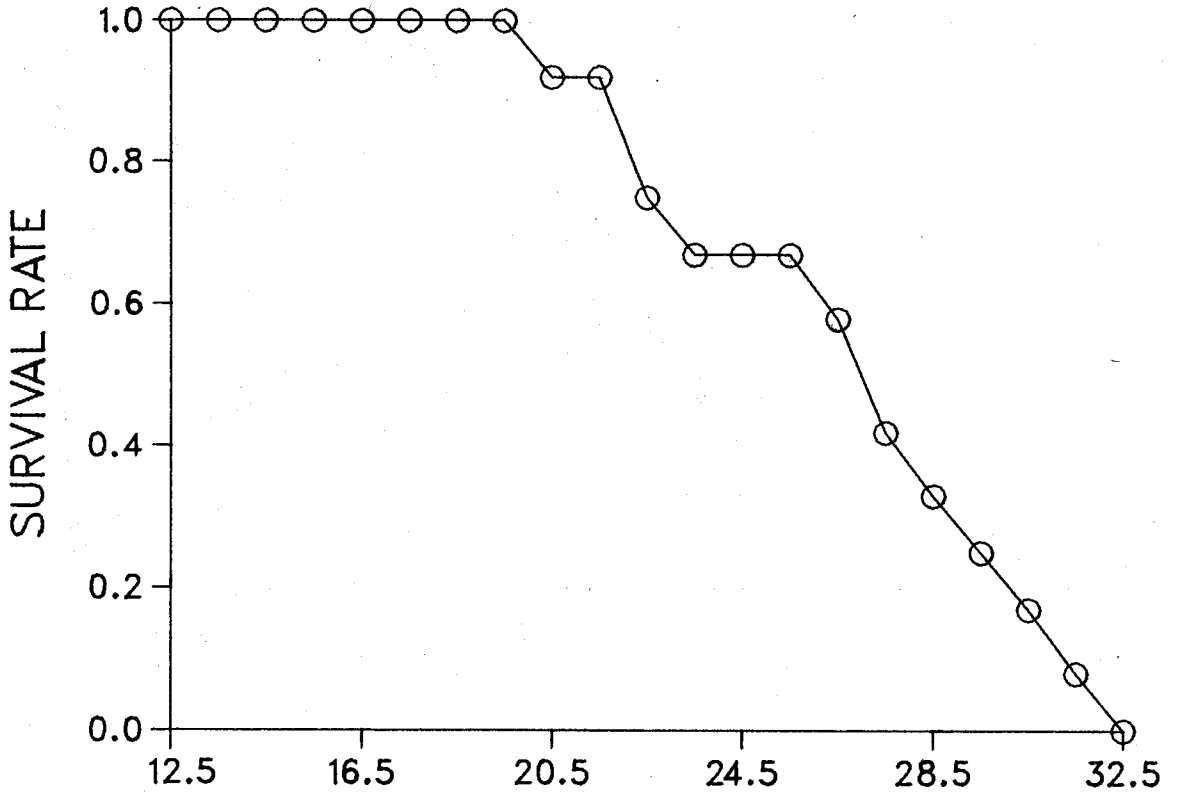
In Table 1, m_x was calculated for different sex ratios and for numbers of "effective eggs" and "total eggs". The values for effective eggs correspond to the numbers of hosts attacked each day, i.e., in superparasitized hosts, supernumerary eggs are considered wasted. However, as superparasitsm occurs rarely in the field among Aphidiidae (Campbell 1973), the values for total eggs provide a more realistic measure of m_x.

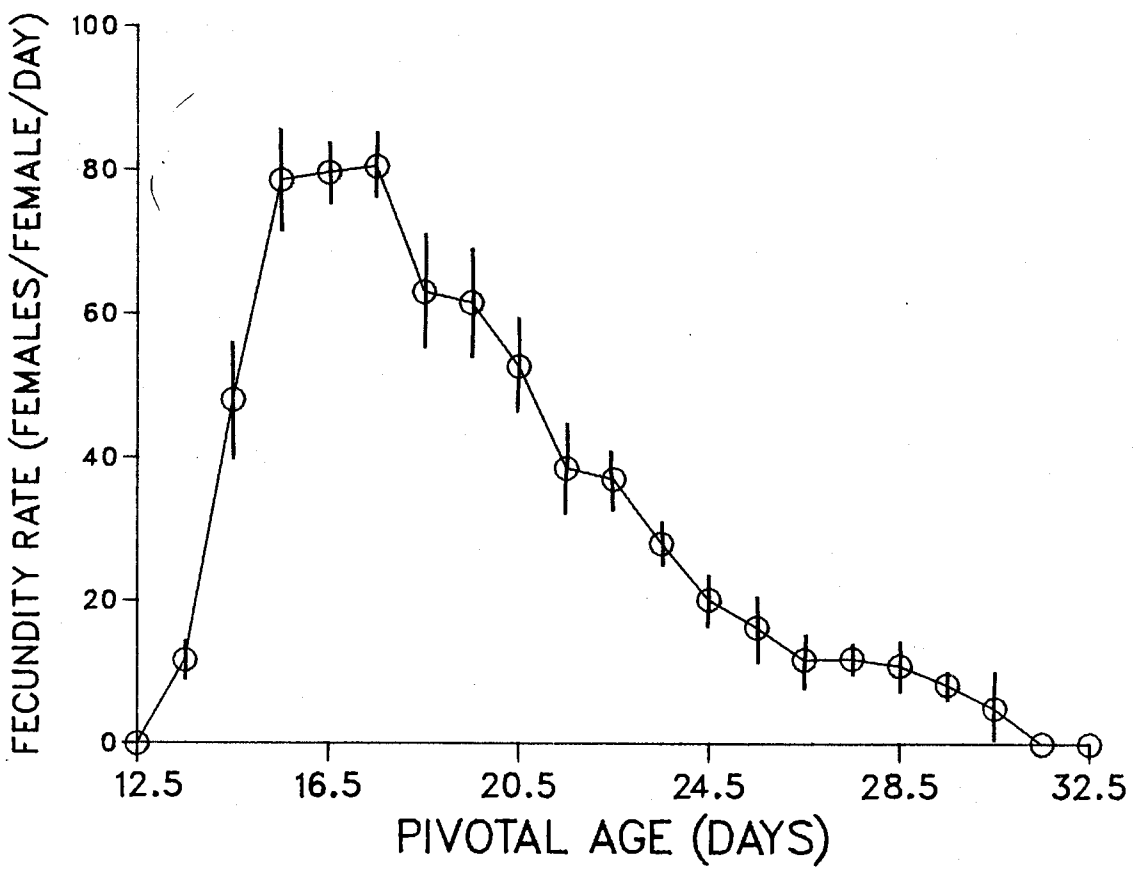
As m_x is expressed in units of females/female/day, the value of this statistic varies with the sex ratio of offspring. The observed sex ratio of emerged parasites in this experiment was 0.17, but, for reasons detailed in the discussion, it was felt that this figure was not based on an objective sample of parasites. In Table 1, sex ratios of 0.50 and 0.66 (the observed sex ratio of *E. californicus* on the lupine aphid in nature, see discussion), were applied to m_x. The fecundity rate rose sharply for the first two days of adult life (pivotal age 13.5-14.5 days) to a sustained peak at 15.5-17.5 days, and then declined gradually (Fig. 1b). The survival rate also declined gradually, following the death of the first female at 20.5 days (Fig. 1a).

Adult longevity ranged from 7 to 19 days (Appendix A). In order to test the correlation of fecundity with longevity, only

Figure 1a. Age-specific survival rate of *Ephedrus californicus* at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod

Figure 1b. Age-specific fecundity rate of *Ephedrus californicus* (±SE) at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod


SURVIVAL RATE
1.0
0.8
0.6
0.4
0.2
0.0
12.5
16.5
20.5
24.5
28.5
32.5


FECUNDITY RATE (FEMALES/FEMALE/DAY)
100
80
60
40
20
0
12.5
16.5
20.5
24.5
28.5
32.5
PIVOTAL AGE (DAYS)

data for the period of intensive egg laying (Mackauer 1983) were used. This period is defined as "the time from day one [of adult life] to that day in each parasite's life when oviposition showed a marked decline, and about one half or more of available aphids escaped parasitization" (Mackauer 1983). Thus, days at the end of a parasite's life, when reproductive activity had essentially ceased, were not included. Fecundity was significantly correlated (r=0.78, $P \leq 0.01$) with the period of intensive egg laying (Fig. 2).

The intrinsic rate of natural increase (r) (Table 2) was calculated by use of a computer program (written by A. Campbell) which iteratively solved the equation

$$\Sigma e^{-rx} l_x m_x = 1.$$

The gross reproductive rate (GRR = Σm_x), net reproductive rate ($R_0 = \Sigma l_x m_x$), finite rate of increase ($\lambda = e^r$), generation time ($T = ln R_0/r$), and doubling time ($DT = ln 2/r$) (Andrewartha and Birch 1954) were also calculated (Table 2).

When r was calculated beginning with the first day of adult life, it increased rapidly from day one to day six (pivotal age 13.5-18.5 days), but remained at the maximum of 0.371 after day ten of adult life (pivotal age 22.5 days) (Fig. 3).

Superparasitism of hosts was heavy during the most active days of parasite egg laying. As many as nineteen larvae were found in a single host (Fig. 4).

Figure 2. Relation between fecundity and period of intensive egg laying of *Ephedrus californicus* at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod

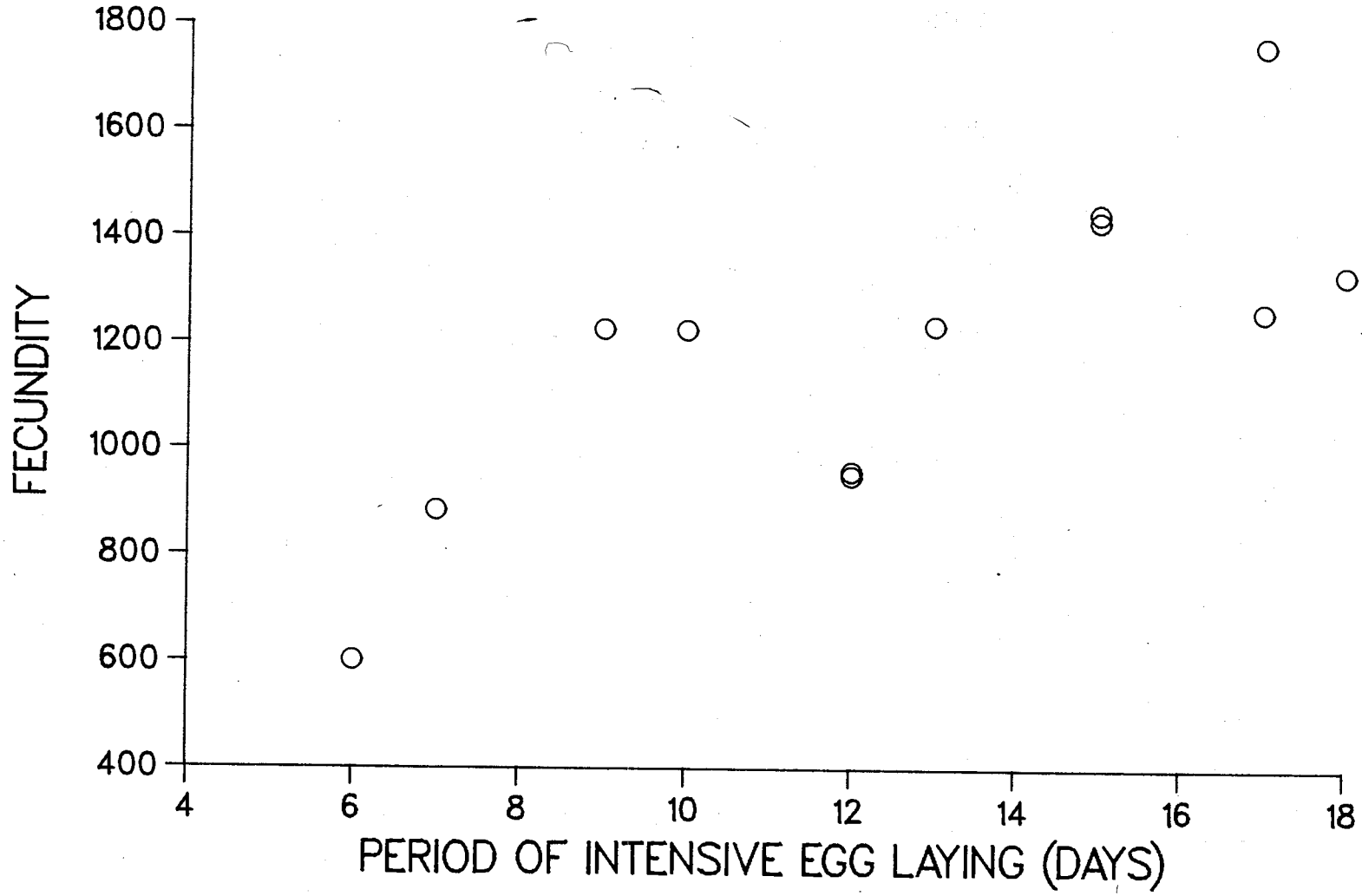

FECUNDITY
1800
1600
1400
1200
1000
800
600
400
4
6
8
10
12
14
16
18
PERIOD OF INTENSIVE EGG LAYING (DAYS)

Table 2. Life table statistics of *Ephedrus californicus* at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod, calculated according to total eggs and effective eggs, and according to different sex ratios

Population growth	Sex ratio=0.50		Sex ratio=0.66		Sex ratio=1.00	
	Total eggs	Effect. eggs	Total eggs	Effect. eggs	Total eggs	Effect. eggs
GRR[1]	664.644	247.585	877.357	326.811	1329.329	495.169
R_0[2]	596.549	202.773	801.402	267.659	1193.098	405.544
r[3]	0.371	0.301	0.389	0.318	0.414	0.344
λ[4]	1.449	1.353	1.476	1.374	1.513	1.411
T[5]	17.227	17.590	17.189	17.578	17.071	17.457
DT[6]	1.868	2.295	1.782	2.180	1.670	2.015

[1]Gross reproductive rate (females/female/generation)
[2]net reproductive rate (females/female/generation)
[3]intrinsic rate of natural increase (females/female/day)
[4]finite rate of natural increase (females/female/day)
[5]generation time (days)
[6]doubling time (days)

Figure 3. Increase of the intrinsic rate of natural increase (r) of *Ephedrus californicus* with female age in pivotal days, at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod

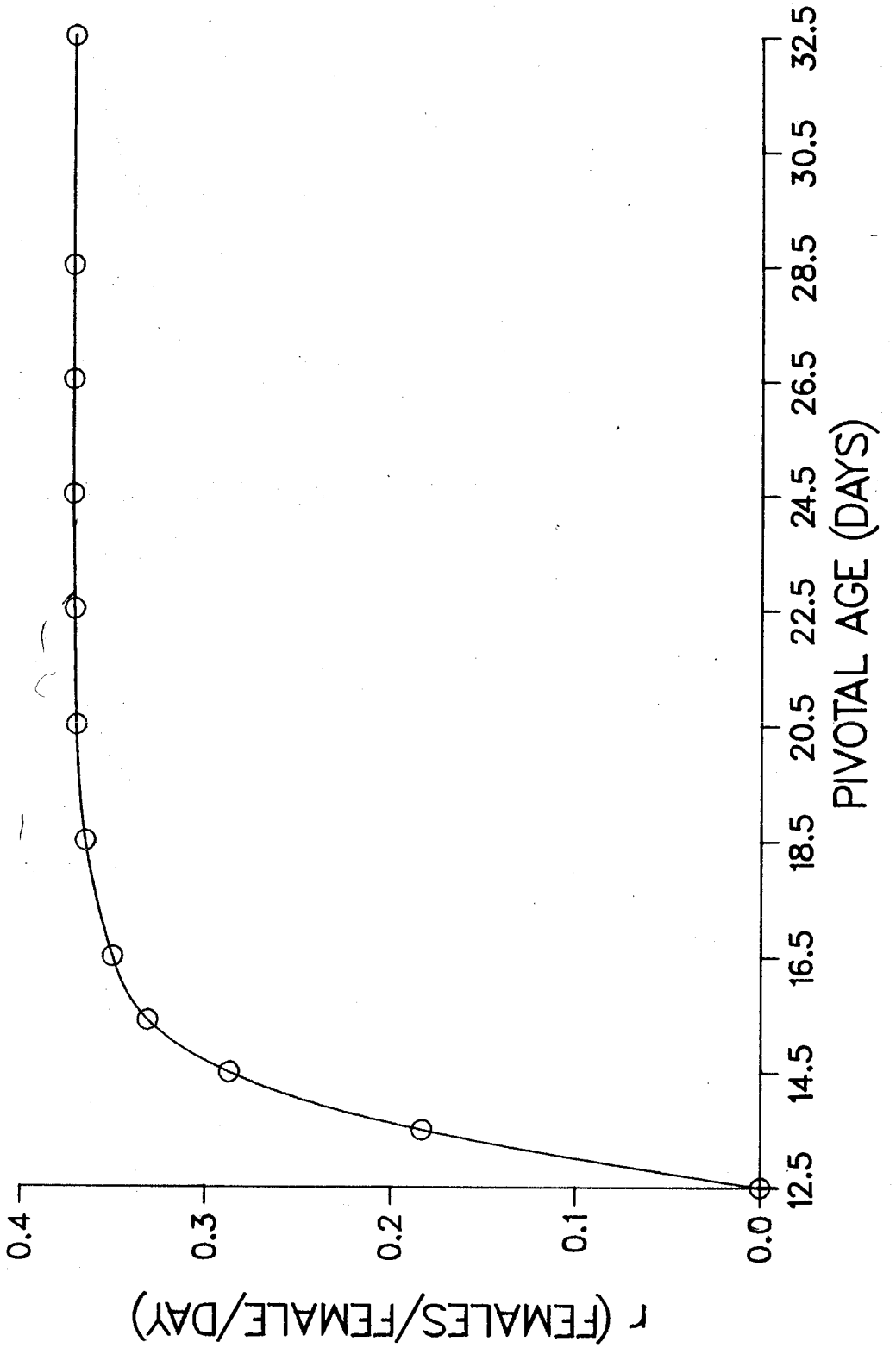
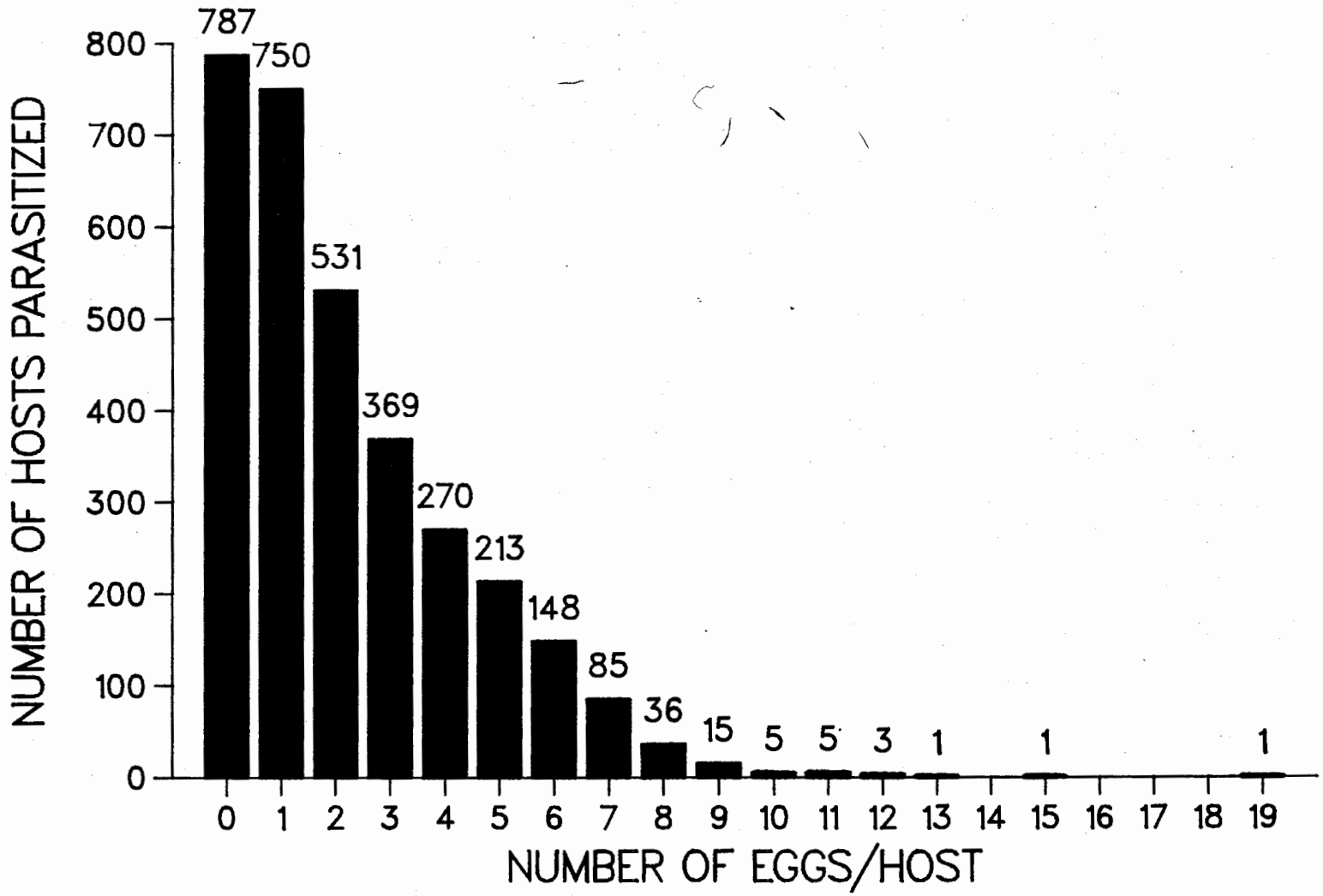

r (FEMALES/FEMALE/DAY)
0.0
0.1
0.2
0.3
0.4
12.5
14.5
16.5
18.5
20.5
22.5
24.5
26.5
28.5
30.5
32.5
PIVOTAL AGE (DAYS)

Figure 4. Distribution of eggs by *Ephedrus californicus*, based on dissection of 20 (out of 40) hosts provided/day at 23±1°C, 65±10% R.H., and a 16L:8D h photoperiod


NUMBER OF HOSTS PARASITIZED
800
700
600
500
400
300
200
100
0
787
750
531
369
270
213
148
85
36
15
5
5
3
1
1
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
NUMBER OF EGGS/HOST

D. Discussion

Fecundity

The mean fecundity of *E. californicus*, determined in this experiment, is the highest recorded mean fecundity for any aphidiid species. However, a review of the literature on the fecundity of aphidiids suggests that the potential egg production of most species has been underestimated because of unsuitable experimental methods. A sample of aphidiid fecundities from various studies is shown in Table 3.

Dissection of ovaries in order to count the number of eggs is a method which has been used extensively in work on Aphidiidae (Stary 1970). However, this method is only appropriate for species that are proovigenic, i.e., in which "ovigenesis is largely if not entirely complete before oviposition begins" (Flanders 1950). By contrast, with synovigenic species, "ovigenesis is not complete before oviposition begins but is more or less continuous throughout the life of the female" (Flanders 1950), and counting the eggs in the ovaries of a parasite at any one time is not a measure of potential fecundity.

Stary (1970) stated that, with the exception of a few suspected cases of proovigeny, the Aphidiidae are characterised by a reproductive system which is intermediate between proovigeny and synovigeny, i.e., that all eggs which a female is capable of producing are in the ovaries at birth, although some

Table 3. Fecundity and adult longevity of selected species of Aphidiidae (Hymenoptera)

Parasite species	Host species	Method of assessment	Fecundity (±SE)	Adult longevity (days) ±SE
Aphidius ervi[6]	*Acyrthosiphon pisum*	Host dissection	567±56.0	7.7±0.69
A. nigripes[1]	*Macrosiphum euphorbiae*	Mummy counting	374±43	20.5±1.9
A. pisivorus[6]	*A. pisum*	Host dissection	316±38.4	6.4±0.39
A. rosae[10]	*Macrosiphum* sp.	Ovary dissection	180-200	
A. rhopalosiphi[9]	*Sitobion avenae*	Ovary dissection	144±17.8	
A. rhopalosiphi[9]	*S. avenae*	Mummy counting	212±69	13.1±1.3
A. smithi[6]	*A. pisum*	Host dissection	774±86.1	7.3±0.73
A. urticae[2]	*Hyalopteroides humilis*	Ovary dissection	257±8.5	
A. urticae[2]	*H. humilis*	Mummy counting	270±35	
A. uzbekistanicus[2]	*Metopolophium dirhodum*	Ovary dissection	478±22	
Ephedrus californicus[12]	*A. pisum*	Host dissection	1193±88.4	13.4±1.12
E. cerasicola[4]	*Myzus persicae*	Mummy counting	51	17.9±0.63
E. incompletus[11]	*Macrosiphum rosae*	Mummy counting	53.2	
E. persicae[10]	*Dysaphis reamuri*	Ovary dissection	340-370	
E. plagiator[5]	*Schizaphis graminum*	Mummy counting	255	22
Praon exsoletum[7]	*Therioaphis trifolii*	Ovary dissection	155	18.3±2.30
P. exsoletum[3]	*T. trifolii*	Host dissection	578±32.2	6.9±0.65
P. pequodorum[6]	*A. pisum*	Host dissection	199±18.5	
P. volucre[10]	*H. arundinis*	Ovary dissection	340-370	
Trioxys complanatus[8]	*T. trifolii*	Ovary dissection	152	14.3±1.23
T. complanatus[3]	*T. trifolii*	Host dissection	844±56.8	

[1]Cloutier *et al.* (1981), [2]Dransfield (1979), [3]Force and Messenger (1964), [4]Hofsvang and Hagvar (1975), [5]Jackson *et al.* (1974), [6]Mackauer (1971), [7]Schlinger and Hall (1960), [8]Schlinger and Hall (1961), [9]Shirota *et al.* (1983), [10]Sorokina (1970), [11]Withington (1909), [12]This study.

are in an immature or undeveloped form. The immature eggs can be counted, and the presence of both developed and undeveloped eggs in the ovaries of newly emerged aphidiids has been noted by several authors (Stary 1970). For example, Schlinger and Hall (1960a, 1961) counted the eggs present in the ovaries of *Praon exsoletum* and *Trioxys complanatus* and found respective means of 155 eggs (93 developed and 62 undeveloped) and 152 eggs (all developed, undeveloped eggs "few in number").

However, Force and Messenger (1964) found fecundities of 578 and 845 eggs for *P. exsoletum* and *T. complanatus*, respectively, by counting the number of progeny produced when the parasites were provided with hosts throughout adult life. Thus, these two parasites are synovigenic. Similarly, Shirota *et al.* (1983) determined the mean fecundity of *Aphidius rhopalosiphi* De Stephani Perez as 144.3 eggs by dissection, but as 212.4 eggs by counting progeny.

In summary, the existence of the intermediate form of reproductive system, proposed by Stary (1970), has not been demonstrated. Rather, based on a comparison of the findings of Schlinger and Hall (1960a, 1961) and Force and Messenger (1964), and the findings of Shirota *et al.* (1983), it is likely that most, but perhaps not all, species of Aphidiidae are in fact synovigenic, and that the counting of eggs in dissected ovaries results in a substantial underestimation of fecundity. In addition, ovary dissection does not appear to provide a relative estimate of fecundity, as the significantly higher fecundity of

T. complanatus as compared with that of *P. exsoletum* was not indicated by the egg counts made by Schlinger and Hall (1960a, 1961).

A second general method of measuring fecundity is to count the actual number of progeny produced when parasites are provided with hosts for the duration of adult life. If properly conducted, this method is more accurate than ovary dissection as it measures total egg production throughout the life of the parasite. Determination of the number of progeny can be made by counting the number of mummies formed, or by dissecting hosts following parasite egg hatch to count parasite larvae. Dissection is the more accurate technique, as mummy counts do not disclose cases of superparasitism, where more than one egg per host is laid. A second important consideration in using progeny counting to determine fecundity is that new hosts should be supplied to parasites daily, and the old hosts removed. If hosts are left exposed to parasite attack for prolonged periods, considerable pre-mummification mortality may result as the aphids are continually scattered from the host plant and are unable to feed.

Several recent studies on aphidiids have used counts of mummies produced, rather than of eggs laid, in order to estimate fecundity (Dransfield 1979; Cloutier *et al.* 1981; Shirota *et al.* 1983). The use of this method has probably persisted because it requires considerably less work than host dissection, and may often provide information sufficient for the needs of the

experimenter. Dransfield (1979) estimated the fecundity of *Aphidius urticae* Haliday as 270±SE 35 offspring. He counted the number of mummies produced, then attempted to account for superparasitism by estimating the number of eggs laid from the number of mummies produced, by use of the model of Thompson (1924). However, this model assumes random oviposition (Dransfield 1979), and it has been shown (Shirota *et al.* 1983; Cloutier 1984) that aphidiids do not distribute their eggs randomly. The advantage of host dissection is exemplified in the work of Shirota *et al.* (1983), who counted a mean of 212.4±SE 69 mummies produced by *A. rhopalosiphi*, but dissected the hosts attacked by one parasite and found a total of 318 larvae. They concluded that the actual fecundity of *A. rhopalosiphi* was approximately 1.5 times the estimate obtained by counting mummies.

The fecundities of four *Ephedrus* species have been investigated. Stary (1962) dissected the ovaries of *E. persicae*, and found "about 70 developed eggs and a big quantity of undeveloped eggs" in each of the parasites' two ovaries. Sorokina (1970) dissected the ovaries of this same species and counted a total of 340-370 eggs.

Jackson *et al.* (1974) studied the fecundity of *E. plagiator* attacking four hosts at different temperatures. Measuring fecundity as the number of mummies produced, the highest mean achieved was 255 mummies, with *Schizaphis graminum* (Rondani) as host at 21°C. There are, however, numerous problems with the

method used, which make this result a poor estimate of the fecundity of *E. plagiator*. Each parasite was caged with 25 third- to fourth-instar aphids; no further hosts were provided for the remainder of the experiment except for the offspring of the original 25 aphids. It can be estimated that the fourth-instar aphids did not begin to reproduce for at least two days (accounting for the molt to the adult stage and the pre-reproductive period). By this time, extensive superparasitism would certainly have occurred. As parasitized hosts were left continually exposed to parasite attack, pre-mummification mortality was probably considerable. Finally, the numbers of mummies produced may have been limited by the reproductive capacity of the original 25 aphids.

The fecundity of *E. cerasicola* was studied by Hofsvang and Hagvar (1975). In their experiment, ten female parasites were caged with "an excess" of *Myzus persicae* on one paprika plant. The parasites were transferred to a new cage with a new aphid-infested host plant each day. The mean fecundity of the ten parasites was found to be 51. This is a suspiciously low figure, and can probably be accounted for by superparasitism, pre-mummification host mortality, mutual interference (Hassel 1978) among parasite females, or a combination of the above. Withington (1909) measured the fecundity of *E. incompletus* by caging individual parasites with 200 rose aphids, *Macrosiphum rosae*, and counted a mean of 53.2 mummies per female.

Given the various inadequacies of the methods used by previous investigators, it can be stated that the present study is the first accurate evaluation of the fecundity of an *Ephedrus* species. Whether high fecundities are characteristic of this genus is thus unknown.

The results of this study can be compared most meaningfully to the results of Force and Messenger (1964) and Mackauer (1971), all of whom used host dissection to determine fecundity, although there are some differences between the methods used which should be considered. An important difference may be the food supplied to adult parasites, known to be a factor influencing parasite longevity (Stary 1970). In this study, parasites were allowed to feed on honey for four hours before the start of the experiment, then were able to feed on aphid honeydew for the duration of the experiment. Force and Messenger (1964) provided fresh honey daily. Mackauer (1971) did not supply honey, which may account for the shorter longevities obtained, if honey is a nutritionally superior food to honeydew or if insufficient quantities of honeydew were available.

Host density has also been shown to influence fecundity, with the number of eggs laid per female generally rising as host density is increased (Messenger and Force 1963; Mackauer 1983). It has been shown that aphidiids can discriminate between unparasitized and parasitized hosts, and avoid laying their eggs in the latter (Force and Messenger 1965; Hofsvang and Hagvar 1983; Chow and Mackauer 1984). Although this restraint breaks

down if unparasitized hosts are not found (Hofsvang and Hagvar 1983), discrimination results in an increased expenditure of time per egg laid. At lower host densities, there is a relatively shorter period of time during which unparasitized hosts are available, and a relatively greater period of time during which only parasitized hosts can be found. This results in a decreased number of eggs laid. In both this study and that of Mackauer (1971), a density of 40 hosts per day was used. Force and Messenger (1964) used a higher density of 50-80 hosts per day, which likely resulted in a relatively greater number of eggs laid per female.

In conclusion, it appears that the differences in experimental methods between this study and that of Force and Messenger (1964) do not fully account for the higher fecundity of *E. californicus* as compared to those of *P. exsoletum* and *T. complanatus*. It is possible that, if fed honey, the fecundities of *A. ervi* and *A. smithi* may approach that of *E. californicus*. However, it is clear that *E. californicus* has a very high fecundity compared to other aphidiids.

Sex ratio

As noted above, the sex ratio of progeny produced in this experiment, 0.17, was considered to be unrealistically low compared to the population sex ratio of *E. californicus* in nature. Based on an analysis of field-collected parasites, Mackauer (1976) found the sex ratio of several species of

aphidiids to be about 0.6. This figure is close to the sex ratio of 0.66 determined for a sample of 293 *E. californicus* reared from field-collected lupine aphids in 1984 (M. Cohen, unpublished data).

Several factors appear to explain the low sex ratio of parasites produced in the experiment described above. First, five of the twelve parasites produced no female offspring. This indicates that either they had not mated, had mated with sterile males, or were otherwise incapable of fertilizing their eggs. Second, the sex ratio obtained from emerged parasites, referred to as the tertiary sex ratio, may differ from the primary sex ratio, i.e., the sex ratio of eggs laid. In cases of superparasitism, the sex of only one egg laid in a host can be determined, as only one parasite survives larval competition. It is not known if, in cases of larval competiton, there is a competitive advantage of one sex over the other. Third, no parasites emerged from 527 of the 1874 mummies collected (=28.12%), probably because diapause was induced in the field-collected parasite strain while the experiment was underway in September and October. A sample of 137 mummies from which no parasites had emerged was dissected, and 74.45% contained diapausing larvae. After 15 months of storage in the laboratory, no further parasites emerged from the remaining mummies. A further sample was then dissected and all diapausing larvae were found to have died. The incidence of diapause among the mummies collected may have influenced the sex ratio, if

there is a differential occurrence of diapause between male and female *E. californicus*. Finally, parasites which produced female offspring were eventually depleted of spermatozoa (after 3-9 days), and subsequent offspring were all male.

Intrinsic rate of natural increase

A comparison of the intrinsic rates of natural increase (r) of four aphidiids (Table 4) shows that the rate of *E. californicus* is consistently higher than that of *P. exsoletum*, and approximately equal to those of *A. smithi* and *T. complanatus*. Values of r for two hosts of *E. californicus*, the lupine and pea aphids, have also been published. At 24.2°C, r for the lupine aphid was determined as 0.278 females/female/day (Frazer and Gill 1981). Studies of the pea aphid on broad bean (*Vicia faba*, the host plant used in this experiment), have determined r as 0.404 (Frazer 1972) and 0.366 (Mackauer 1973) females/female/day, at 20°C.

However, as fecundity, longevity, and developmental time (data necessary for computation of r) can vary depending on experimental conditions and methods, the meaningfulness of comparisons of r determined in different studies is uncertain. This is one difficulty limiting the use of r as a parasite rating, as was proposed by Messenger (1964). Another difficulty is evaluating the usefulness of r in predicting parasite performance in the field, or in interpreting field data. Calculation of r assumes a stable age distribution (Andrewartha

Table 4. Intrinsic rates of natural increase[1] (r) of selected species of Aphidiidae (Hymenoptera)

Parasite species	Host density (aphids/day)	Sex ratio=0.50		Sex ratio=1.00	
		Total eggs	Effect. eggs	Total eggs	Effect. eggs
A. smithi[4]	40		0.309		
	60		0.326		
E. californicus[5]	40	0.371	0.301	0.414	0.344
P. exsoletum[2]	50-80	0.283	0.247	0.327	0.288
T. complanatus[3]	50-80	0.38[6]			

[1]Females/female/day
[2]Force and Messenger (1964)
[3]Force and Messenger (1964), Messenger (1964)
[4]Mackauer (1983)
[5]This study
[6]sex ratio=0.59.

and Birch 1954). Carter *et al.* (1978) have shown that aphid populations in the field rarely achieve a stable age distribution, in large part because the number of generations per year (approximately 5) is too few, and the same may be true for parasites. A second problem is that life table experiments in the laboratory are carried out under near-optimal conditions. It is likely that, in the field, various elements of environmental resistance are more important in limiting parasite population increase than are fecundity or other life table parameters. Environmental factors such as unfavorable temperatures may reduce egg production and shorten longevity, while factors such as predation of larvae, mummies or adults decrease the survival rate.

Nonetheless, the life table analysis of *E. californicus* in this chapter did yield information that was useful in discussing the abundance of *E. californicus* on pea and lupine aphids in the field (Chapter VI). For example, previous studies of other *Ephedrus* species suggested that this genus may have had an especially low fecundity (Jackson *et al.* 1974; Hofsvang and Hagvar 1975), but it is now clear that this is not so for *E. californicus*. Furthermore, while it is known that the adult longevity of aphidiids is considerably shorter in the field than in the laboratory (Gilbert and Gutierrez 1973; Mackauer and van den Bosch 1973), this short adult life would appear not to limit the effectiveness of *E. californicus*. The intrinsic rate of increase for this parasite approaches its maximum value by day 5

of adult life (Fig. 3), compared to a mean longevity of 13.42 days.

III. Effect of Temperature on Parasite Developmental Time in the Pea Aphid

A. Introduction

Study of the relationship between insect rate of development and temperature can contribute to an understanding of the abundance and seasonal occurrence of insect populations. Two thermal characteristics are of particular use: the developmental threshold, or temperature below which no measurable development takes place; and the developmental time, or time from oviposition to adult emergence, expressed in degree-days above the threshold (Campbell *et al.* 1974). In Chapter II, the developmental time of *E. californicus* was used to construct a life table and to estimate the intrinsic rate of natural increase. In Chapters V and VI, the developmental threshold of the parasite was used in order to gain an understanding of parasite appearance and impact on host populations in the spring. The response of insect rate of development to temperature has been widely investigated by entomologists, and the topic has recently been reviewed by Schaffer (1983) and Wagner *et al.* (1984).

As insects are poikilothermic, their rate of development is not constant, but varies with the ambient temperature (Fig. 5).

The response of insect rate of development to increasing temperature yields a shallow sigmoid curve, but many different models can describe this relationship (Wagner *et al.* 1984). For a central range of temperatures, the rate of development (1/D, where D is the developmental time) increases in direct proportion to increasing temperature. At some point, higher temperatures become detrimental, and the rate of development increases at a slower rate. Eventually, it begins to decline.

For temperatures near the developmental threshold, the relationship between rate of development and temperature again departs from linearity, tailing to the left. Because of high mortality and the long time required for completion of development, it is not practical to experimentally determine developmental time at temperatures in this range. Therefore, the technique of estimating the threshold by extrapolation of the linear portion of the curve to the temperature axis has been widely used. This method was also used in this study, and its accuracy and application are considered in the discussion.

The developmental times at one or more temperatures have been determined for numerous aphidiids and their hosts (Stary 1970), but only a few studies have provided a regression equation and extrapolated developmental threshold (Hughes 1963; Gilbert and Gutierrez 1973; Campbell *et al.* 1974; Campbell and Mackauer 1975). For species of *Ephedrus*, the developmental times at various temperatures have been determined for *E. plagiator* (Jackson *et al.* 1974) and *E. cerasicola* (Hofsvang and Hagvar

1975), but no study has included a regression of rate on temperature or a developmental threshold.

B. Materials and Methods

The following experimental method was followed twice for each of four constant temperatures: 17.6, 20.9, 24.0, and 26.4 °C. The first trial at each temperature was a dry run to obtain an approximation of the median emergence time and the range of time over which parasites emerged, and only data from the definitive experiments will be presented and discussed. All temperatures quoted are ±1°C.

For each temperature, a cohort of aphids for parasitization was reared at 21.1°C for 72±4 h. On the day of parasitization, aphids were placed singly into clear gelatin capsules (size 00). Parasitization was accomplished by placing a parasite in a capsule with an aphid and allowing it to strike the aphid once. Parasitization was divided into five 30-min periods, during which each of 15-20 females was used from one to four times. Thus, five approximately equal subgroups, each containing 22-45 parasitized aphids, were obtained for each temperature, and the time of parasitization for the aphids in each subgroup was known with an accuracy of ±15 min.

Parasitized aphids were reared in a growth chamber on cut bean plants in 8.5 cm diameter cages (Mackauer and Bisdee 1965a), with 10-15 aphids in each cage. The temperature inside

the cages was determined by use of a digital thermometer, with probe. Continuous light and a R.H. of 55-70% were used for all temperatures. After mummification, mummies were transferred to wax paper cups with mesh covers; the temperature inside the cups was the same as that inside the cages.

The median developmental time (or median emergence time, ET_{50}) at each temperature was determined by quantal response analysis (Finney 1971, Hewlett and Plackett 1979). Each of the five subgroups was observed once, at pre-determined times spaced evenly around the expected median emergence time, and the proportion of parasites emerged in each cage was recorded. Proportions were later adjusted to account for mummies from which adults did not emerge after 48 h of additional observation. The probit values corresponding to the proportions of adults emerged at each time check were plotted against the log to base ten of time after oviposition, and a regression line was fitted to the data. The median emergence time, its standard error and 95% confidence limits, the slope and its standard error, and the y-intercept of the regression were estimated by maximum likelihood analysis (Finney 1971).

After the median emergence time at each temperature had been determined, the corresponding rates of development ($1/ET_{50}$) were plotted against temperature, in order to calculate a regression equation.

C. Results

The proportion of emerged parasites generally increased with increasing time from oviposition (Table 5). Although, for each experiment, one point was an exception to this trend, regressions calculated for probit of proportion emerged on log of time after oviposition (Table 6) were significant ($P \leq 0.05$). Data for male and female emergence at each temperature (Table 5) did not differ significantly (median test, $P \leq 0.05$) and were combined.

The rate of development of *E. californicus* increased linearly from 17.6 to 24.0°C (Fig. 5). However, upon examination, it was evident that the point for 26.4°C was not in the linear range of the relationship, but rather in the non-linear range of deleterious, higher temperatures. This observation was supported by the significantly decreased proportion of viable mummies obtained at this temperature (Table 6). Thus, the point for 26.4°C was not included in the calculation of the regression equation, which was determined as

$$y = 0.00437\ x - 0.0299,$$

where y is the rate of development ($1/ET_{50}$, ET_{50} in days), and x is the temperature in °C. The developmental threshold, or x-intercept of the regression line, is 6.84±SE 0.384°C [SE calculated using the formula of Campbell *et al.* (1974)].

Table 5. Quantal response data for developmental times of *Ephedrus californicus* at four constant temperatures, 55-70% R.H., and continuous light

Temp. (±1°C)	Emergent group no.	Total no. viable mummies	Time after ovip. (h)	No. parasites emerged			% emergence at time of observation
				Total	Female	Male	
17.6	1	34	503	2	0	2	5.88
	2	39	508	17	2	15	43.59
	3	41	513	22	3	19	53.66
	4	39	518	30	2	28	76.92
	5	30	523	20	7	13	66.67
20.9	1	42	380	6	1	5	14.29
	2	45	385	13	5	8	28.89
	3	40	390	32	10	22	80.00
	4	44	395	32	15	18	72.73
	5	37	400	35	17	18	94.59
24.0	1	39	317	7	2	5	17.95
	2	39	321	25	11	14	64.10
	3	39	325	32	14	18	82.05
	4	39	329	30	9	21	76.92
	5	40	333	36	16	20	90.00
26.4	1	22	280	1	0	1	4.55
	2	39	290	17	5	12	43.59
	3	40	300	28	8	20	70.00
	4	32	310	20	8	12	62.50
	5	32	320	28	13	15	87.50

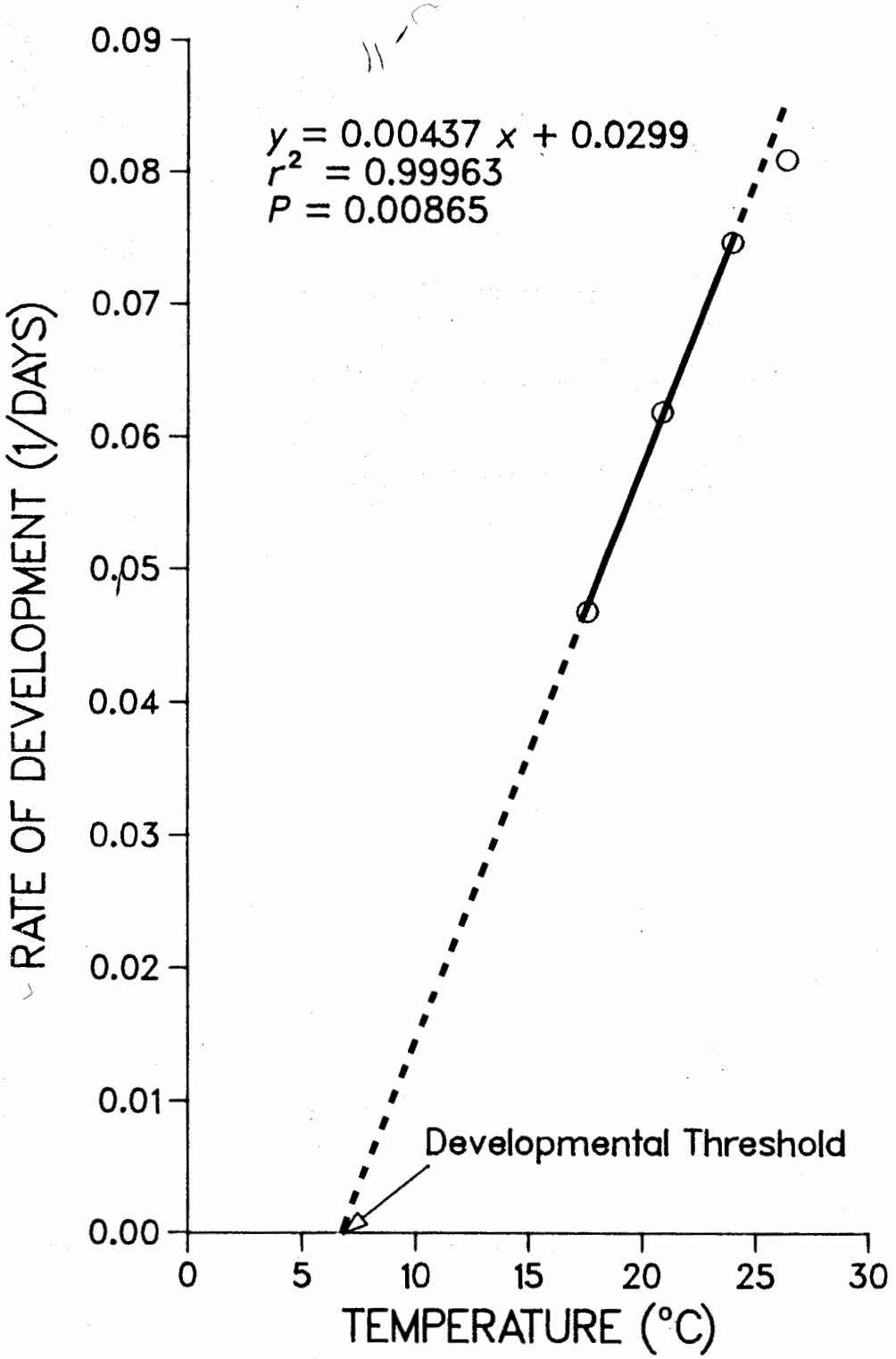
Table 6. Sample size, final percent parasite emergence, median developmental time, developmental rate, and regression statistics of percent emergence on time after oviposition of *Ephedrus californicus* at four constant temperatures, 55-70% R.H., and continuous light

Temp. (±1°C)	Total no. mummies	Final no. parasites emerged	% parasite[1] emergence	ET_{50}[2] ±SE (days)	$1/ET_{50}$[3]	95% C.I.[4] of ET_{50}	Slope[5] ±SE	y-inter-[5] cept
17.6	198	183	92.42a	21.37 ± 0.06	0.047	21.25 - 21.48	84.76 ± 15.52	-224.71
20.9	218	208	95.41a	16.13 ± 0.06	0.062	16.10 - 16.22	132.22 ± 16.53	-337.58
24.0	208	196	94.23a	13.38 ± 0.04	0.075	13.30 - 13.44	99.22 ± 15.09	-243.71
26.4	200	165	82.50b	12.34 ± 0.09	0.081	12.15 - 12.51	35.56 ± 6.10	- 83.93

[1]Percentages sharing the same letter form homogeneous subsets ($P \leq 0.05$), Unplanned Test of Homogeneity (Sokal and Rohlf 1981, p. 728).
[2]Median emergence time
[3]Rate of development
[4]Confidence interval
[5]Regression of probit of emergence on log time after oviposition

Figure 5. Regression of developmental rate of *Ephedrus californicus* on temperature, at 55-70% R.H. and continuous light

Broken portions of the curve represent extrapolations.


$y = 0.00437\ x + 0.0299$
$r^2 = 0.99963$
$P = 0.00865$
RATE OF DEVELOPMENT (1/DAYS)
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
5
10
15
20
25
30
TEMPERATURE (°C)
Developmental Threshold

D. Discussion

As noted in the introduction, many models have been proposed to describe the response of insect rate of development to temperature. The linear model used in this chapter is relatively simple, and has a long history of use (Wagner *et al.* 1984). It is sometimes referred to as the method of "degree-day summation". A degree-day is a measure of the period of time (in days) during which temperature exceeds the developmental threshold, multiplied by the degrees above the threshold maintained during that period. The reciprocal of the slope of the temperature-rate regression, in this case 228.83 °C-days, is the developmental time expressed as the number of degree-days above the threshold (Campbell *et al.* 1974).

There are constraints on the application of this model in that it is valid only for predictions of the rate of development in a central range of temperatures where the response is linear. In addition, extrapolation of the line to the temperature axis (in order to estimate the developmental threshold) is known to result in overestimation of the threshold (Campbell *et al.* 1974; Wagner *et al.* 1984), as , at low temperatures, the curve actually tails to the left. However, many authors have continued to find that this linear model provides an accurate basis for predicting development in the field (e.g., Johnson *et al.* 1979; Butts and McEwen 1981; Obrycki and Tauber 1982; Laing and Heraty 1984). Moreover, it is simpler and easier to use than complex

biophysical models which describe the developmental rate over a full range of temperatures (e.g., Sharpe and DeMichelle 1977; Wagner *et al.* 1984).

When comparing the developmental times and thresholds of species from different areas (Table 7), it must be remembered that these thermal constants vary from population to population, reflecting adaptations to local climate and host ecology. The developmental time may also vary with host quality (Bodenheimer and Swirski 1957; Campbell *et al.* 1974; Dransfield 1979). Among species of *Ephedrus*, *E. californicus* has a shorter developmental time than *E. plagiator* and *E. cerasicola* (Table 7). However, all three *Ephedrus* species require relatively more time to adult emergence than the other parasites shown, with the exception of *P. exsoletum*.

In Table 8 are the developmental thresholds for Vancouver strains of some parasites and their hosts. Campbell *et al.* (1974) have shown that the threshold of a parasite generally exceeds that of its host, ensuring that hosts will be available at the time of parasite emergence in the spring. In contrast to developmental time, it would seem that the threshold should not change with host quality or host species (Campbell *et al.* 1974), as the threshold is not dependent on nutrition but only on the enzymes of the parasite (which are temperature-dependent). Thus, the threshold of *E. californicus* on the lupine aphid, *Macrosiphum albifrons*, has been assumed to be the same as that determined with the pea aphid, *Acyrthosiphon pisum*, as host.

Table 7. Developmental times of selected species of Aphidiidae (Hymenoptera)

Parasite species	Host species	Origin of parasite colony	Temp. (°C)	Develop. time (days)
Aphidius ervi[3]	*Acyrthosiphon pisum*	Kamloops, B.C.	21	13.2
A. pisivorus[3]	*A. pisum*	Kamloops, B.C.	21	12.6
A. smithi[3]	*A. pisum*	Kamloops, B.C.	21	12.0
Diaeretiella rapae[2]	*Brevicoryne brassicae*	Berkeley, Calif.	21.1	13.8
Ephedrus californicus[7]	*A. pisum*	Vancouver, B.C.	21	16.2
E. cerasicola[5]	*Myzus persicae*	Jeloya, Norway	21	21.6
E. plagiator[6]	*Schizaphis graminum*	Taiwan	21	17.2
Monoctonus paulensis[1]	*A. pisum*	Albany, Calif.	21.1	14-15
Praon exsoletum[4]	*Therioaphis trifolii*	Dos Palos, Calif.	21.1	17.2
P. pequodorum[3]	*A. pisum*	Kamloops, B.C.	21	14.1
Trioxys complanatus[4]	*T. trifolii*	Dos Palos, Calif.	21.1	14.4

[1]Calvert and van den Bosch (1973), [2]Campbell *et al.* (1974), [3]Campbell and Mackauer (1975), [4]Force and Messenger (1964), [5]Hofsvang and Hagvar (1975), [6]Jackson *et al.* (1974), [7]This study.

Table 8. Developmental thresholds of selected species of Vancouver area aphids and their parasites

Host species	Threshold (°C)±SE	Parasite species	Threshold (°C)±SE
Acyrthosiphon pisum[1]	4.0±0.28	*Aphidius ervi*[1]	4.2±0.38
		Ephedrus californicus[3]	6.8±0.38
Brevicoryne brassicae[1]	4.7±0.80	*Diaeretiella rapae*[1]	4.9±0.94
Macrosiphum albifrons[2]	4.0±0.59	*E. californicus*[3]	6.8±0.38
Masonaphis maxima[1]	3.9±0.47	*A. rubifolii*[1]	5.3±0.41

[1]Campbell *et al.* (1974)
[2]Frazer and Gill (1981)
[3]This study

Unfortunately, the subject of parasite thresholds on different host species does not appear to have been further discussed in the literature.

The differences between the threshold of *E. californicus* (6.84°C) and that of *M. albifrons* (3.95°C) and *A. pisum* (4.0°C) are considerably larger than those between other parasites and their hosts (Table 8). These data suggest that, in the spring, *E. californicus* would appear much later than the lupine aphid. Field data to test this prediction, and the implications of the high threshold of *E. californicus* on its potential as a biological control agent, are discussed in Chapters V and VI.

In common with other aphidiids, there was no significant difference between the developmental times of male and female *E. californicus*. Similar findings have been reported for *Aphidius ervi*, *A. pisivorus*, *A. smithi*, and *Praon pequodorum* (Campbell 1973); *A. urticae* and *A. uzbekistanicus* Luzhetski (Dransfield 1979); and *Ephedrus cerasicola* (Hofsvang and Hagvar 1975).

IV. Parasite Preference for and Development on Lupine and Pea Aphids

A. Introduction

Ephedrus californicus is a polyphagous parasite, and in this thesis it has been studied on two of the hosts which it has been recorded to attack in nature, the lupine and pea aphids. A comparison of the parasite's preference for, and ability to complete development on, these two aphid species was necessary for a further understanding of the ecology of *E. californicus* on the lupine aphid (Chapter V) and of the rare occurrence of this parasite on the pea aphid.

Two previous chapters have investigated basic biological parameters of *E. californicus*, with the pea aphid as host. In Chapter II, the parasite was found to have the highest recorded fecundity of any aphidiid; and in Chapter III, the developmental time of *E. californicus* was found to be faster than those of other *Ephedrus* species previously studied. One conclusion which can be drawn from these results is that the pea aphid is a very suitable host for *E. californicus*, as, on poorly-suitable hosts, parasites have been found to have reduced fecundities (e.g., Smith and Pimentel 1969; Dransfield 1979) and slowed developmental rates (e.g., Dransfield 1979; Wallner and Grinberg

1984).

For interpretation of the data on the ecology of *E. californicus* attacking the lupine aphid (Chapter V), it was important to know whether the lupine aphid is as suitable a host as the pea aphid, i.e., whether the parasite has a similar developmental time and high fecundity when reared on the lupine aphid. As large laboratory experiments using the lupine aphid were found to be impractical because of difficulties in growing potted lupines, an indirect approach was taken comparing the sex ratio, survivorship, and weight of parasite progeny on the two hosts. The significance of these factors in assessing host suitability is examined in the discussion.

Although the pea aphid has been shown to be a suitable host for *E. californicus* in the laboratory (Gutierrez 1968, and this study), it has been only rarely found to attack this host in nature (Gutierrez 1968; Halfhill *et al.* 1972). The experiments in this chapter examined one possible explanation for the absence of *E. californicus* from the pea aphid in nature: that when given a choice between the pea aphid and a host commonly attacked in the field (in this case the lupine aphid), the parasite might show a strong preference for the latter.

B. Materials and Methods

Pea aphids and parasites reared from them were obtained from stock colonies, as described in Chapter I. Lupine aphids were obtained as first- or second-generation progeny of adult lupine aphids collected from the field and reared in the laboratory on lupine cuttings. Parasites reared from lupine aphids were collected as mummies from lupine plants, or were first-generation progeny from lupine aphids attacked in the laboratory by these field-collected parasites.

Aphids of both species were reared for 96±4 h in a controlled environment chamber at 21.1±1°C, 55-70% R.H., and continuous light. At this age, individuals of the two aphid species were approximately the same size. When used for experiments, female parasites were 2-6 days old, and had been caged with males and honey (but no hosts) in the same controlled environment chamber as the aphids. Experiments were carried out in two sessions, separated by three weeks. In each session, parasites reared from both host species were tested. Totals of 15 parasites reared from lupine aphids and 16 reared from pea aphids were used.

On the first day of the experiment, 20 aphids of each species were randomly placed in wax paper cups (9.5 cm diameter x 6.5 cm), closed with 9 cm disposable petri dishes. The cups were placed on a laboratory bench under cool white fluorescent lights; the temperature in the cups was measured as 24.0±1°C.

One parasite was placed in each cup for a 90 minute period, during which parasites were observed to search, oviposit, and rest for varying periods of time. After removal from the cups, the parasites were caged individually in numbered cups and stored overnight in the controlled environment chamber. On the next day, the entire procedure was repeated.

After exposure to parasite attack, lupine and pea aphids were separated (the two are easily distinguished based on color, and on the presence of waxy scales on the lupine aphid) and the aphids from each cup were reared separately on host plant cuttings in small plastic cages (Mackauer and Bisdee 1965a). After five days, samples of ten aphids (out of 20) of each species from each cup were dissected and the parasite larvae in each host were counted. The remaining ten aphids were reared to mummification and held for emergence of adult parasites. Mummies from which no adults emerged were dissected and the contents were noted as to diapausing larvae, or dead larvae, pupae, or adults. Emerged male and female parasites were stored for approximately four months, then dried at 80°C for 24 h and weighed on a Mettler UM 3 balance.

The results of the experiments were analyzed by three-way analysis of variance (ANOVA) utilizing three factors: the host species attacked, the host species from which the parasite was reared, and the experience of the parasite (day one, inexperienced; day two, experienced). Thus, each ANOVA had eight subgroups, e.g., pea aphid attacked, pea aphid-reared parasites,

day one; lupine aphid attacked, pea aphid-reared parasites, day two; etc. Separate ANOVAs were run for each of the following dependent variables: numbers of eggs laid, hosts attacked, mummies produced, proportion of mummies from which parasites emerged, and proportion of females among all parasites emerged (sex ratio). The significance of the main effects and two- and three-way interactions were tested. In order to test the dependent variables of sex ratio (the proportion of females among all emerged parasites) and survivorship (the proportion of all mummies from which parasites emerged), the proportions (for each host species in each cup) were transformed, using the following arcsine transformation (Zar 1974):

$$X' = \sqrt{(n+1/2)}\arcsin\sqrt{(f+3/8)/(n+3/4)}$$

where n is the total number of parasites (or mummies), and f is the number of females (or mummies from which parasites emerged).

Two additional, two-way ANOVAs were run on the weights of male and female parasites which emerged from the two host species. The factors were host species attacked and host species from which the parasite was reared (data for days one and two were combined).

C. Results

There was no significant difference between the mean number of eggs laid in lupine and pea aphids (Table 9). However, there was a difference in the way the eggs were distributed, with

Table 9. Summary of ANOVA of success of *Ephedrus californicus* reared from two hosts and parasitizing the same two hosts in the laboratory[1]

Dependent variable	Main[2] effect	Treatment	Mean[3]	n	*F*
No. eggs laid	HAT	Pea aphid	6.66	62	2.610
		Lupine	5.68	62	
	HRE	Pea	5.98	64	0.394
		Lupine	6.37	60	
	DAY	1	6.10	62	0.057
		2	6.24	62	
No. hosts attacked	HAT	Pea aphid	6.00	62	9.283*
		Lupine	4.66	62	
	HRE	Pea	5.44	64	0.252
		Lupine	5.22	60	
	DAY	1	5.27	62	0.066
		2	5.39	62	
No. mummies produced	HAT	Pea aphid	6.29	62	27.819*
		Lupine	4.23	62	
	HRE	Pea	5.28	64	0.015
		Lupine	5.23	60	
	DAY	1	5.03	62	1.331
		2	5.48	62	
Propor. parasites emerged	HAT	Pea aphid	0.92	62	21.188*
		Lupine	0.88	62	
	HRE	Pea	0.92	64	0.520
		Lupine	0.89	60	
	DAY	1	0.89	62	1.938
		2	0.92	62	
Sex ratio (all parasites)	HAT	Pea aphid	0.42	62	1.090
		Lupine	0.45	62	
	HRE	Pea	0.43	64	0.073
		Lupine	0.43	60	
	DAY	1	0.43	62	0.243
		2	0.43	62	

Table 9 continued

Dependent variable	Main[2] effect	Treatment	Mean	n	*F*
Sex ratio ("mated" parasites only)	HAT	Pea aphid	0.62	40	2.024
		Lupine	0.67	40	
	HRE	Pea	0.60	44	0.305
		Lupine	0.70	36	
	DAY	1	0.63	40	0.437
		2	0.66	40	
Male weight (mg)	HAT	Pea aphid	0.155	40	2.899
		Lupine	0.162	40	
	HRE	Pea	0.160	40	0.585
		Lupine	0.157	40	
Female weight (mg)	HAT	Pea aphid	0.205	40	27.271*
		Lupine	0.231	40	
	HRE	Pea	0.220	40	0.713
		Lupine	0.216	40	

[1]Complete ANOVA tables can be found in Appendix B
[2]HAT=host species attacked
HRE=host species from which parasites were reared
DAY=day of experiment
[3]Untransformed values
*significant at P=0.01

significantly more pea than lupine aphids attacked. The difference in numbers of hosts attacked was reflected in the numbers of mummies formed, with significantly more pea aphid mummies resulting. However, two-way interactions for the number of hosts attacked and the number of mummies formed were not significant (Appendix B).

The proportion of mummies from which parasites emerged was significantly lower on the lupine aphid than on the pea aphid (Table 9). Moreover, there was a significant interaction between survivorship and the host species from which attacking parasites were reared (Appendix B). Survivorship of parasites in lupine aphid mummies produced by parasites reared from lupine aphids was significantly lower than among other classes of mummies, and this was a result of a high incidence of "gregarious mummies" (Table 10). Gregarious mummies of *E. californicus* may result when two parasites survive larval competition in a superparasitized aphid (Cohen *et al.*, in prep.). The incidence of superparasitism was significantly higher among lupine aphids attacked by parasites reared from lupine aphids (Table 11).

The sex ratio of parasites which emerged from the two host species did not differ significantly for any of the main effects (Table 9). However, six of the fifteen lupine aphid-reared parasites, and five of the sixteen pea aphid-reared parasites did not produce any female offspring (on either host or on either day of the experiment). Under the possibility that these females were unmated, had mated with sterile males, or were

Table 10. Percentages of parasite emergence and numbers of gregarious mummies produced by *Ephedrus californicus* reared from two hosts and exposed simultaneously to the same two hosts in the laboratory

Treatment HRE[1]	HAT[2]	Tot. no. mummies produced	Tot. no. parasites emerged	% parasites emerged[3]	No. gregar. mummies
Pea aphid	Pea aphid	198	19	90.40a	0
Lupine	Pea	192	12	93.75a	0
Pea	Lupine	140	7	95.00a	1
Lupine	Lupine	122	20	83.61b	12

[1]Host species from which parasites were reared
[2]Host species attacked
[3]Percentages sharing the same letter form homogeneous subsets ($P \leq 0.05$), Unplanned Test of Homogeneity (Sokal and Rohlf 1981, p.728).

Table 11. Levels of superparasitism produced by *Ephedrus californicus* reared from two hosts and exposed simultaneously to the same two hosts in the laboratory

Treatment HRE[1]	HAT[2]	Total no. hosts attacked	Total no. eggs laid	No. super-numerary eggs	% eggs[3] super-numerary
Pea aphid	Pea aphid	193	209	16	7.66a
Lupine	Pea	155	174	19	10.92a
Pea	Lupine	179	204	25	12.25a
Lupine	Lupine	134	178	44	24.72b

[1]Host species from which parasites were reared
[2]Host species attacked
[3]Percentages sharing the same letter form homogeneous subsets ($P \leq 0.05$), Unplanned Test of Homogeneity (Sokal and Rohlf 1981, p.728).

otherwise incapable of fertilizing their eggs, the sex ratio of progeny from only those parasites which produced at least one female was analyzed. Again, none of the main effects was significant.

Female parasites which emerged from lupine aphids were significantly heavier than those from pea aphids, but the weight of male parasites which emerged from the two hosts did not differ significantly (Table 9).

D. Discussion

Host preference

The apparently conflicting data showing that the numbers of eggs laid in each host species by *E. californicus* did not differ significantly, but that there were significantly more pea than lupine aphids attacked (Table 9) indicate that there was a more clumped distribution of eggs in the lupine aphid. This distribution may be a result of variation among lupine aphids, e.g., some aphids may have more vigorously resisted attempts to oviposit in them, or some may not have been accepted by parasites for oviposition. Given the origin of the aphid species used in this experiment, it is possible that there was more variation among lupine aphids than pea aphids. The former were first- or second-generation progeny of females collected from a large field population, while the latter were from a laboratory colony kept under standardized conditions for over ten years.

A decision on whether *E. californicus* showed a preference for the pea aphid would depend on which factor, total eggs laid or total hosts attacked, is considered the best indicator of host preference. Regardless, most important to the objectives of this chapter is the fact that *E. californicus* readily attacked the pea aphid, even when lupine aphids were available. This is of interest to consideration of the absence of *E. californicus* from the pea aphid in the field, which is further discussed in Chapter VI.

Hopkins (1916, cited in Wood 1963), working with scolytid beetles, proposed a "host selection principle" which states that "...a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted." Several investigators have tested this hypothesis with entomophagous insects (Vinson 1976), and some have found it to explain experimental results (e.g., Salt 1935, Thorpe and Jones 1937; Ohgushi 1960; Eijsackers and van Lenteren 1970). However, in the experiments of this chapter, there was no significant interaction between the effects of the host from which the parasite was reared and the host species attacked, for any of the dependent variables concerned with host preference (Appendix B). Thus, the form of conditioning proposed by Hopkins (1917) did not influence the preference of *E. californicus* for lupine or pea aphids. Similarly, parasite experience (based on the day of the experiment, where on day one the parasites were inexperienced) had no significant effect on host preference

(Appendix B).

Host suitablility

Several factors quantified in the choice test conducted can be used to compare the suitabilities of the lupine and pea aphids as hosts for *E. californicus*. These include: host preference, sex ratio and weight of emerged parasites, and the proportions of mummies from which parasites emerged. Literature on these topics as they apply to host suitability is discussed below.

Host preference. Among the Aphidiidae (Griffiths 1960; Calvert 1973), as among some other parasitic Hymenoptera (e.g., Lewis and Vinson 1971; Vinson 1975), host acceptance and host preference are not always reliable indicators of host suitability, as parasites have been found to oviposit readily into hosts unsuitable for development. *Monoctonus crepidis* (Haliday) attacked with equal frequency several species of aphids reared on lettuce although only one, *Nasonovia ribis-nigri* Mordvilko, was suitable for development (Griffiths 1960). However, the parasite did not oviposit in any aphids reared on host plants other than lettuce. Calvert (1973) caged *M. paulensis* (Ashmead) with four aphid species simultaneously. All were attacked with equal frequency, although only two were suitable for development. When offered together, *Acyrthosiphon pisum*, a suitable host, was attacked more often than *Therioaphis trifolii* (Monell), an unsuitable host, but the two species were

attacked with equal frequency when offered separately. Similarly, no significant difference was found in the number of attacks on *Sitobion fragariae* (Walker), suitable, and *Rhopalosiphum padi* (L.), unsuitable, when they were offered together. However, some aphidiids do not oviposit in, or show less preference for, certain aphid species. *Ephedrus plagiator* did not probe or attempt to oviposit in *T. trifolii* or *Sipha flava* (Forbes), although it was not determined if these hosts were suitable or unsuitable for development (Jackson *et al.* 1974). *Aphidius uzbekistanicus* showed less preference for *Hyalopteroides humilis* (Walker) (which was less suitable for development) when it was offered simultaneously with *Metopolophium dirhodum* (Walker) (Dransfield 1979).

Sex ratio. Most Hymenoptera have haplodiploid sex determination, which provides females with control over the sex of their offspring (Charnov 1982). Females may lay proportionately more fertilized eggs in suitable hosts than in unsuitable hosts (Flanders 1965). Progeny emerging from poorly-suitable hosts may be predominantly male for the additional reason that males may survive better than females in such hosts (Flanders 1956, 1965; Wylie 1966).

Among the Aphidiidae, Jackson *et al.* (1974) found that *E. plagiator* produced more females on *Schizaphis graminum* and *Rhopalosiphum maidis* (Fitch) than on two less preferred hosts. These results were apparently due to selective oviposition of fertilized eggs in the preferred hosts, rather than selective

mortality of females in the less preferred hosts, as the proportion of unemerged mummies was low and did not differ among different hosts. By contrast, Dransfield (1979) found no consistent difference between the sex ratio of the offspring of *A. uzbekistanicus* on *M. dirhodum*, a suitable host, and *H. humilis*, a less suitable host.

In studying host preference and host transfers with populations of three *Aphidius* species, Pungerl (1984) found that on some hosts, which were apparently less preferred or less suitable (as parasites produced fewer offspring when caged with them), only male progeny were produced. For example, when transferring a population of *A. ervi*, collected on *A. pisum*, to *M. persicae*, approximately 70 offspring, all males, were recorded from six females. Similarly, a population of *A. rhopalosiphi*, collected on *M. dirhodum*, produced only male offspring on *Sitobion avenae* (F.) (approximately 65 offspring from four females). However, it was not verified that the females were mated, and no data were presented on pre-emergence mortality.

In his study of host preference in *M. paulensis*, Calvert (1973) found large proportions of dead larvae and unemerged mummies on the unsuitable hosts *T. trifolii* and *R. padi*. Of the few parasites which emerged from these hosts, all were short-lived males with deformed wings.

Weight. It has often been shown that insect fecundity is positively correlated with weight (e.g., Salt 1935, 1940; Murdie

1969; Frazer and Gill 1981). Assuming this relationship to be true for *E. californicus*, then, as female parasites reared from lupine aphids were heavier than those reared from pea aphids (Table 9), there is no reason to expect parasites reared from the lupine aphid to be less fecund on the basis of size.

Pre-emergence mortality. Pre-emergence mortality would seem to be a clear indicator of poor host suitability. It may result from a number of factors, including host immunity, nutritional unsuitability, and host toxins (Vinson and Iwantsch 1980). In the experiments described in this chapter, there was a significant interaction between the host reared from and the host attacked, for the dependent variable of survivorship. Specifically, a larger proportion of parasites in lupine aphid mummies resulting from attack by parasites reared from lupine aphids did not emerge (Table 10). Of the 20 mummies in this group from which no parasites emerged, 12 were gregarious.

Cohen *et al.* (in prep.) have found that the incidence of gregarious mummies is positively correlated with increasing levels of superparasitism. This trend can in part explain the large number of gregarious mummies found among lupine aphids attacked by lupine aphid-reared parasites, as for reasons not clear, this treatment had the highest level of superparasitism (expressed as the number of supernumerary eggs, Table 11.) Interestingly, the levels of superparasitism produced in the experiments of this chapter were moderate, and the incidence of gregarious mummies higher, as compared with those of Cohen *et*

al. (in prep.), where gregarious mummy formation was studied with only the pea aphid as host. Thus, it is possible that gregarious mummies are more likely to be produced with the lupine aphid as host.

No parasites emerged from the thirteen gregarious mummies produced in the experiments of this chapter. Although one or even both parasites in a gregarious mummy may often emerge (Cohen *et al.*, in prep.), they are reduced in size and, presumably, fitness. Thus, the formation of gregarious mummies would be detrimental to the parasite species. As gregarious mummies occurred more frequently with the lupine aphid as host, the lupine aphid might be classed as a less suitable host than the pea aphid for *E. californicus*. However, gregarious mummies can result only in cases of superparasitism, which among the Aphidiidae occurs infrequently in the field (Campbell 1973). Of 542 *E. californicus* lupine aphid mummies collected from the field in 1984, 9 (1.66%) were gregarious, suggesting that the formation of gregarious mummies is not likely to be an important mortality factor for *E. californicus* in nature. Therefore, the occurrence of gregarious mummies does not appear to justify the categorization of the lupine aphid as a less suitable host for this parasite.

In summary, the following results suggest that the lupine and pea aphids are equally suitable hosts for *E. californicus*, and that fecundity and developmental time on the two hosts should be similar:

1. the sex ratio of progeny emerged from the two host species did not differ significantly;
2. although pre-emergence mortality was higher on the lupine aphid, this can be explained by the formation of gregarious mummies, which is probably not an important mortality factor in nature;
3. females emerging from lupine aphids were heavier than those from pea aphids, and males were equally as heavy; and
4. on the basis of total hosts attacked (but not total eggs laid), *E. californicus* may have shown a preference for the pea aphid, but both aphid species were readily attacked.

V. Ecology and Distribution of the Lupine Aphid and its Associated Parasites in Southwestern British Columbia

A. Introduction

Lupines (*Lupinus*, family Leguminosae), while regarded only as wildflowers and ornamentals in Canada, are being studied for a variety of commercial uses in many parts of the world, including the southern United States, South America, Europe, and Australia. Lupine seed has a higher protein content than soybean, and can be used as a supplement to animal and human foods. In addition, as lupines become readily established in poor soils, and enrich the soil with nitrogen, they can be used as agricultural cover crops, or to reclaim mining sites or prepare ground for afforestation (Carter *et al.* 1984).

The lupine aphid, *Macrosiphum albifrons*, is a holocyclic species restricted to *Lupinus*. It is indigenous to North America, where it is found on both the east and west coasts, as well as in the Rocky Mountain region (Smith and Parron 1978), but has recently become a pest of cultivated lupines in the United Kingdom, where it was first recorded in 1981 (Stroyan 1981). By 1982, the aphid was well established in several counties, and was spreading rapidly (Carter *et al.* 1984). As yet, there are no further records of *M. albifrons* outside of the

United States and Canada.

M. albifrons is a large aphid (adults may be up to 5 mm long), and has a prodigious fecundity (Frazer and Gill 1981). Essig (1911) stated that the aphid is "quite effectively preyed upon by the larvae of syrphid flies, coccinellids, and by internal parasites, which are very large." However, no systematic survey of parasites attacking the lupine aphid has been undertaken. Liu (1977) described *Aphidius lupini* Liu, reared from the aphid in California. Two earlier records of parasites reared from the aphid, *A. pisivorus* (Schlinger and Hall 1960b), and *Praon simulans* (Provancher) (MacGillivray and Spicer 1953), were considered to be based on doubtful identifications (Mackauer and Stary 1967).

In order to provide background information relative to the potential for biological control of the lupine aphid in introduced habitats, this chapter presents the results of a survey of the distribution of the lupine aphid and its parasites in southwestern British Columbia, and describes seasonal changes in lupine growth and in aphid and parasite abundance in the Vancouver area.

B. Materials and Methods

Ecology of the lupine aphid and its parasites in the Vancouver area.

During 1983 and 1984, several lupine fields were studied in

the Vancouver area (Table 13). In addition to observations on plant growth and the size and distribution of aphid colonies, weekly collections of aphids were made at three sites from June to September, 1984, in order to monitor parasite activity. The three sites were:

A1, north side of Upper Levels Highway at the 15th Street exit, in West Vancouver, a south-facing hillside with several patches of *Lupinus polyphyllus* Lindl,

A3, northwest corner of Grandview Highway and Rupert Street in Burnaby, a level, vacant lot with a community of *Lupinus* sp. (possibly a hybrid of *L. arcticus* S. Wats.), and

A4, east side of Boundary Road between Southeast Marine Drive and Rumble Steet in Burnaby, a west-facing hillside extensively covered with *L. polyphyllus*.

The method of collection consisted of a traverse across the lupine site, with stops made at two meter intervals. At each stop, aphid colonies (if present) on one or several plants were sampled by placing a tray beneath a colony and tapping the plant. On selected dates, mummies were also collected at each stop.

In the laboratory, a known number of second-, third-, and fourth-instar aphids was taken for each site. Each instar sample was reared on lupine cuttings in small plastic cages (Mackauer and Bisdee 1965a) at 23-25°C. After eight days, dead,

parasitized aphids (mummies) and aphids killed by the pathogen *Entomophthora* sp. were removed and counted. Field-collected mummies were placed in gelatin capsules and kept outdoors, sheltered from the rain, in order to monitor diapause and hyperparasitism.

Although rearing the second, third, and fourth aphid instars cannot determine the percentage parasitism of the entire aphid population, it can reliably determine the relative importance of each parasite species. Monitoring only one aphid instar can provide misleading results if a later host instar is preferred by a parasite, or if parasitized aphids wander from the colony. By contrast, monitoring first instars and adults adds little information, as these life stages are seldom preferred by parasites (Hagen and van den Bosch 1968).

Survey of the distribution of the lupine aphid and its parasites in southwestern British Columbia.

During July of 1983 and 1984, lupine fields were visited throughout southwestern British Columbia. Each site was noted for its biogeoclimatic characteristics (Beil *et al.* 1976), and lupines were collected for later identification according to Dunn and Gillett (1966). If aphids were found, a sample was collected and reared (as described above) in order to determine the identity and approximate abundance of any parasites present.

C. Results and Discussion

Ecology of the lupine aphid and its parasites in the Vancouver area.

Seasonal changes in aphid abundance. Lupines began to produce new foliage in March, with racemes beginning to form in late April. Aphids were found to overwinter as nymphs as well as eggs, and the first small colonies of the year appeared in April. In June, one or two isolated areas of heavy infestation, covering four to ten plants, were formed at each site, while most other plants remained almost free of aphids. In late June, the aphid populations at these foci "crashed", but the foliage and racemes were wilted and did not recover. Dispersal of alates from the foci led to a progressively more evenly distributed aphid population. Throughout July and most of August, aphid colonies were present on the racemes of most plants. Although at times extensively covered with aphids and honeydew (Fig. 6), most lupines continued to grow and produced mature seed pods. Aphids became less numerous in mid-August, and by September only a few small colonies or scattered individuals remained.

Seasonal changes in parasite abundance. Two parasites, *Aphidius lupini* and *Ephedrus californicus*, were found attacking the lupine aphid in the Vancouver area; in addition, many aphids were killed by *Entomophthora* sp. (Figs. 7-9). *A. lupini* was clearly the more common parasite until late August, when *E. californicus* became more abundant on all instars at site A1, and

Figure 6. Lupine aphids on *Lupinus polyphyllus*. a) heavy infestation on raceme at time of flowering; b, c) heavy infestation on raceme, seed pod formation almost completed; d) leaf with mummies of *Ephedrus californicus* (black) and *Aphidius lupini* (brown).


a
b
c
d

Figure 7. Seasonal mortality of second-instar lupine aphids at three Vancouver area sites, 1984

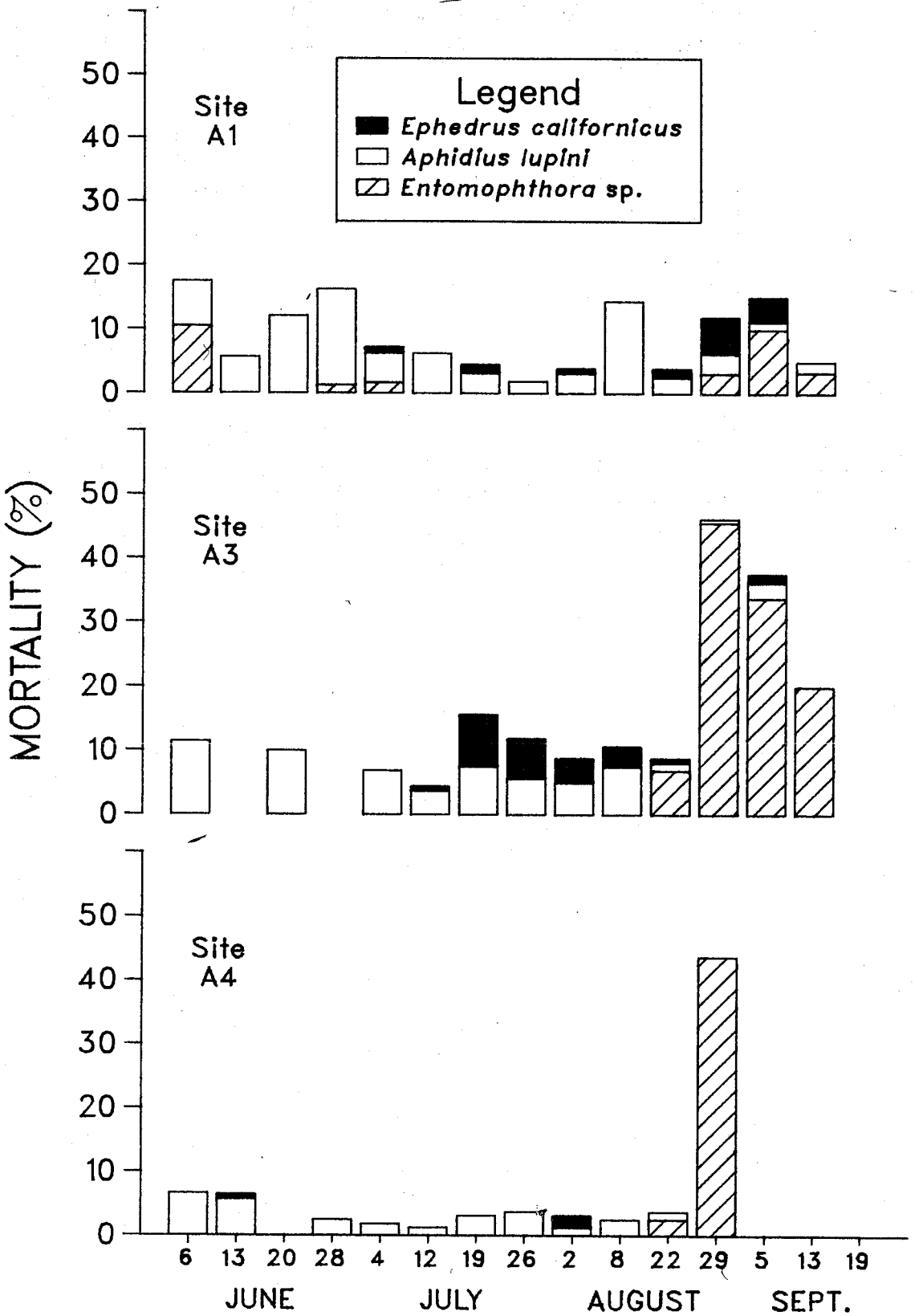

Legend
Ephedrus californicus
Aphidius lupini
Entomophthora sp.
Site A1
Site A3
Site A4
MORTALITY (%)
0
10
20
30
40
50
6 13 20 28 4 12 19 26 2 8 22 29 5 13 19
JUNE
JULY
AUGUST
SEPT.

Figure 8. Seasonal mortality of third-instar lupine aphids at three Vancouver area sites, 1984

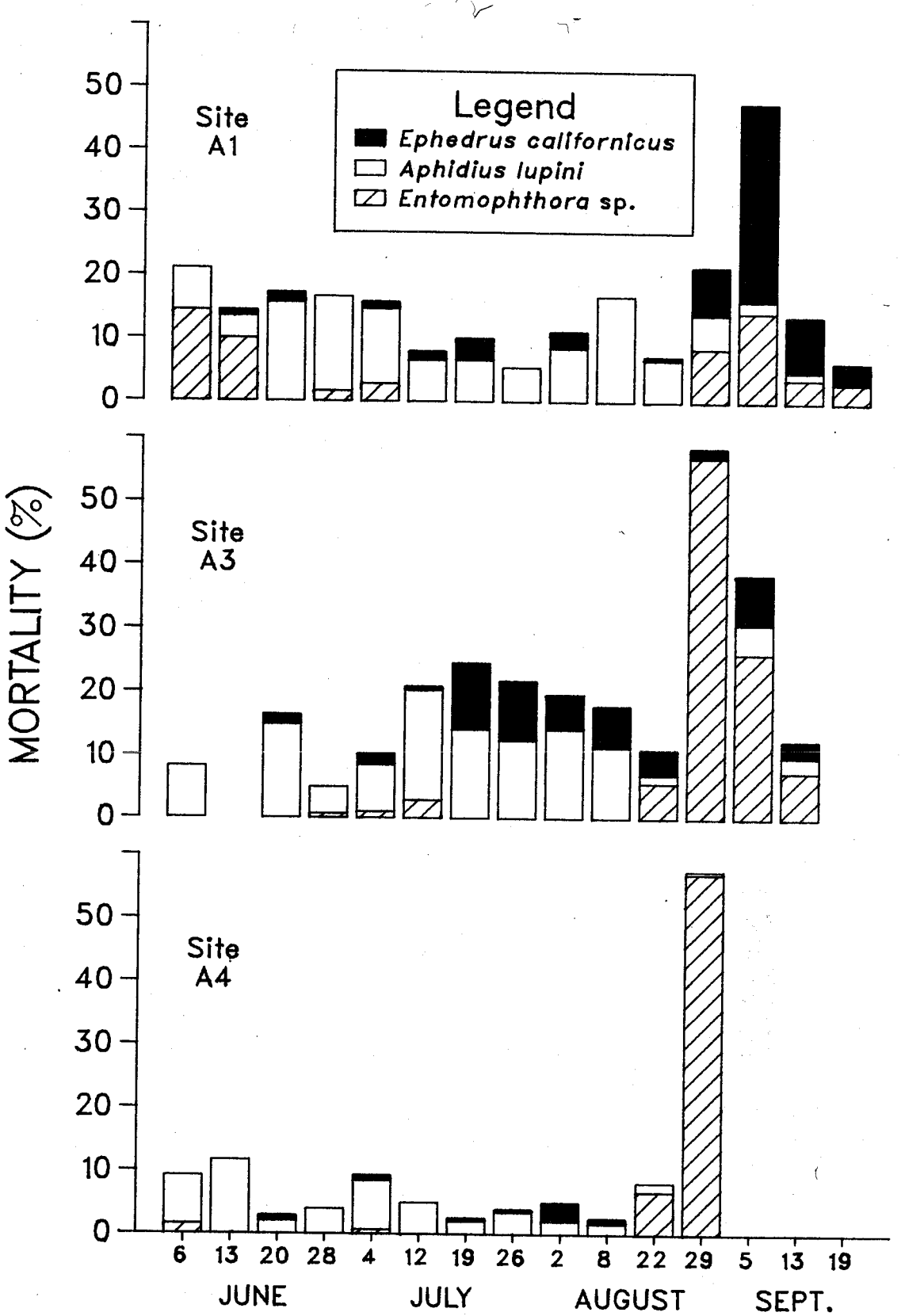
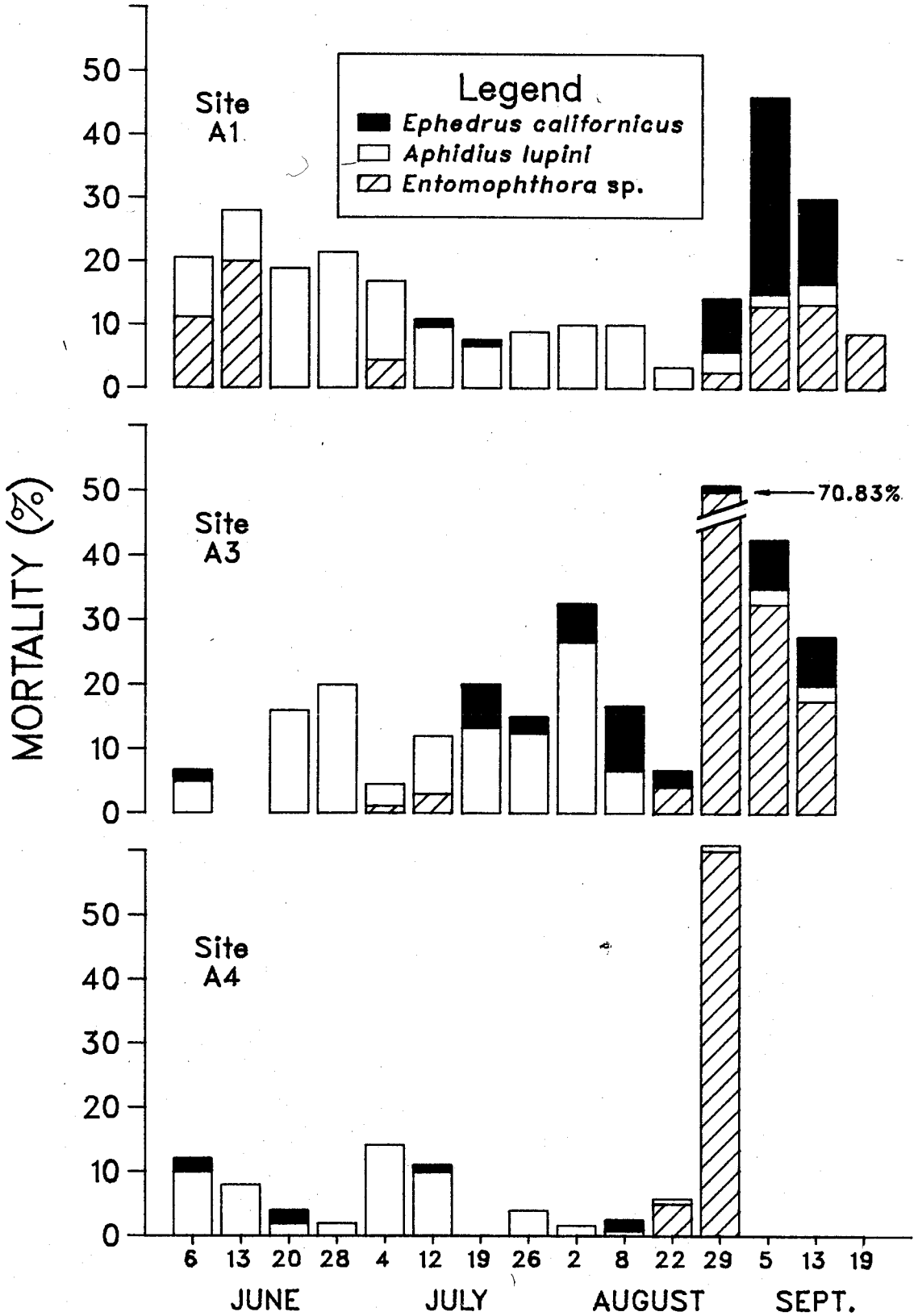

Legend
Ephedrus californicus
Aphidius lupini
Entomophthora sp.
Site A1
Site A3
Site A4
MORTALITY (%)
0
10
20
30
40
50
6 13 20 28 4 12 19 26 2 8 22 29 5 13 19
JUNE
JULY
AUGUST
SEPT.

Figure 9. Seasonal mortality of fourth-instar lupine aphids at three Vancouver area sites, 1984


Legend
Ephedrus californicus
Aphidius lupini
Entomophthora sp.
Site A1
Site A3
Site A4
70.83%
MORTALITY (%)
0
10
20
30
40
50
6 13 20 28 4 12 19 26 2 8 22 29 5 13 19
JUNE
JULY
AUGUST
SEPT.

on third and fourth instars at site A3. *E. californicus* was also common on all instars in July at site A3, but was never abundant at site A4.

A. lupini mummies on new lupine foliage were first observed in May, indicating that the parasite is well synchronized with the early appearance of lupine aphid colonies. In addition, 90 of 208 (43.3%) second to fourth instar aphids collected at site A1 on May 12 were found to contain *Aphidius* larvae upon dissection in the laboratory, suggesting that *A. lupini* may be important in containing lupine aphid outbreaks early in the spring.

By contrast, *E. californicus* was very scarce until about July, when it became common at site A2. This is probably in part attributable to its relatively high threshold temperature for development, 6.84±SE 0.38°C (Chapter III), as compared to that of the lupine aphid in Vancouver, 3.95±SE 0.59°C (Frazer and Gill 1981). Other aphidiids have been found to have thresholds considerably closer to those of their hosts (Campbell *et al.* 1974). Collection and laboratory rearing of the rose aphid, *Macrosiphum rosae*, an important host of *E. californicus* (Schlinger and Hall 1960b), did not reveal the presence of *E. californicus* until June 15, confirming the scarcity of this parasite until early summer (M. Cohen, unpublished data).

The reasons for the decreased parasitism of lupine aphids by *A. lupini* and increased parasitism by *E. californicus* in late August are unclear. There was considerable variation in the

degree of hyperparasitism at both sites A3 and A5 (Table 12). On August 2, *A. lupini* was clearly more frequently attacked by hyperparasites than *E. californicus*, but all other percentages overlap in their 95% confidence intervals. On both dates, the proportion of both parasites in diapause was low (Table 12).

Mortality from the pathogen Entomophthora *sp.* Aphids killed by *Entomophthora* sp. were found only during the generally rainy weeks of June, early July, late August, and September (Figs. 7-9). Mortality from the pathogen in spring was substantial only at site A1. However, late-summer mortality was high at all sites, occasionally exceeding 50% of aphids collected at sites A3 and A4.

Distribution of the lupine aphid and its parasites in southwestern British Columbia.

The lupine aphid was found in all four survey areas, i.e., the greater Vancouver area, the Squamish area, southern Vancouver Island, and the southern and central Interior (Fig 10, Table 13). However, it was noticeably absent from two locations within these areas: the Victoria area on Vancouver Island, and the dry, low elevation sites of the Interior (Fig. 10, Table 13).

Two types of lupine sites were surveyed in the Victoria area: the coastal bluffs, where *Lupinus densiflorus* Benth. and *L. bicolor* Lindl. occur, and roadsides along Highway 1, where *L. polyphyllus* Lindl. is abundant. The absence of the aphid from

Table 12. Contents of field-collected lupine aphid mummies from two Vancouver area sites, August, 1984

Site	Date	Parasite species	No. mummies	Primary parasites			Hyper-parasites	% mummies primary parasites (95% C.I.)[1]	% mummies hyper-parasites (95% C.I.)[1]
				Emerged	Unemerged				
					Dead	Diapause			
A3	Aug. 2	*A. lupini*	65	8	20	1	36	44.62 (32.8-56.7)	55.38 (43.3-67.2)
		E. californicus	53	24	24	0	5	90.57 (81.3-96.9)	9.43 (3.1-18.7)
	Aug. 22	*A. lupini*	41	2	8	3	28	31.71 (18.5-46.6)	68.29 (53.4-81.5)
		E. californicus	38	7	6	0	25	34.21 (20.2-49.8)	65.79 (50.2-79.8)
A5	Aug. 2	*A. lupini*	47	1	13	0	33	29.79 (17.7-43.5)	70.21 (56.5-82.3)
		E. californicus	33	7	11	1	14	57.58 (40.6-73.7)	42.42 (26.3-59.4)
	Aug. 22	*A. lupini*	23	2	3	0	18	21.74 (5.7-52.1)	78.26 (59.5-92.3)
		E. californicus	12	2	1	0	9	25.00 (5.7-52.1)	75.00 (47.9-94.3)

[1]C.I.=confidence intervals

Figure 10. Lupine sites in southwestern British Columbia sampled for the lupine aphid and its associated parasites, 1983-1984

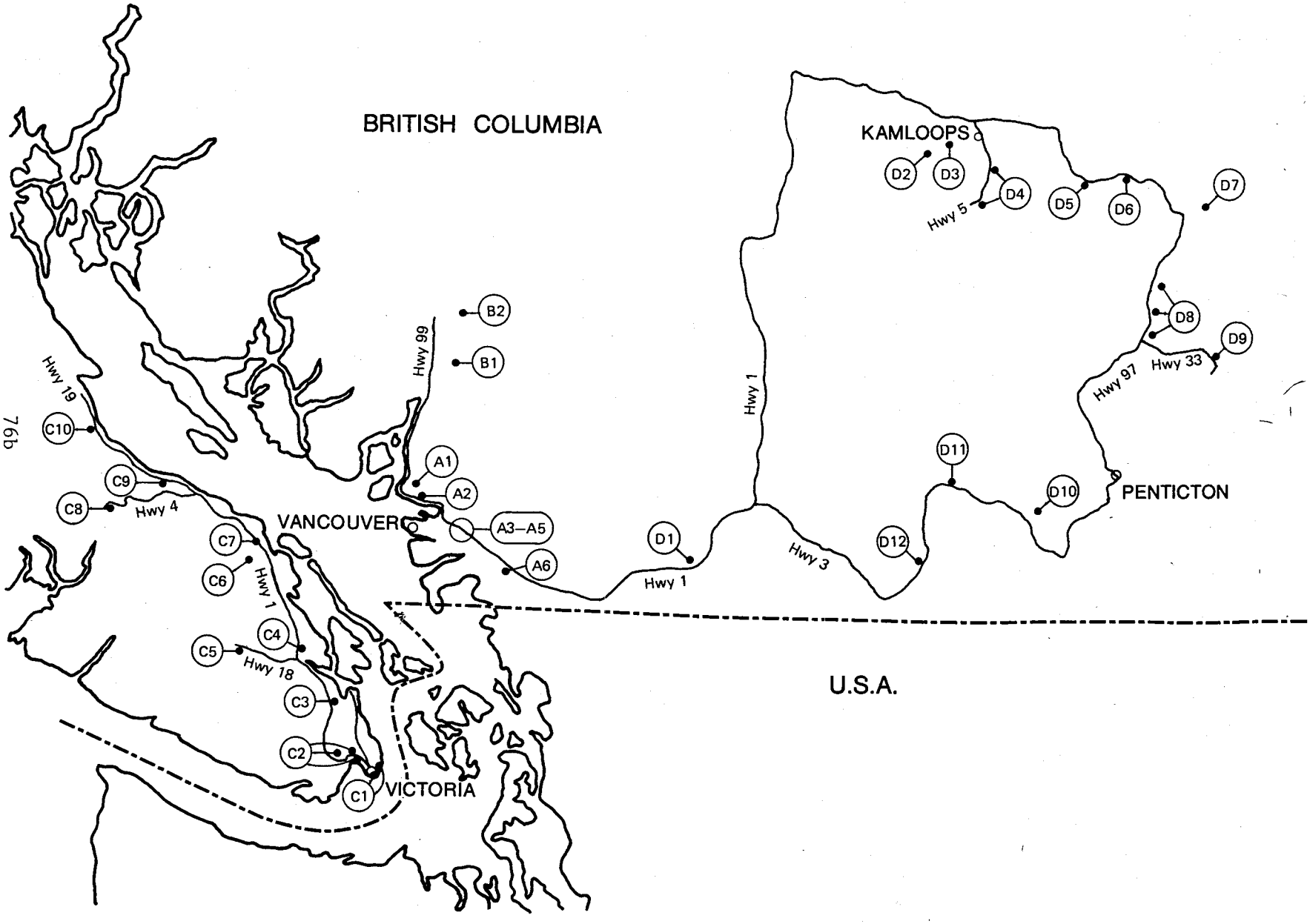

BRITISH COLUMBIA
KAMLOOPS
D2
D3
D4
D5
D6
D7
Hwy 5
B2
B1
Hwy 99
Hwy 19
C10
C9
C8
Hwy 4
A1
A2
VANCOUVER
A3–A5
A6
Hwy 1
D1
Hwy 1
Hwy 3
D12
D11
D10
PENTICTON
D8
D9
Hwy 97
Hwy 33
C7
C6
Hwy 1
C4
C5
Hwy 18
C3
C2
C1
VICTORIA
U.S.A.

Table 13. Distribution of lupines, lupine aphids, and lupine aphid parasites in southwestern British Columbia, 1983-1984

Area of survey	Site	Location[1]	Elev. (m)	Para-sites[2]	Lupine species
Greater Vancouver	A1	W. Vancouver	150	A,E	*L. polyphyllus*
	A2	Cypress P.P.	760	A,E	*L. arcticus*, *L. polyphyllus*
	A3	S. Burnaby	80	A,E	*Lupinus* sp.
	A4	S. Burnaby	80	A,E	*L. polyphyllus*
	A5	S.F.U.	300	A,E	*L. polyphyllus*
	A6	Cloverdale	150	A,E	*L. polyphyllus*
Squamish Area	B1	Diamond Head	900	A,E,Po	*L. arcticus*
	B2	Black Tusk Tr.	1150	A	*L. arcticus*
Southern Vancouver Island	C1	Beacon Hill Pk., Victoria	3	-	*L. bicolor*, *L. densiflorus*
	C2	Esquimault	10	-	*L. polyphyllus*
	C3	Mill Bay	120	A	*L. arcticus*
	C4	Duncan	30	A,E	*L. polyphyllus*
	C5	Lk. Cowichan	180	A,E,Po	*L. arcticus*
	C6	Nanaimo	150	A,E	*L. arcticus*
	C7	Nanaimo	120	A,E,Po	*L. polyphyllus*
	C8	Pt. Alberni	300	A,E,Po	*L. arcticus*
	C9	Qualicum Beach	20	A,E	*L. polyphyllus*
	C10	Buckley Bay	40	A	*L. polyphyllus*
Southern, Central Interior	D1	Chilliwack	120	-	*L. polyphyllus*
	D2	Chewhels Mtn.	1520	A,E,Po	*L. arcticus*
	D3	L. LaJeune P.P.	750	-	*L. sericeus*
	D4	Stump Lake	750	-	*L. sericeus*
	D5	Westwold	600	*	*L. sericeus*
	D6	Falkland	600	A	*L. sericeus*
	D7	Silver St. P.P.	1370	A,E	*L. arcticus*
	D8	Hwy. 97, Oyama to Rutland	400 -450	-	*L. sericeus*
	D9	Tamarac Park	840	A	*L. polyphllus*
	D10	Apex Alpine	1600	A,E,P	*L. arcticus*
	D11	Princeton	1220	A	*L. arcticus*
	D12	Manning P.P.	1010	A	*Lupinus* sp.

[1]P.P.=Provincial Park
[2]A=*Aphidius lupini*, E=*Ephedrus californicus*, P=*Praon* sp., Po=*Praon* sp. nr. *occidentale*, - =Lupine aphid absent, * =Lupine aphid present, no parasites found

the harsh shoreline environment might be expected, but reasons for its absence from the roadside plants are less clear, as large aphid colonies were found on *L. polyphyllus* at other roadside locations on Vancouver Island.

At low elevations of the Interior (400-750 m), *L. sericeus* Pursch forms extensive communities, found with *Artemisia* spp. or underneath *Pinus ponderosa* Dougl. The lupine aphid was not found in this dry environment, with the exception of sites D2 and D3, where small colonies were found in 1983. However, the aphid was often present at the more moist, higher elevations (840-1600 m) of the Interior, where *L. polyphyllus* and *L. arcticus* S. Wats. occur.

In addition to the two parasites collected in the Vancouver area, *Praon* sp. nr. *occidentale* Baker and *Praon* sp. were found attacking the lupine aphid in the survey of southwestern British Columbia. With one exception (site D2), *A. lupini* was present at all sites where lupine aphids were found. Where more than one parasite species was present, *A. lupini* was either the most abundant or was as abundant as the other parasite species.

E. californicus was present at most sites, but was generally much less abundant than *A. lupini*. *Praon* sp. nr. *occidentale* was abundant at site B1, but was collected only in small numbers at the other locations at which it was found. *Praon* sp. was numerous at site D10, the only location at which it was collected. Both *Praon* species were entirely absent from the Vancouver area.

In summary, the lupine aphid formed large colonies on *L. polyphyllus* and *L. arcticus* throughout most of southwestern British Coumbia. However, these plants are robust and appeared to suffer appreciable damage only during the early stages of raceme formation in June, when the lupine aphid formed dense colonies in small areas (4-10 plants) of infestation. It is possible that the early activity of *A. lupini* restricts spring outbreaks of the lupine aphid, when lupines are most vulnerable to damage, as has been observed for the aphidiid *Trioxys complanatus* attacking *Therioaphis trifolii* on alfalfa in California (Hagen and van den Bosch 1968).

A. lupini was the most abundant and most widespread parasite in the area of survey, and is well synchronized with its host. In addition, the parasite has been recorded only from the lupine aphid (Liu 1977), and is probably specific to this host. These characteristics of host specificity and synchronicity are some of the features generally suggested as important for successful biological control agents (Huffaker *et al.* 1976; Beddington *et al.* 1978), and it would appear that *A. lupini* is the best parasite for biological control of the lupine aphid in the United Kingdom.

In contrast to *A. lupini*, *E. californicus* did not appear until June, and is known to have a broad host range (Mackauer and Stary 1967). The parasite became abundant in late August, but by this time lupines had completed seed production and were entering fall senescence.

VI. General Discussion and Conclusions

Before this study was undertaken, little was known of the biology and ecology of *Ephedrus californicus*, or of the identity and importance of parasites attacking the lupine aphid in North America. However, the experiments and field observations of the preceding chapters have contributed new information on these topics. In this chapter, the findings and conclusions of this thesis are reviewed, and areas for future research are suggested.

Ecology of *E. californicus* on the lupine aphid

As discussed in Chapter V, *Aphidius lupini* would appear to be the most effective parasite of the lupine aphid in southwestern British Columbia. It was the most abundant and widespread species collected, is host specific, and is well synchronized with the spring emergence of its host. While almost as widespread as *A. lupini*, *E. californicus* was only occasionally abundant, and is poorly synchronized with the lupine aphid.

Although some authors have recently questioned the conventional wisdom of preferring specialized over polyphagous natural enemies for biological control programs (e.g., Ehler and Miller 1978, Murdoch *et al.* 1985), it appears that some of the

established arguments against polyphagy are important in explaining the lack of effectiveness of *E. californicus* against the lupine aphid. For example, polyphagous parasites are, in general, not synchronized with any particular host (Murdoch *et al*. 1985), and might be expected to have high developmental thresholds (as does *E. californicus* in comparison with the lupine aphid, and, apparently, in comparison with the specialized parasite *A. lupini*). A high developmental threshold would be advantageous for polyphagous parasites in that spring emergence would be delayed until numerous host species were available. It might not be advantageous for *E. californicus* to be synchronized with the lupine aphid, which appears early in the spring, well before many other host species are active.

Once *E. californicus* does begin seasonal activity (in June), its polyphagous habit may help explain its unexpected lack of abundance on the lupine aphid. Results from this thesis suggest that *E. californicus* should be an abundant parasite. In Chapter II it was found that the parasite has a high fecundity, and that it rapidly achieves a high intrinsic rate of natural increase. In the field, the parasite was found to have a sex ratio of 0.66, comparable to other aphidiids (Mackauer 1976). However, it may be that the parasite disperses to other, perhaps preferred, host species. For example, the parasite appears to be more numerous on the rose aphid in the Vancouver area (Dr. M. Mackauer, pers. comm.). It has also been suggested that polyphagous natural enemies do not respond numerically to pest

population density, and therefore do not provide control should a pest population exceed a threshold level (related to the saturation of the functional response) (Beddington *et al.* 1978). However, this suggestion has been disputed (Murdoch *et al.* 1985), and there appears to be a lack of experimental evidence on this topic. Other factors such as poor searching ability may account for the low numbers of *E. californicus* on the lupine aphid, but additional study is necessary to provide more definitive answers to these questions.

Absence of *E. californicus* from the pea aphid

The results of this study can also provide a basis for discussing the absence of *E. californicus* from the pea aphid in alfalfa, although it appears that this phenomenon cannot yet be fully understood. It may be helpful to consider the problem in terms of the steps necessary for a successful host-parasite relationship, which have been described as host habitat location, host location, host acceptance, host suitability (Salt 1935, 1938; Doutt 1959), and host regulation (Vinson 1975). The available information on these processes for the *E. californicus*-pea aphid relationship are reviewed below.

While no attempt was made here to determine if (and how) *E. californicus* regulates the physiology of its hosts, the performance of the parasite on the pea aphid in the laboratory indicated no difficulties in exploiting this host. Similarly, the favorable fecundity, longevity, and developmental time of

the parasite (Chapters II, III) suggest that the pea aphid is a suitable host for *E. californicus*.

The pea aphid was readily accepted by *E. californicus*, even when the lupine aphid, a host commonly attacked in the field, was offered simultaneously (Chapter IV). While host location by *E. californicus* was not investigated in this study, females successfully located pea aphids when searching on bean plants in laboratory colonies, and it seems likely that the parasite would be able to locate this host were it searching for it in the field on alfalfa.

It thus remains to consider whether host habitat location can explain the absence of *E. californicus* from the pea aphid in alfalfa. One factor which requires further investigation concerns the "search image" which the parasite uses in locating host habitats. It may be that *E. californicus* does not search for fields with a flat, uniform profile (such as alfalfa fields), but rather for fields with a more heterogeneous appearance such as those where lupines or roses can be found, mixed with trees, shrubs, and other vegetation. It might be expected, then, that pea aphids in such heterogeneous habitats would be attacked by *E. californicus*. In fact, the pea aphid is a polyphagous species and has been collected on Scots' broom, *Cytisus scoparious* (L.), and clover, *Trifolium* spp. (Forbes and Chan 1978), two legumes often found with lupines in the Vancouver area. *Ephedrus* mummies have not been found in the course of casual observation of pea aphid colonies on these

plants (Dr. M. Mackauer, pers. comm.), but study of such aphids may reveal the presence of *E. californicus*.

Were *E. californicus* to attack the pea aphid in alfalfa, there are reasons to expect that it would contribute to biological control of this pest. The intrinsic rate of increase of *E. californicus* compares favorably to that of *Aphdius smithi* (Table 4), the most fecund of the parasites attacking the pea aphid in North America (Mackauer 1971). In addition, the polyphagous habit of *E. californicus* might well be an advantage in the alfalfa ecosystem. The alfalfa crop is cut three times during the growing season. Following each cut, populations of both the pea aphid and its parasites are drastically reduced, but the aphid recovers faster and often escapes control (van den Bosch *et al.* 1967). "Strip cutting" of alfalfa is widely used in California to maintain a stable environment and control of the pea aphid, but this technique is not used in British Columbia. Of the parasites attacking the pea aphid, it is possible that, following each cut, *E. californicus* alone would be able to disperse to other hosts, maintain its numbers, and then switch back to the pea aphid as it reappeared. This adaptability is an advantage of polyphagous parasites emphasized by Murdoch *et al.* (1985). The other aphidiids attacking the pea aphid in North America are oligophagous to varying degrees (Mackauer and Stary 1967), but it is not known if alternate hosts for these species are available or attacked adjacent to alfalfa fields.

As has been observed with the lupine aphid as host, however, *E. californicus* would not be expected to be effective against the pea aphid in early spring. Its developmental threshold is considerably higher than those of both the pea aphid and its numerically dominant parasite, *A. ervi* (Table 8).

APPENDIX A: FECUNDITY AND LONGEVITY OF *EPHEDRUS CALIFORNICUS* AT 23 ± 1°C, 65 ± 10% R.H., AND A 16L:8D H PHOTOPERIOD.

Extrapolated values of total eggs laid per day based on dissection of 20 (out of 40) hosts exposed to a single parasite/day.

Female age (days)	Parasite number 1	2	3	4	5	6	7	8
1	46	24	10	26	20	34	14	0
2	110	74	14	104	66	180	118	116
3	186	224	72	224	112	146	184	170
4	134	198	106	150	208	156	160	142
5	110	190	138	192	150	180	162	214
6	72	168	134	130	46	130	116	138
7	108	134	154	58	0	166	108	180
8	78	140	158	0		114	80	122
9	24	74	78	0		82	100	112
10	46		92			80	78	54
	24		70			52	72	46
11	12		66			48	34	58
12	0		52			44	8	38
13			54			12	0	30
14			24			8		26
15			24			2		
16			16					
17								
18								
19								
Total	950	1226	1262	884	602	1434	1234	1446

continued

Female age (days)	Parasite number 9	10	11	12	Total eggs for day (par.1-12)	Mean eggs for day (±SE) (parasites 1-12)
1	12	32	4	60	282	23.50 ± 5.06
2	38	146	16	172	1154	96.17 ± 16.13
3	164	174	96	134	1886	157.17 ± 13.67
4	160	158	150	190	1912	159.33 ± 8.16
5	166	164	114	152	1932	161.00 ± 8.94
6	58	240	98	184	1514	126.17 ± 15.86
7	164	162	100	144	1478	123.17 ± 15.11
8	114	150	108	96	1160	105.46 ± 13.13
9	94	156	74	56	850	77.27 ± 12.62
10	80	116	86	36	668	74.22 ± 8.29
11	52	78	56		450	56.35 ± 6.11
12	32	18	56		324	40.50 ± 6.93
13	50	68	2		262	32.75 ± 9.79
14	36	34	0		166	23.71 ± 7.68
15	34	28			120	24.00 ± 4.34
16	34	28			88	22.00 ± 6.98
17	24	10			50	16.67 ± 4.06
18	20	0			20	10.00 ± 10.00
19	0				0	0.00 ± 0.00
Total	1332	1762	960	1224	14 316	1193.00 ± 88.41

APPENDIX B: ANOVA TABLES FOR CHAPTER IV

Analysis of Variance

Number of eggs laid

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	35.187	3	11.729	1.020	0.386
HAT	30.008	1	30.008	2.610	0.109
DAY	0.653	1	0.653	0.057	0.812
HRE	4.526	1	4.526	0.394	0.532
2-way interactions	2.734	3	0.911	0.079	0.971
HAT DAY	2.331	1	2.331	0.203	0.653
HAT HRE	0.399	1	0.399	0.035	0.852
DAY HRE	0.004	1	0.004	0.000	0.985
3-way interactions	8.035	1	8.035	0.699	0.405
HAT DAY HRE	8.035	1	8.035	0.699	0.405
Explained	45.956	7	6.565	0.571	0.778
Residual	1333.487	116	11.496		
Total	1379.444	123	11.215		

Analysis of Variance

Number of hosts attacked

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	57.462	3	19.154	3.200	0.026
HAT	55.556	1	55.556	9.383	0.003
DAY	0.395	1	0.395	0.066	0.798
HRE	1.510	1	1.510	0.252	0.616
2-way interactions	1.450	3	0.483	0.081	0.970
HAT DAY	0.073	1	0.073	0.012	0.913
HAT HRE	0.756	1	0.756	0.126	0.723
DAY HRE	0.622	1	0.622	0.104	0.748
3-way interactions	2.307	1	2.307	0.385	0.536
HAT DAY HRE	2.307	1	2.307	0.385	0.536
Explained	61.219	7	8.746	1.461	0.188
Residual	694.225	116	5.985		
Total	755.444	123	6.142		

Analysis of Variance

Total mummies produced

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	138.523	3	46.174	9.722	0.000
HAT	132.129	1	132.192	27.819	0.000
DAY	6.323	1	6.323	1.331	0.251
HRE	0.071	1	0.071	0.015	0.903
2-way interactions	17.666	3	5.889	1.240	0.299
HAT DAY	3.226	1	3.226	0.679	0.412
HAT HRE	2.100	1	2.100	0.442	0.507
DAY HRE	12.340	1	12.340	2.598	0.110
3-way interactions	0.603	1	0.603	0.127	0.722
HAT DAY HRE	0.603	1	0.603	0.127	0.722
Explained	156.792	7	22.399	4.716	0.000
Residual	550.950	116	4.750		
Total	707.742	123	5.754		

Analysis of Variance

Proportion of parasites emerged

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	16.683	3	5.561	7.852	0.000
HAT	14.944	1	14.944	21.118	0.000
DAY	1.371	1	1.371	1.938	0.167
HRE	0.368	1	0.368	0.520	0.472
2-way interactions	6.450	3	2.150	3.038	0.032
HAT DAY	1.396	1	1.396	1.972	0.163
HAT HRE	2.801	1	2.801	3.958	0.049
DAY HRE	2.253	1	2.253	3.184	0.077
3-way interactions	0.200	1	0.200	0.283	0.596
HAT DAY HRE	0.200	1	0.200	0.283	0.596
Explained	23.333	7	3.333	4.710	0.000
Residual	82.084	116	0.708		
Total	105.417	123	0.857		

Analysis of Variance

Sex ratio (of progeny from all parasites)

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	1.759	3	0.586	0.469	0.705
HAT	1.364	1	1.364	1.090	0.299
DAY	0.303	1	0.303	0.243	0.623
HRE	0.092	1	0.092	0.073	0.787
2-way interactions	1.769	3	0.590	0.471	0.703
HAT DAY	0.752	1	0.752	0.601	0.440
HAT HRE	0.873	1	0.873	0.698	0.405
DAY HRE	0.144	1	0.144	0.115	0.735
3-way interactions	0.021	1	0.021	0.017	0.897
HAT DAY HRE	0.021	1	0.021	0.017	0.897
Explained	3.549	7	0.507	0.405	0.897
Residual	145.150	116	1.251		
Total	148.699	123	1.209		

Analysis of Variance

Sex ratio (of progeny from "fertilized" parasites only)

by: Host species attacked (HAT)
Day of experiment (DAY)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	2.837	3	0.946	0.922	0.435
HAT	2.076	1	2.076	2.024	0.159
DAY	0.448	1	0.448	0.437	0.511
HRE	0.313	1	0.313	0.305	0.582
2-way interactions	2.911	3	0.970	0.946	0.423
HAT DAY	1.177	1	1.177	1.148	0.288
HAT HRE	1.566	1	1.566	1.527	0.221
DAY HRE	0.168	1	0.168	0.164	0.687
3-way interactions	0.062	1	0.062	0.061	0.806
HAT DAY HRE	0.062	1	0.062	0.061	0.806
Explained	5.810	7	0.830	0.809	0.582
Residual	73.836	72	1.026		
Total	79.646	79	1.008		

Analysis of Variance

Weight of male progeny (mg)

by: Host species attacked (HAT)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	0.001	2	0.001	1.742	0.182
HAT	0.001	1	0.001	2.899	0.093
HRE	0.000	1	0.000	0.585	0.447
2-way interactions	0.001	1	0.001	2.255	0.137
HAT HRE	0.001	1	0.001	2.255	0.137
Explained	0.002	3	0.001	1.913	0.135
Residual	0.028	76	0.000		
Total	0.031	79	0.000		

Analysis of Variance

Weight female progeny (mg)

by: Host species attacked (HAT)
Host species from which the parasite was reared (HRE)

Source of variation	Sum of squares	df	Mean square	*F*	Signif of *F*
Main effects	0.014	2	0.007	13.992	0.000
HAT	0.013	1	0.013	27.271	0.000
HRE	0.000	1	0.000	0.713	0.401
2-way interactions	0.001	1	0.001	2.224	0.140
HAT HRE	0.001	1	0.001	2.224	0.140
Explained	0.015	3	0.005	10.069	0.000
Residual	0.037	76	0.000		
Total	0.051	79	0.001		

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