EFFECTS OF STARVATION ON DEVELOPMENT AND REPRODUCTION OF THE PEA APHID, *ACYRTHOSIPHON PISUM*: INFLUENCE ON HOST SELECTION AND FITNESS OF THE PARASITOID WASP *EPHEDRUS CALIFORNICUS*.

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EFFECTS OF STARVATION ON DEVELOPMENT AND REPRODUCTION OF THE PEA APHID,

ACYRTHOSIPHON PISUM: INFLUENCE ON HOST SELECTION AND FITNESS OF THE

PARASITOID WASP EPHEDRUS CALIFORNICUS.

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ABSTRACT

The effects of food availability on growth, development and reproduction of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), and the effects of aphid size on oviposition preference, development time and size of the aphid parasite, *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae), were investigated in the laboratory. When pea aphids were allowed to feed intermittently on bean plants, their rate of growth and adult size were reduced, they started reproducing later and they produced fewer offspring than fully fed aphids; and mortality was higher among starved aphids than non-starved aphids. These effects increased with the length of daily starvation.

In choice tests, *E. californicus* attacked and parasitized more small, starved than large hosts, irrespective of the age of the host. Among aphids of equal size, starved individuals were attacked more frequently than fed aphids, but each size class was equally accepted for oviposition. When aphids were anesthetized with CO_2, wasps showed no clear preferences in the rates of attacks, but small hosts were preferred for oviposition over large ones. These findings indicate that preference in *E. californicus* depends on aphid size and defensive behaviour.

E. californicus eggs developed in all three groups of aphids. The developmental times, recorded by video camera, were shorter for parasites from small hosts than for those from large

hosts; parasite size was correlated with host size.

RESUMÉ

Les effets de la disponibilité de nourriture sur la croissance, le développement et la reproduction du puceron du pois, *Acyrthosiphon pisum* (Harris) (Homoptère: Aphididae), ainsi que les effets de la grosseur du puceron sur le choix du parasite *Ephedrus californicus* Baker (Hymenoptère: Aphidiidae), pour l'oviposition, la longueur du temps de développement et la grosseur, ont été examinés au laboratoire. Lorsque le puceron était privé de nourriture pendant un certain temps par jour, sa croissance et sa grosseur au stade adulte étaient réduites. De même, sa reproduction était retardée, sa fécundité réduite et sa mortalité accrue. Ces effets étaient plus accentués avec la longueur du temps de privation.

Dans des expériences de selection, les pucerons qui étaient privés de nourriture, de petite taille, étaient attaqués d'emblée et plus parasités que les larges hôtes, quel que soit l'âge du puceron. Avec des pucerons d'égale grosseur, les individus privés de nourriture étaient plus attaqués mais tous les groupes étaient parasités avec la même intensité. Lorsque les pucerons étaient anesthesiés par le CO_2, il n'y avait pas de préférence nette en ce qui concerne les attaques, mais les petits hôtes étaient les plus parasités. Ces resultats indiquent que le choix du hôte chez *E. californicus* dépend de la grosseur et du comportement de l'hôte.

Les oeufs de *E. californicus* deposés dans les trois groupes de puceron se sont bien developpés. Le temps de développement était plus court pour les parasites dans les petits pucerons que celui des parasites dans les gros hôtes; cepandant, les parasites sortis des gros pucerons étaient les plus gros et les plus lourds.

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CHAPTER I

GENERAL INTRODUCTION

The effectiveness of a parasite in controlling its host depends on several factors, including the biological characteristics of the host and the parasite and the interactions between them (Mackauer and van den Bosch, 1973; Doutt *et al*, 1976). For example, the rates of growth and reproduction of a pest may constitute important information for planning and executing an effective control program.

In the field, seasonal variations may induce drastic changes in the development of plants. Thus, variation in quality and quantity of food is expected for phytophagous insects. Also, in species of aphids, several developmental stages (instars) may be available simultaneously, owing to the presence of overlapping populations (Dixon, 1985a). As a result, several aphid size groups will be present at any given time and may cause crowding; crowding can cause serious food shortages which may affect aphid life history characteristics (Murdie, 1969a,b; Sutherland, 1969).

When several potential host types are available, a parasite usually shows a preference for one type over others. This preference may be based on several factors, including host size and behaviour. Studies have shown that rates of development of immature parasites depend on attributes of the host at the beginning of parasitization. However, most of these investigations have focused on the host's stage of development rather than on host size as such.

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), is a common pest of legumes, especially alfalfa, *Medicago sativa* L., and peas, *Pisum sativum* L.. The insect colonizes leaves, stems, and flower buds (Dunn and Wright, 1955; Pollard, 1973). While probing plant tissues, the aphid secretes saliva containing substances which modify the structure of plant tissues, usually to the benefit of the aphids (Way and Cammell, 1970; Dixon and Wratten, 1971). The pea aphid overwinters in the egg stage on leaves and stems of alfalfa and clover. The surviving eggs hatch in March-April, giving rise to a parthenogenetic generation of fundatrices which, in turn, give birth to parthenogenetic viviparous females. These latter can be wingless (apterae) or winged (alatae). Apterous forms are predominant during the summer months and under most laboratory conditions. From birth to the adult stage, the pea aphid completes four nymphal instars (R.E. Campbell 1926; A. Campbell, 1974).

Ephedrus californicus Baker is a solitary hymenopteran endoparasite belonging to the family Aphidiidae. Stary (1970) has reviewed in detail the biology of this family. The Aphidiidae are parasites of aphids (Homoptera: Aphididae); some introduced species are examples of successful biological control agents. In North America, *E. californicus* has a wide range of hosts, including the pea aphid (Smith, 1944; Cohen, 1985).

The life cycle begins with the female ovipositing in the host. Generally, *E. californicus* takes a relatively long time of 6 sec or more for a successful attack (Chow and Mackauer, 1986). The eggs hatch and the parasite larvae start to feed selectively on non-vital host tissues. The fourth and final instar consumes the remainder of the internal tissues and kills the host. The parasite spins a cocoon inside the dead host and pupates; the dead host is called a mummy. From the mummy, a single adult parasite emerges. The life cycle of *E. californicus*, from oviposition to emergence, takes approximately 13 days at 20°C under laboratory conditions (Cohen, 1985). Although this parasite is not common in pea aphids in the field, the system pea aphid-*E. californicus* has been extensively used in laboratory studies to investigate some aspects of host-parasite interactions.

In this study, I used the pea aphid and its parasite *E. californicus* to examine the following questions:

1. How, and to what extent, does intermittent feeding affect the growth, development and reproduction of the pea aphid ?
2. Are oviposition preference and developmental time of *E. californicus* influenced by variations in aphid size resulting from starvation ?

CHAPTER II

EFFECTS OF STARVATION ON GROWTH, DEVELOPMENT AND REPRODUCTION OF THE PEA APHID

INTRODUCTION

The effects of starvation on the life table characteristics of insects have received considerable attention in recent years, especially with regard to growth, development and reproductive biology. For example, Thomas (1989) showed that when larvae of the spruce budworm, *Choristoneura fumiferana*, fed on low-quality host plants, they consumed 40% less food than on high-quality plants. As a consequence, their relative growth rate was reduced by about 53% and the mean developmental time was increased by 26%. The author concluded that those effects resulted from the larvae's inability to increase the efficiency of their food utilization in order to compensate for the reduced food consumption.

Direct relationships have been shown in a number of insects between the rate of food intake and daily growth, as measured by weight gain, and between the rate of food intake and the developmental time. Examples are found in the grasshopper, *Poecilocerus pictus* (Muthukrishnan and Delvi, 1974), in the lepidopterans *Pseudaletia unipuncta* (Mukerji and Guppy, 1970) *Danaus chrysippus* (Mathavan and Muthukrishnan, 1976), *Calocalpe* *undulata* (Schroeder, 1976); and in the milkweed bug *Oncopeltus fasciatus* (Slansky, 1980). Starved insects may also show a loss from their initial fresh weight (Slansky, 1980) and generally heavy mortality as well as a delay in the onset of reproduction.

A low growth rate caused by starvation can be coupled with small size and low weight in adults. In time, these effects can cause a reduction in the number of progeny, resulting from an arrest of embryogenesis (Bell and Bohm, 1975; Clements and Boocock, 1984) or a delay in the maturation of the reproductive system.

In aphid species, effects of starvation have been described for the black bean aphid, *Aphis fabae* (Dixon *et al.*, 1982; Hardie, 1985), the rose-grain aphid, *Metopolophium dirhodum* (Grüber and Dixon, 1988), and the vetch aphid, *Megoura viciae* (Ward and Dixon, 1982; Ward *et al.*, 1983; Walters *et al.*, 1988; Brough and Dixon, 1989, 1990). Only limited information is available concerning the effects of starvation in the pea aphid, *Acyrthosiphon pisum*. McClean and Kinsey (1967) observed that individuals reared on non-host-plants, such as lettuce and cowpea, were unable to survive for longer than five days and they produced fewer offspring than did those of comparable age reared on broad bean. Investigating the causes and effects of size variation in this aphid, Murdie (1969a) showed that starvation decreased antennal length.

My objective was to investigate the effects on the pea aphid, of the limitation of feeding on its growth, developmental time, and reproduction. The results will be discussed in terms of food utilization and resource allocation.

MATERIALS AND METHODS

Aphid colonies

Colonies of pea aphids were maintained in the laboratory on potted broad bean plants, *Vicia faba*, seeded in garden mix soil. To obtain a synchronous colony of aphids, I transferred reproducing adults to fresh bean plants for 15 to 17 h. After this period, all adults were removed from the plants with a camel hair brush. The newly born nymphs were reared in a controlled environment chamber at 21±1°C, 65±5% RH and under continuous light.

Experiments

Aphids of 24±2.5h old were obtained by keeping reproducing adults on bean plants for 5 h. Newly-born nymphs with wet weights averaging 0.1136±0.0157 mg (mean±SE, n = 50) were divided into three groups, as follows:

Group 1: aphids permitted to feed continuously on bean plants (CF);

Group 2: aphids starved for 4h/day (4H);

Group 3: aphids starved for 6h/day (6H);
A 4th group, starved for 8h/day (8H), was also used in some experiments.

Aphid growth

Aphids of groups 1, 2, and 3 were kept in plastic cages (15.5 diam x 4 cm high) containing the growing tip of a bean plant kept in tap water. Starvation was imposed by removing young aphids from the plants with a camel-hair brush and keeping them in 4 cm diam petri dishes in the controlled environment chamber. After the end of the predetermined starvation times, the aphids were returned to fresh bean plants. Daily, one cage in each group was removed; the aphids in these cages were anesthetized with CO_2 and weighed to determine their wet weights with a Mettler UM3 microbalance; they were then dried at 100°C in a PS Thelco drier for 48h to determine their dry weights. These procedures were continued until the aphids were 20 days old. For each treatment, the aphids' mean relative growth rates before and after the onset of reproduction were calculated on a wet weight basis according to the following equation (Fisher, 1921)

$$MRGR = (\ln WW_2 - \ln WW_1)/(t_2 - t_1)$$

where MRGR is the mean relative growth rate (in mg/mg/day) and WW_1 and WW_2 are the wet weight (in mg) at times t_1 and t_2 (in days), respectively.

Aphid development and reproduction

Aphids, aged 24 h (±2.5), were divided into four starvation groups and placed singly in small, numbered clip cages (Noble, 1958). The clip cages were attached to the lower surfaces of bean leaves, one cage per leaf, and maintained in the controlled environment chamber. During their daily starvation treatments, the aphids were kept singly in numbered gelatine capsules (size 00). All the cages were examined at the same time daily (between 10 a.m. and 12 noon) before starvation, always starting with the continuously feeding group. All offspring produced were counted and removed from the cage. The numbers of cast skins were recorded to determine the duration of developmental time. At day 15, the length of the aphid's body from head to cauda and of the hind tibia were measured by means of a stereomicroscope equipped with a micrometer. The aphids were then dried for 48 h and weighed. Demographic characteristics, such as prereproductive period (PRP), survival rate (lx), and average daily fecundity (mx) were determined, and life tables were constructed for the four groups of aphids.

The data were statistically analysed on the SFU main frame computer using the BioMedical Data Process (BMDP), the SAS or the SPSS-X Statistical Softwares.

RESULTS

Aphid growth:

The effect of starvation on the growth of pea aphids was assessed by the fitting of growth curves to the cumulative wet weights separately for each group of aphids i.e. 0h, 4h, and 6h starvation. A derivative-free nonlinear regression (least square method) was used to fit a curve to the observed data. In all three groups, the cumulative wet weight increased as an exponential function of age and could be predicted from the equation of the general form:

$$\hat{y} = a/(1 + \exp(b - cx))$$

where $\hat{y}$ is the predicted aphid weight at age x, and a, b, and c are fitted parameters: a represents the upper asymptote; b the height of the curve from the *x*-axis, and c the rate of growth. For the continuous feeding group the equation was:

$$\hat{y} = 3.377/(1 + \exp(3.900 - 0.773x))$$

(regression MS=1390.43, $F(3,574)=16.36$, $P \leq 0.001$). Values of a, b, and c for each treatment are shown in Table 2.1.

Pea aphids fed continuously on potted broad bean plants steadily increased in wet weight from birth to day 7 (Fig.1) with a mean relative growth rate of 0.467±.033 mg/mg/day (Table 2.1). After this period, daily wet weight gain decreased and the growth curve reached a maximum, with wet weight remaining relatively constant around 3.44±0.090 mg (mean±SE, n = 15). Starved aphids (4H and 6H) showed a growth pattern similar to unstarved aphids (Fig. 1), but their final adult weights were significantly lower than that of unstarved aphids (Oneway ANOVA, F=64.53, df=2,40; P≤0.001; SNK, P≤0.05). Also, starved aphids (4H and 6H) required longer than CF-aphids for their wet weights to approach a maximum (Fig.1). With 4h-starvation, the decrease in wet weight gain was observed on day 8, and the maximun was reached on day 10 with a mean wet weight of 2.380±0.074mg (mean±SE, n = 14) which was significantly less than that of normally fed individuals of the same age (Twosample T-test, t=41.33, df=18.0, P≤0.001). With 6h-starvation, the preplateau period was 11 days and the mean wet weight at the plateau was 2.100±0.099mg (mean±SE, n = 14) which also was significantly lower than that of the 4h-starved aphids of the same age (Twosample T-test, t=6.54, df=17.2, P≤0.001). In aphids fed continuously, the dry weight:wet weight ratio was slightly lower (mean±SE = 0.210±0.001, n = 577) than in starved aphids (4h: 0.220±0.027 n=418; 6h: 0.218±0.029 n=456)(Oneway ANOVA df=2,1448 F=17.02 P≤0.001). However, the ratio did not show any obvious trend, correlated with aphid age.

The lower weights were associated with lower mean relative growth rates in the starved aphids. The MRGRs during the prereproductive period of 4h- and 6h-starved aphids were 0.301±.034mg/mg/day and 0.192±.005mg/mg/day respectively (Table 2.1), statistically different from that of non-starved aphids. However, MRGRs after the onset of reproduction did not significantly differ between the three treatments (Oneway ANOVA, df=2,67 F=0.352 P=0.075).

Aphid developmental time (time-to-adult)

Starvation had a marked effect on the aphids' developmental time. Starved aphids had their 4th moult after a significantly longer growth period than that of normally fed aphids (Oneway ANOVA, df=1,161 MS=8.39 F=26.17 P≤0.001). In aphids fed continuously, 81.25% reached the adult stage in 6.5 days (pivotal age), and 18.75% became adults one day later, whereas in 4h-hour starved aphids, only 63.64% of individuals became adults at age 6.5 days, 31.18% at 7.5 days and the last 4.55% at 8.5 days. In the group starved for 6h, these percentages were 52.94, 41.18, and 5.88 respectively. In the 8h-starvation experiments, the moult from the 4th instar to the adult stage occurred mainly at age 8.5 days (73.68%) and 9.5 days (23.68%), which were 2 and 3 days later than the unstarved aphids.

Body and tibia lengths

In 15-day-old starved aphids, the body and hind tibia (Table 2.2) were significantly shorter than those of unstarved aphids (body length: Oneway ANOVA, df=3,140 F=251.20 P ≤ 0.001; SNK, P ≤ 0.05; hind tibia: Oneway ANOVA, df=3,140 F=91.79 P ≤ 0.001; SNK, P ≤ 0.05). In starved aphids, the lengths of the body and hind tibiae decreased with increasing starvation time. In 4h-starved aphids, these measurements were 3.98±0.05mm and 2.83±0.02mm respectively, which were significantly longer than those of 6h-starved aphids (3.61±0.07mm and 2.69±0.03mm) which again, were longer than those of 8h-starved aphids (2.87±0.06mm and 2.48±0.02mm) (SNK multiple range test, $P \leq 0.05$).

Reproduction

The duration of the prereproductive period and fecundity depended on starvation time (Table 2.2). Increased starvation time lengthened the prereproductive period: 89.36% of aphids allowed to feed normally on bean plants began to produce offspring by the pivotal age of 6.5 days. On day 7.5, all aphids of this group were reproducing, and the average daily fecundity in nymphs/female/day, increased to reach a maximum of 12.36 ($n = 47$). Thereafter, it remained nearly constant until day 11.5, then steadily declined (Fig. 2). In starved aphids, reproduction was significantly delayed compared with that of the controls. The delay, as represented by the prereproductive period, was correlated with the length of daily starvation and could be described by a linear regression equation of the form:

$$\hat{y} = 5.96 + 0.647x$$

($r^2=0.609$, regression: df=1,143, MS=105.37, F=222.26) where $\hat{y}$ is the predicted prereproductive period and x is the duration of daily starvation. The prereproductive periods were: 7.35±0.36 days for the 4h-starved group, 7.50±0.37 days for the 6h-starved, and 8.81±0.99 days for the 8h-starved group (Table 2.2). The total numbers of offspring produced showed a negative correlation with the duration of daily starvation.

Table 2.1. Characteristics of the growth curves of *A. pisum* undergoing two starvation treatments, and a control.

Daily starv. (h)	a* (mg)	b* (mg)	c* (mg)	DF	MS	P	n	MRGR(1)† (mg/mg/day)	MRGR(2)† (mg/mg/day)
0	3.377	3.900	0.773	3,574	1390	≤.001	577	0.467±0.033	0.054±0.037
4	2.331	3.906	0.577	3,415	366.76	≤.001	418	0.301±0.034	0.055±0.006
6	2.318	5.221	0.864	3,453	486.48	≤.001	456	0.192±0.005	0.028±0.004

* a = upper asymptote of weight curve;

* b = height of the curve from the x-axis;

* c = rate of growth;

† MRGR = Mean relative growth rate: (1) before, and (2) after the onset of reproduction.

Table 2.2. Development and reproduction of *A. pisum* undergoing three starvation treatments, and a control.

Daily starva- tion (h)	No. cast skins	Body length (mm)	Hind tibia length (mm)	Pre reprod. period (days)	Mean fecundity (to 15 days)	Aver. daily fecund.	Wet weight* (mg)	Dry weight (mg)	Develop mental time (Days)	Survival rate (to 15 days)
0 (n=47)	4.21±.06	4.73±.02	2.99±.01	6.60±.31	91.89±1.7	11.97	3.44±.09	.727±.01	5.68±.39	.94
4 (n=41)	4.20±.03	3.98±.05	2.83±.02	7.35±.36	68.56±1.40	8.50	2.38±.07	.421±.02	5.92±.65	.82
6 (n=30)	4.07±.07	3.61±.07	2.69±.03	7.50±.37	52.63±1.50	6.60	2.10±.09	.311±.02	6.00±.62	.63
8 (n=26)	3.88±.48	2.87±.06	2.48±.02	8.81±.99	28.54±1.52	4.06	--	.160±.05	6.74±.59	.51

* Means are based on sample sizes of n=15 (CF), n=14 (4H) and n=14 (6H).

Figure 1. Daily changes in the wet weight of pea aphids caged singly on broad bean leaves in a climate chamber, under two regimes of daily starvation periods, plus control, at 21±1°C and constant light (Δ = CF; o = 4H; □ = 6H).

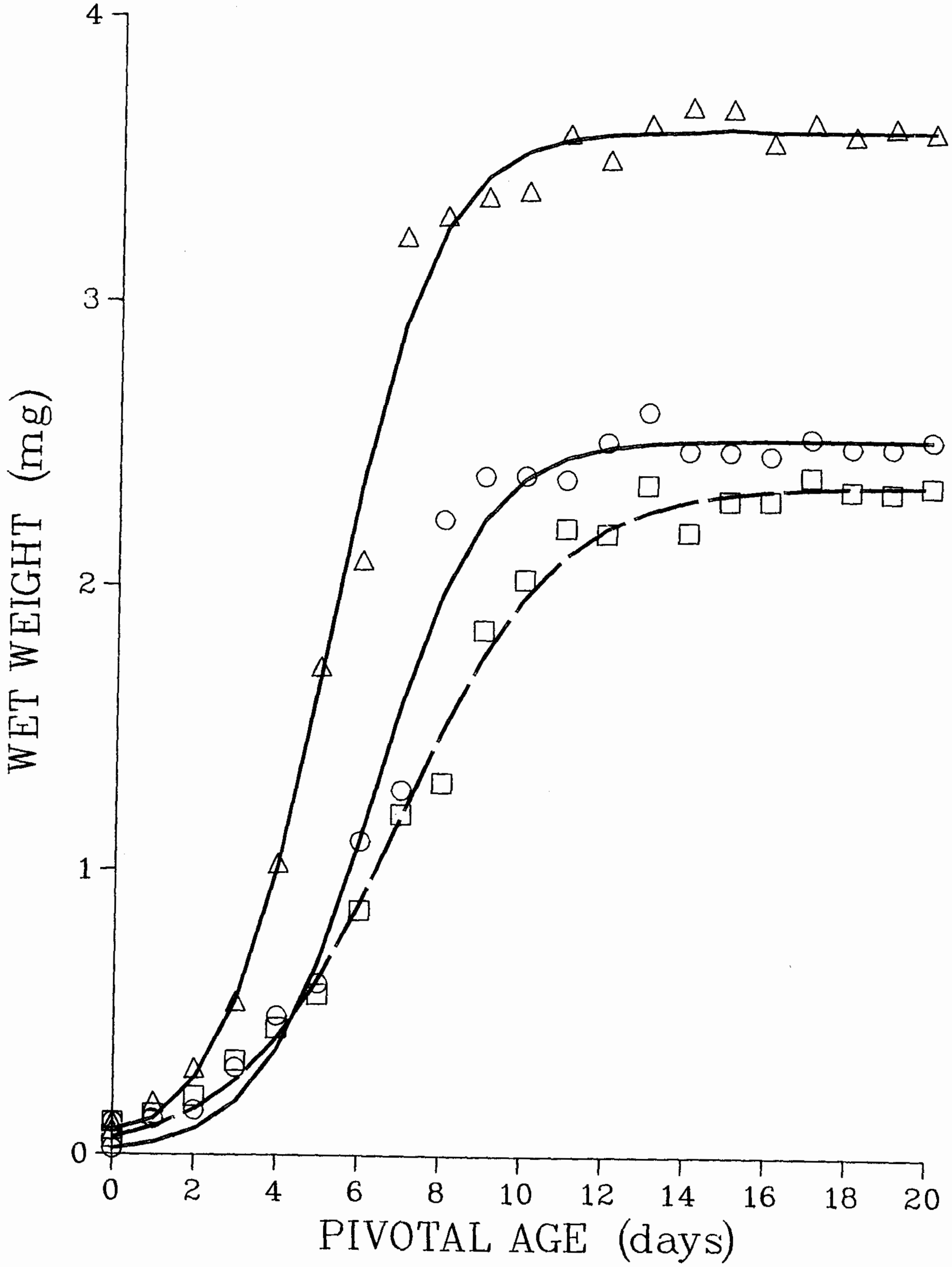

WET WEIGHT (mg)
4
3
2
1
0
0
2
4
6
8
10
12
14
16
18
20
PIVOTAL AGE (days)

Figure 2. Changes in average daily fecundity (mx) of pea aphids caged singly on broad bean leaves in a climate chamber, under three regimes of daily starvation periods, plus control, at 21± 1°C and constant light (Δ = CF; o = 4H; □ = 6H; ●= 8H); Error bars are the SEM.

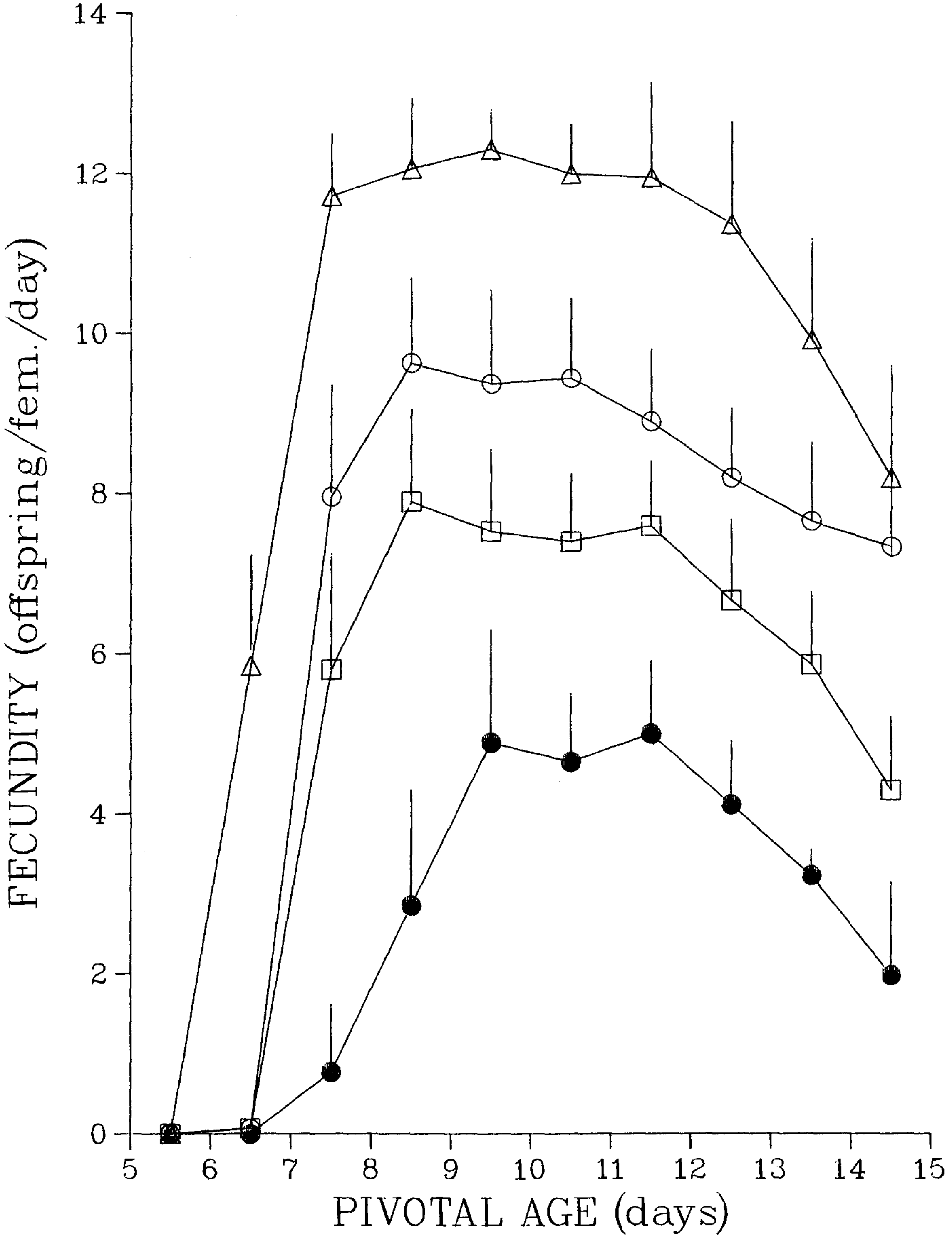
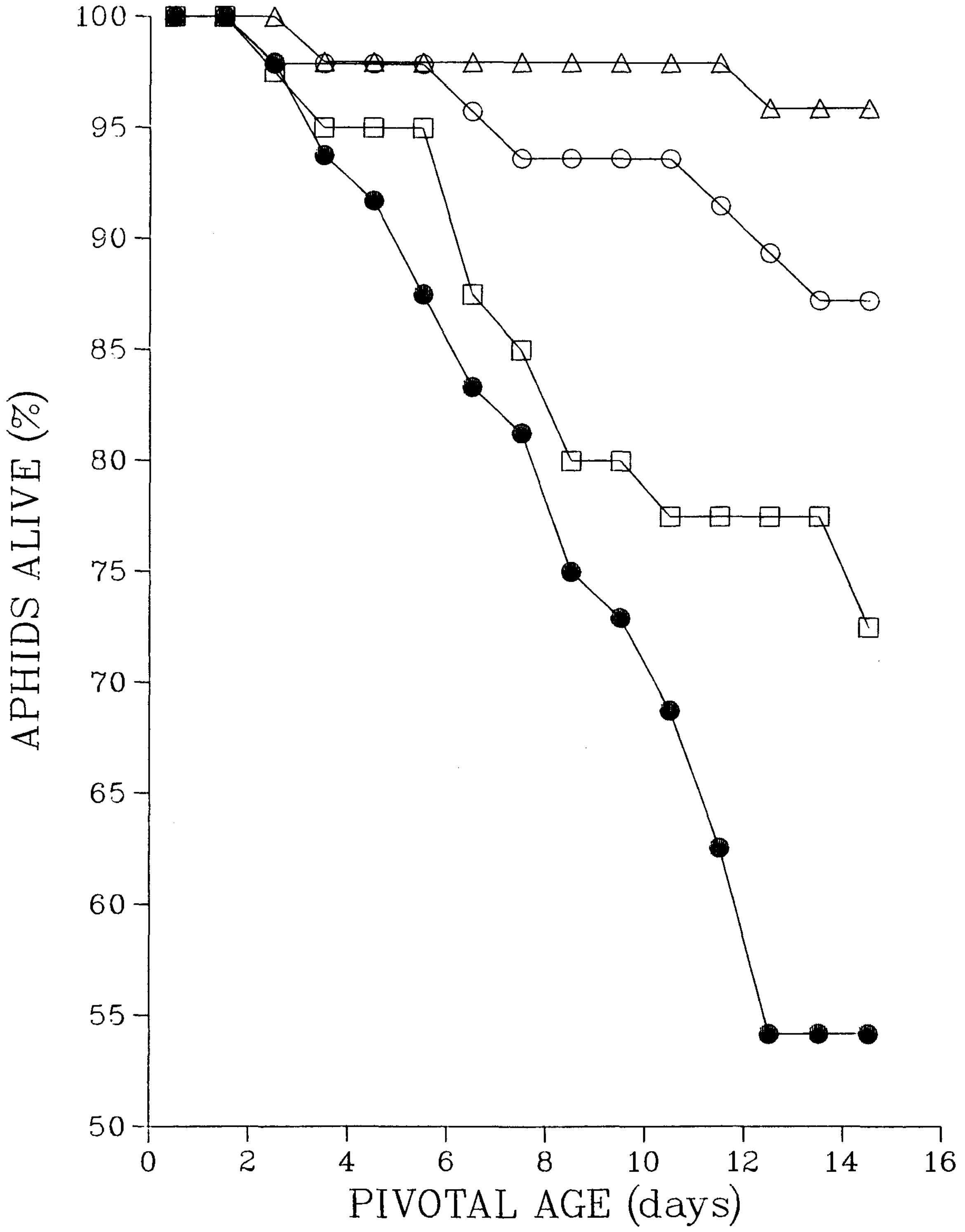

FECUNDITY (offspring/fem./day)
PIVOTAL AGE (days)
0
2
4
6
8
10
12
14
5
6
7
8
9
10
11
12
13
14
15

Figure 3. Survival rates of pea aphids caged singly on broad bean leaves in a climate chamber, under three regimes of daily starvation periods, plus control, at 21± 1°C and constant light (Δ = CF, o = 4H; □ = 6H; ● = 8H).



APHIDS ALIVE (%)
100
95
90
85
80
75
70
65
60
55
50
PIVOTAL AGE (days)
0
2
4
6
8
10
12
14
16

A linear regression equation was satisfactorily fitted to the data. The form of the equation was:

$$\hat{y} = 114 - 21.2x$$

($r^2=0.855$; regression: df=1,142; F=840.73) where $\hat{y}$ is the predicted number of offspring produced and x the duration of daily starvation. A curvilinear regression fitted to the data showed that the number of offspring produced by an aphid was correlated with adult dry weight. The regression equation was

$$\text{Number(Offsp)} = .0076(\text{Adult DW})$$

($r^2=0.947$; df=1,142 MS=439.89, F=137.59 $P\leq0.001$), where dw stands for dry weight in mg.

Mortality

During the 15 days of the experiment, mortality was much higher in starved (≥ 18%) than in the non-starved (6%) aphids. At 4h-starvation, mortality was 18% as compared with 40% at 6h. The 8h-starvation caused the highest mortality rate of 48% (Fig.3).

DISCUSSION

For insects which feed almost continuously, any restriction of feeding time can result in adverse effects (Murdie, 1969a; Schroeder, 1976; Mathavan and Muthukrishnan, 1976; Slansky, 1980; Brough and Dixon, 1990). In the pea aphid, a limit on the feeding time lengthened the time for reaching maturity and produced adults which were small. Nymphs starved every day grew much more slowly than those allowed to feed continuously. Starvation delayed the onset of reproduction, decreased eventual fecundity and shortened lifetimes. Like quality, the importance of quantity of food in relation to negative effects on aphids has been pointed out by several workers (Murdie, 1969ab; Dixon and Dharma, 1980; Dixon *et al.*, 1982; Brough and Dixon, 1990). Investigating the causes of size variation in the pea aphid, Murdie (1969a) found that starvation reduced similarly the growth of the antennae in all four instars, and suggested that a kind of growth inhibition might operate from an early stage of development; but neither the mechanism of inhibition, nor the levels at which it may occur, have been determined. The small size of starved aphids is the consequence of their slow growth resulting from the low quantity of food ingested and utilized. This slow growth may account for the longer than normal time to reach final adult size, which I have shown to be reduced.

The food ingested by an aphid is the source of energy for growth, development and maintenance of metabolic activities necessary for survival. The amount of energy required for each activity and its distribution may be genetically programmed. When aphids are starved for a certain period every day, they ingest proportionately less food than if they were kept on a plant. They appear to be unable to increase their rate of intake. Thus, their food will give proportionately less energy, which normally is used for maintenance, growth and development. A high growth rate is achieved only when aphids are under conditions which enable them to ingest large quantities of food to gain enough energy to satisfy the maintenance cost. In the starved insects, this cost is increased by high respiration losses resulting from increased activity for food seeking, and by a reduced growth rate (Schroeder, 1976). Confronted with decreasing resource input and increasing energy demand, the insect appears to allocate its resources to survival. In effect, when resources become scarce, the pea aphid allocates the available energy primarily to survival. The higher growth rate of the 4h-starved aphids compared with that of the 6h-starved aphids indicates that in the latter group the energy left over for growth and development was much lower. A similar imbalance in the energy requirements for basic metabolism and growth was proposed to account for the slow growth of the black bean aphid (Müller, 1966). Müller explained that, at high temperatures, catabolism consumes most of the available energy and little is left for anabolism in which the building of somatic tissues occurs. Considering the low level of energy available in starved individuals, it appears that the pea aphid does not have the ability to store nutrients or to compensate for the energy loss during the periods of starvation by increasing its feeding rate. By contrast, Mathavan and Muthukrishnan (1976) found that the monarch butterfly, *Danaus chrisyppus*, compensated by increased feeding rates for any reduced food intake during earlier periods.

Efficiency in utilization of food ingested by an insect is also essential for its growth rate (Waldbauer, 1968). Although limited information is available concerning the effects of starvation on food consumption and assimilation, and conversion efficiencies in aphids, much is known in other insect groups: starvation can increase or reduce these indices. For example, the cutworm, *Prodenia eridania*, compensates for a diminishing intake of food by increased assimilation (Soo Hoo and Fraenkel, 1966) whereas in the grasshopper, *Poecilocerus pictus*, the compensation is partly by increasing conversion efficiency rather than by assimilation (Muthukrishnan and Delvi, 1974). Long periods of food deprivation during larval development of the cherry scallop moth, *Calocalpe undulata*, reduce the efficiency of conversion of matter, energy and nitrogen to larval tissue (Schroeder, 1976). In the light of work on other aphid species, it is likely that starvation might modify food utilization indices in the pea aphid. However, the mechanisms of these modifications and their nature and importance are not known. Whatever the mechanisms are, the results of my experiments suggest that food limitation was not compensated for or, if it occurred, was not sufficient.

Starvation is known to have marked effects on both the development and the reproductive potential of insects (Lea *et al.*, 1978; Tadkowski and Jones, 1979; Slansky, 1980; Khan *et al.*, 1982; Ward and Dixon, 1982; Leather *et al.*, 1983; Hardie, 1985). When pea aphid nymphs were starved for 4h/day or longer, they became adults after a significantly longer period than when they were allowed to feed normally. Similar effects of nutrient stress on other aphid species have been reported recently for *Metopolophium dirhodum* starved from the onset of the fourth instar (Grüber and Dixon, 1988), for *Megoura viciae* (Brough and Dixon, 1989, 1990). The fact that pea aphids reach maturity even when intermittently starved throughout nymphal development indicates that, in this species, growth and development proceed relatively independently. However, the delay observed in starved nymphs in reaching the adult stage might be accompanied by a delay in the development and maturation of the reproductive system, e.g., oviduct and gonads. In *M. viciae* under starvation, a decrease in size of the soma was coupled with an arrest in the growth of the gonads. This resulted in a decrease of the number of mature embryos and offspring produced (Brough and Dixon, 1990). Conversely, embryos of *M. dirhodum* starved from the onset of the 4th instar and those of unstarved individuals matured at the same time and produced similar numbers of offspring during the first three weeks (Grüber and Dixon, 1988). The difference was probably due to the timing of the different levels of starvation experienced by the two species: starvation in *M. dirhodum* was imposed only at the 4th instar; at this stage most of the systems, especially the reproductive system, are practically formed and the nymphs have accumulated resources for future development. Under normal conditions, aphid somatic and gonadal growth occur simultaneously, i.e. the gonads develop throughout larval life (Dixon, 1987). Therefore, it is unlikely that the gonads of pea aphids starved from birth and those of unstarved individuals, will mature at the same time.

The reproductive immaturity of starved aphids was shown by their long prereproductive period. This demonstrates that the development of gonads lags behind that of somatic tissues (Brough and Dixon, 1990) and that, under stress conditions, aphids allocate resources primarily to ensure maintenance at the expense of reproduction. The high mortality observed in the starved aphids can be explained by the fact that these individuals run out of reserves. Maintaining living costs at the expense of reproductive potential when resources are limited is a widespread phenomenon in insects. *M. viciae* resorb their smallest embryos and continue to mature their largest (Ward and Dixon, 1982), whereas in the majority of insect species it is the largest oocyte in an ovariole which is resorbed (Bell and Bohm, 1975; Trepte and Trepte-Feuerborn, 1980). This respnse is seen as a reproductive strategy (Tadkowski and Jones, 1979; Clements and Boocock, 1984) which enables stressed animals to adjust their activities to the available resources, because species with a high reproductive investment have poor resistance to starvation (Ward *et al.*, 1983).

Resorption of the smallest embryos has been shown to occur in pea aphids under stress by parasitism (Soldan and Stary, 1981). Delay in the maturation of gonads and probable resorption of embryos may partly explain why starved pea aphids had lower fecundity than unstarved ones.

CHAPTER III

PREFERENCES BY *EPHEDRUS CALIFORNICUS* FOR DIFFERENT SIZES OF ITS PEA APHID HOST

INTRODUCTION

Host preference has been defined as the behaviour of a parasite to distribute its eggs in a non-random and regular way over the available hosts (van Lenteren *et al.*, 1978). Preference is shown if the relative frequency of host types attacked or parasitized differs from the relative frequencies of the host types available. Parasite preference may strongly influence the relationship between host and parasite because it can affect the mortality rate and reproduction of the host (Hogg and Nordheim, 1983; Sequeira, 1987), and the feeding rate and thus, the damage done to the host plants (Brewer and King, 1978). All these factors may affect parasite fitness (Jones and Lewis, 1971; Miles and King, 1975; Beckage and Riddiford, 1978). Hence, a knowledge of this subject will contribute to an understanding of the population dynamics of host and parasite species.

In general, a female parasite may oviposit and successfully develop her offspring in several kinds of hosts, i.e. species, developmental stage, or size class; however, parasites will often show a preference for one or two kinds over others when given a choice among a wide range of potential hosts (van Alphen and Vet, 1986; van Dijken *et al.*, 1986; Hagley and Barber, 1986; van Driesche *et al.*, 1987; Fransen and van Montfort, 1987; Heinz and Parrella, 1989; Picket *et al.*, 1989.

The size of the host is an important component of selection by a parasite because host sizes may differ in their profitability to the parasite. In addition, encounter rates, handling time, success of attack, developmental time, and size of progeny may all vary with host size (de Jong and van Alphen, 1989; Martin *et al.*, 1989).

However, most of the authors who investigated host preference considered the age of the host to be the standard of choice. Those who dealt with host size considered the developmental stage. Thus, in spite of their pertinence, these approaches tend to be confusing because they do not distinguish between the size or instar or age of the host. As a consequence, it is not clear whether, for example, the preference for second and fourth instar pea aphids by *Praon pequodorum* (Sequeira and Mackauer, 1987) is due to physical attributes, i.e, the effect of size of the host, or also due to physiological causes making certain instars more suitable than others (Mackauer,1973).

In this chapter, I examine the effects of host size alone, apart from instar, on attack and oviposition decisions of *E. californicus* in the laboratory, using the pea aphid's weight as the measure of its size. Different hypotheses to explain the selection and its physical and physiological implications will be discussed.

MATERIALS AND METHODS

Aphid colonies

The conditions and methods of culture and maintenance of the pea aphid are described in chapter II above.

Parasite colonies

A culture of *E. californicus* was started by collecting from colonies of the lupine aphid, *Macrosiphon albifrons*, in West Vancouver, British Columbia, in 1983 (Cohen, 1985). The culture was maintained in the laboratory, on pea aphids. To produce new parasites, a cohort of 8 to 10 mated females was confined in wax paper cups with 80 to 100 third and early fourth instar aphids. After 8-9h, the parasites were removed, and the aphids were transferred to fresh bean plants in plexiglass rearing cages (33 x 34 x 44cm). The cages were kept in a controlled atmosphere chamber at 21±1°C, 75±5% RH and under continuous light, until the aphids became mummies. The parasites of the new generation emerging from the mummies were kept in a paper cup and fed with a 50% honey solution streaked across a petri dish lid. The stock colony of wasps was maintained at 10°C until parasites were needed.

Experiments

Two series of experiments, I and II, were designed to investigate the preference of *E. californicus* between aphids of three sizes, based on aphid wet weight at the time of the experiments. Observations reported in the previous chapter showed that, for a given age, aphids feeding continuously were bigger and heavier than aphids starved for 4h daily, which were bigger and heavier in turn than those starved for 6h daily. It was also shown that aphid body length was correlated with wet weight (regression equation $W = -0.722 + 0.297BL$; $r^2=0.856$; df=1,142; $P \leq 0.001$). Thus, wet weight could be used as an index of aphid size. Series I and II differed in the kind of arena used. Series I experiments were performed in plastic cages, 15.5 cm diam x 4 cm high, each containing a broad bean shoot placed in tap water (Mackauer and Bisdee, 1965). In series II, the experimental arena was a petri dish, 5.5 cm diam x 1 cm high. Prior to each experiment, the parasites intended for use were exposed during about 1 h to some aphids, to give them experience.

I considered that preference had been shown if, at the 95% confidence interval, the number of eggs laid or the number of hosts attacked in a particular group exceeded the number of eggs laid or the number of hosts attacked in a different group exposed simultanuously to the parasite.

Series I experiments

Three groups of apterous aphids on broad bean plants were obtained by the methods previously described: i.e. continuously feeding (CF); starved daily for 4 h (4H); or for 6h (6H). The aphids were exposed in a plastic cage to a single female parasite either in pairs (CF+4H, CF+6H, 4H+6H) or all three groups together (CF+4H+6H).

For the paired experiments, 44 aphids of 5 day-old (±2.5h), 22 of each group, were introduced in a plastic cage 5 to 6 h before the trial so that they could settle on the plant. A mature, mated female parasite was then released in the cage. To distinguish the aphids of the paired groups, each group was marked by clipping the terminal segment of one antenna following the method of Mackauer (1972). The parasite was removed after 6h. The exposed aphids were kept on the plant and were allowed to develop for a further 72h under the conditions described above. All the surviving aphids were then dissected in 70% alcohol under a stereomicroscope. The number of aphids parasitized and the number of eggs laid per aphid were recorded. The experiment was repeated 11 times or more, each replicate being performed with a different female parasite. The numbers of aphids parasitized in each host groups were summed to obtain two grand totals. Grand totals of the numbers of eggs laid in each group were also obtained.

In the experiment in which all host groups were used together, 15 aphids of 5 days-old(±2.5h) from each group were exposed to a single parasite under the same conditions and following the same procedures described in the paired experiments. The groups were distinguished by amputating the terminal segment of one antenna of 4h-starved and both antennae of 6h-starved aphids. Grand totals were made of the numbers of hosts parasitized and the numbers of eggs laid in each group for each cage.

Series II experiments

These experiments were performed in petri dishes. Three groups of experiments (IIA, IIB, IIC) were set up. In IIA and IIB, three pairs (CF+4H, CF+6H, and 4H+6H) were compared, whereas in IIC, only two pairs (CF+4H and CF+6H) were compared. Twenty aphids, 10 of each group, were introduced into one petri dish (5.5 cm diam). A 4-5-day-old experienced female *E. californicus* was then released in the dish to attack the aphids. The parasite was allowed to attack an aphid only once. An aphid was considered attacked if the parasite inserted her ovipositor into the host for 6 sec or longer (Chow and Mackauer, 1986). Each aphid attacked was removed from the arena and immediately replaced by another individual of the same size group in order to maintain an equal number of hosts of each group in the arena. The parasite remained confined with the hosts until she had attacked about 20 of them. All aphids attacked by one parasite were reared on a fresh bean stalk for 72 h in the controlled environment chamber and dissected under a stereomicroscope to record the number of eggs laid. Each paired experiment was replicated 11 times or more. Every replication was with a new, experienced parasite and with 10 new aphids in each group. The numbers of hosts attacked and eggs laid (= number of aphids parasitized) in each group were pooled to obtained two grand totals.

Experiment IIA: *Aphids of different size but same age*

This experiment was similar to the paired experiments in series I except that it was run in a petri dish and that the attacked hosts were replaced. All aphids were 5 days old (±2.5h).

Experiment IIB: *Aphids of the same size but different ages*

To evaluate the oviposition preference of *E. californicus* for hosts reared under different conditions, I used three groups of aphids in sets of pairs, all of about the same size, but 3 days old (CF) and 5 days old (4H and 6H); the average wet weight difference between individuals of the pairs of groups to be compared was 0.0423mg or less: 0.0423mg between CF and 4H, 0.0364mg between CF and 6H, and 0.0161mg between 4H and 6H.

Experiment IIC: *Anesthetized aphids*

Defensive behaviour in the host has often been invoked to explain why some parasites oviposit preferably in the younger and smaller hosts (Sequiera and Mackauer, 1987). To test this hypothesis with *E. californicus*, I designed the following experiment, in which two paired experiments (CF+4H and CF+6H) were made as described above: 20 experimental aphids, 10 of each group, all of the same age (5 days old ±2.5h), were anesthetized with CO_2 for 4 min before being placed in the petri dish. Individuals of the 2 groups were placed in alternating order with 9 mm between them.

Analysis of data

The data from the paired experiments were analyzed with a paired sample t-test and a oneway analysis of variance (ANOVA) using the total numbers of eggs laid and of hosts attacked in each group to indicate preference. From these numbers I calculated the indices of preference (Cock, 1978; Mackauer, 1983) based on the numbers of hosts parasitized or the numbers of hosts attacked, and the numbers of eggs laid, using the less starved group in each case as the standard.

Data from the experiments in which all three groups were presented together to the parasite were analyzed with a oneway ANOVA followed by a Student-Newman-Keuls (SNK) multiple range test in order to determine the degree of preference between groups, using the unstarved groups as the standard.

RESULTS

Series I experiments

The results showed that *E. californicus* had a distinct preference. When the female parasite was presented simultaneously with two different groups of hosts on plants, aphids from the groups that had been starved were most often parasitized (Table 3.1). The parasite laid significantly more eggs in the most starved rather than in the less- or non-starved aphids. Between two groups of starved aphids, the preference of the parasite appeared to be for the host that had been starved the longest.

Experiments with all three different groups of hosts exposed simultaneously to the parasite showed the same trend (Table 3.2): hosts with the longest starvation period were most frequently parasitized. With all combinations of hosts, the wasps consistently laid more eggs in the starved aphids. The numbers of eggs laid per aphid parasitized averaged from 1.00±0.0 to 1.490±0.246 in the paired comparisons and were 1.042±0.044 to 1.949±0.256 when the three groups were presented together. A high percentage of eggs was wasted due to superparasitism particularly in 6H (46.15 %) and in 4H (32.33 %) aphids. The index of preference confirmed that the preference was in favor of the 6H aphids.

Series II experiments

In the 1st set (IIA) of these experiments, the parasite was presented with two groups of aphids of equal age but different sizes. The results showed that significantly more aphids were attacked when these had been starved for a longer period (Tables 3.3 and 3.4). When CF and 4H aphids were offered together, the starved hosts were readily attacked, 182 individuals of the 4H group as compared with 135 of the CF group. Attacks on 4H aphids resulted in 80.77% successful parasitizations, compared with only 62.22% in the CF group.

In the CF and 6H combination, 104 of 154 6H hosts attacked (67.53%) were parasitized, whereas only 48 of 113 CF hosts (42.48%) were parasitized. In the comparison between the two starved groups, 126 hosts of 6H were attacked and 80 (63.49%) parasitized; 44 hosts (47.83%) of 4H were parasitized as a result of 92 attacks.

The IIB paired experiments were done with aphids of the same size but of different ages. The tests showed the same patterns (Table 3.4): aphids from the long starvation group were mostly attacked and a higher proportion of these were parasitized as compared with those from the non-starved or a shorter starved group.

When aphids of different sizes but the same age were anesthesized and offered by pairs (IIC), the parasite did not have a clear preference (Table 3.5).

Table 3.1. Preferences by *Ephedrus californicus* among two groups of starved aphids, plus control, exposed to a parasite by pairs on plants (n = number of female wasps in each combination).

Combination	CF and 4H[1]		CF and 6H[1]		4H and 6H[1]	
	(n=13)		(n=11)		(n=10)	
No. hosts dissected	288	290	219	214	214	221
No. hosts parasitized	67	208	18	177	58	102
(Mean±SE)	5.15±1.070	16.421±1.20	1.800±.442	17.700±.803	5.80±0.917	10.20±1.470
No. eggs laid	80	304	18	269	66	133
(Mean±SE)	6.15±1.360	23.38±2.17	1.80±.442	26.90±4.34	6.60±1.14	13.30±2.23
% hosts parasitized	23.21±4.790	71.30±4.79	8.23±2.02	79.89±4.75	7.81±4.84	49.57±6.33
No. eggs laid/host:						
(Mean±SE)	1.171±0.05	1.446±0.07	1.00±0.00	1.490±0.246	1.120±0.05	1.29±0.16
% eggs wasted	17.58±4.85	29.14±3.14	0.00	25.30±6.30	9.110±3.81	15.85±6.30

Paired T-Test			
Based on hosts parasitd	12.49***	20.36***	4.97***
Based on eggs laid	9.62***	5.99***	4.79***
Based on eggs/ hosts	3.52**	4.79**	1.48ns
Index of preference	4H/CF	6H/CF	6H/4H
Hosts parasitized	3.98±0.692	10.77±1.99	1.800±0.203

Levels of significance: ns, no significant difference($p>0.05$); **, $P\leq0.01$; ***, $P\leq0.001$.

[1]: CF = continuously fed aphids; 4H = aphids starved 4h/day; 6H = aphids starved 6h/day; all aphids were 5 days-old±2.5h.

Table 3.2. Preferences by *Ephedrus californicus* among two groups of starved aphids, plus control, exposed to a parasite together on plants (n = 10 female wasps).

Treatment	CF[1]	4H[1]	6H[1]	2-WAY ANOVA		
				DF	F	P
No. hosts dissected	149	141	135			
No. hosts parasitized	23	87	117			
(Mean±SE)	2.30±.700a	8.70±.967b	11.70±0.716c[2]	2,18	55.380	0.0001
No. eggs laid	26	129	228			
(Mean±SE)	2.60±0.98a	12.90±1.84b	22.80±3.01c[2]	2,18	35.302	0.0001
Eggs laid/Host:						
Mean	1.038a	1.454b	1.948c[2]	2,18	11.340	0.005
SEM	0.038	0.127	0.257			

Index of preference:	4H/CF	6H/CF	6H/4H
Based on hosts parasitized	5.36±1.170	7.77±1.420	1.53±0.159

[1]: CF = continuously fed aphids; 4H = aphids starved 4h/day; 6H =aphids starved 6h/day; all aphids were 5 days-old ±2.5h;

[2]: Means with the same letter(s) are not significantly different within rows (SNK, $P \leq 0.05$).

Table 3.3. Preferences by *Ephedrus californicus* among two sizes of starved aphids, plus control, exposed to a parasite by pairs in a petri dish (n = number of female wasps in each combination).

Combination	CF	4H[1]	CF	6H[1]	4H	6H[1]
	(n=14)		(n=13)		(n=11)	
No. hosts attacked	136	181	113	153	92	126
(Mean±SE)	9.71±.815	12.93±1.170	8.69±.582	11.77±.993	8.36±.593	11.45±.638
No. hosts parasitized	85	148	48	104	44	80
(Mean±SE)	6.07±.559	10.571±.863	3.69±.674	8.00±1.120	4.00±.603	7.27±.799
% hosts parasitized:						
Based on each group	64.11±4.33	77.00±6.40	41.91±6.47	64.42±6.17	47.50±6.33	65.89±7.69
Based on both groups	28.19±2.45	47.96±2.60	18.25±3.46	38.26±5.00	20.33±3.13	36.65±3.94

Paired T-Test			
For hosts attacked	2.42*	2.25*	2.56*
For hosts parasitized	4.72***	5.59***	4.66***
Index of preference:	4H/CF	6H/CF	6H/4H
For hosts parasitized	1.36±0.108	1.79±0.244	1.51±0.274

Levels of significance: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

[1]: CF = continuously fed aphids; 4H = aphids starved 4h/day; 6H = aphids starved 6h/day;

all aphids were 5 days-old±2.5h.

Table 3.4. Preferences by *Ephedrus californicus* among two groups of starved aphids, plus control, of equal[1] size but different ages exposed to a parasite by pairs in a petri dish (n = number of female wasps in each combination).

Combination	CF	4H[2]	CF	6H[2]	4H	6H[2]
	(n=12)		(n=11)		(n=13)	
No. hosts attacked	90	163	109	147	102	162
(Mean±SE)	7.50±.584	13.58±.633	9.90±.791	13.36±.691	7.85±.355	12.46±.756
No. hosts parasitized	67	126	86	122	69	110
(Mean±SE)	5.58±.583	10.50±.557	7.81±.761	11.09±.680	5.30±.458	8.46±.730
% hosts parasitizd:						
Based on each group	74.55±4.63	77.72±3.45	78.89±3.44	82.85±3.20	63.35±7.53	65.13±7.39
Based on both groups	26.59±2.84	49.87±2.70	33.45±3.16	47.92±3.35	29.85±3.95	42.57±3.73

Paired T-Test			
Based on hosts attacked	5.14***	2.46*	3.39**
Based on hosts parasitized	4.90***	2.49*	4.65***
Index of preference:	4H/CF	6H/CF	6H/4H
Based on hosts parasitized	1.09±.077	1.07±.064	1.08±.123

Levels of significance: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

[1]: Wet weight difference between any 2 groups is less than or equal to 0.0423mg

[2]: CF = continuously fed aphids, age= 3days±2.5h; 4H = aphids starved 4h/day, age = 5days±2.5h;

6H = aphids starved 6h/day, age = 5 days±2.5h.

Table 3.5. Preferences by *Ephedrus californicus* among two groups of starved aphids, plus control, anaesthetized and exposed to a parasite by pairs in a petri dish (n = number of female wasps in each combination).

Combination	CF	4H[1]	CF	6H[1]
	(n=13)		(n=13)	
No. hosts attacked	138	139	157	143
(Mean±SE)	10.63±.559	10.84±.517	12.07±.445	11.00±.424
No. hosts parasitized	76	116	89	101
(Mean±SE)	5.84±.529	8.92±.746	6.84±.741	7.76±.662
% hosts parasitized:				
Based on each group	54.98±4.64	82.43±4.81	56.16±5.56	70.15±4.78
Based on the 2 groups	27.22±2.34	41.56±3.12	29.41±2.90	33.47±2.61

Paired T-Test		
Based on hosts attacked	0.08ns	1.46ns
Based on hosts parasitized	4.70***	1.30ns
Index of preference	4H/CF	6H/CF
Based on hosts parasitized	1.55±.087	1.47±.236

Levels of significance: ns, no significant difference; ***, $P \leq 0.001$.

[1]: CF = continuously fed aphids; 4H = aphids starved 4h/day; 6H =aphids starved 6h/day;

all aphids were 5 days-old±2.5h.

When the numbers of hosts attacked were 138 from CF and 141 from 4H the values were not significantly different (Paired T-Test: t=0.26, P=0.800); similarly, the numbers of hosts attacked (157 and 143) in the CF and 6H combination were not statistically different (Paired T-Test: t=1.46, P=0.543), even though significantly more 6H aphids were parasitized in this combination (Paired T-Test: t=4.70, P≤0.001). The indices of preference of 4H/CF and 6H/CF based on the number of hosts parasitized were 1.550±0.087 and 1.471±0.256.

DISCUSSION

Results presented here indicate that mated, experienced female *E. californicus* preferred to attack aphids starved for 6h, over those starved for 4h or continuously fed. The parasites attacked selectively and oviposited most frequently in the smaller hosts. With aphids of equal size, the starved individuals were more likely to be attacked than the non-starved, but each size class was likely to be accepted equally for oviposition. When the aphids were anesthetized, there was no preference for attack, but still the smaller hosts were preferred for oviposition. These results suggest that attack preference in the parasite may depend on aphid defensive behaviour, whereas oviposition may depend on aphid size.

Numerous studies have been done on parasite host selection. Some of these were reviewed by van Alphen and Vet (1986). The recent studies include those of Nechols and Kikuchi (1985), Hopper (1986), Putters and van den Assem (1988), de Jong and van Alphen (1989), Heinz and Parrella (1989), Martin *et al.*, (1989), Hébert and Cloutier (1990), Reznik and Umarova (1990). These studies showed that parasite preference for small hosts is not common.

In most cases, female parasites have shown a strong preference for relatively older and larger hosts. Mackauer (1973, 1983), working with *Aphidius smithi*, found that females attacked first instar aphids less frequently and laid fewer eggs in these than in older instars and prereproductive adults, which are much larger. Because the degree of preference by the parasite decreases with the difference of age in the hosts, Mackauer (1973) suggested that size in acceptable hosts appears to be an important factor of selection. The fact that *A. smithi* discriminates against smaller hosts was suggested earlier by Wiackowski (1962). In field experiments, the corn earworm parasite, *Microplitis croceipes* (Braconidae), preferred the third instars of *Heliothis zea* and *H. virescens* over younger and smaller instars (Hopper and King, 1984). Opp and Luck (1986) reported that large individuals of the California red scale, *Aonidiella auranti*, were more often parasitized than small ones both by *Aphytis melinus* and *A. lingnanensis* (Aphelinidae). Similarly, *Diglyphus begini* (Eulophidae) oviposited most frequently in large than in small larvae of the dipteran host *Liriomyza trifolii* when larvae of both sizes were provided (Heinz and Parrella, 1989). With the exception of Fox *et al.*

(1967), few authors have concluded that parasitic Hymenoptera will select small over large hosts.

In some cases, a preference is not clearly shown and the parasite may select hosts of intermediate size over small or large individuals. This has been shown to happen with *Aphidius sonchi*; when all instars were simultaneously provided, the parasite attacked preferentially and laid more eggs in the second and third aphid instars (Liu *et al.*, 1984). The third instar larvae of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), was preferred for parasitization by *Campeoletis sonorensis* (Ichneumonidae) over other instars (Isenhour, 1985).

The results of a preference test can be influenced by the experimental methods: Fox *et al.* (1967) measured the preference of *A. smithi* for the pea aphid by offering separately the four instars of the host. He found that early first instars were preferred. However, with the same parasite species, Mackauer (1973, 1983) compared host instars by pairs and was unable to confirm Fox's results. Moreover, he found that this parasite showed a strong preference for large, late instars over the first instar. Liu *et al.* (1984) also found that *A. sonchi* did not show any preference when host instars were presented separately, but selected second and third instars when all instars were available. This shows that evaluation of host size by female wasps is based on a relative rather than an absolute difference.

Several factors are involved in a parasite's host selection. Size is most often suggested to be an important element, because size and behaviour can be related. Liu *et al.* (1984) suggested that the effect of size on host selection success can be explained partly by the fact that parasites find their hosts by random search. In this case, a larger host is more likely to be encountered and parasitized than a smaller one (van Alphen and Drijver, 1982). This argument has been supported recently by work of de Jong and van Alphen (1989). They found that encounter rates between the parasite, *Leptomastix dactylopii*, (Encyrtidae) and its host, the citrus mealybug, *Phenacoccus citri*, increased with the size of the host. However, this hypothesis failed to explain satisfactorily why parasite encounter rates with large reproducing adults were low.

Host defensive behaviour is another contributing factor to the effect of size on parasite host selection. As hosts grow, their defense mechanisms develop and their response to attack increases. For example, large hosts are more likely to fall off the host plant upon parasite attack, and they have more ability to struggle against the parasite by flipping their abdomens, by kicking with their legs (de Jong and van Alphen, 1989), or by walking away from the parasite. Because of these responses, the handling time for large hosts may be prolonged and their parasitization difficult.

The defense mechanisms can be modified by conditions of growth and development. As I have shown here, when the pea aphids were prevented from feeding for a certain period each day, there was no evidence that they had the ability to compensate for energy loss by increased consumption. The limited quantity of nutrients ingested will consequently yield too little available energy. Starved aphids use the available energy to ensure basic functions first of all. For energy saving purposes, non-essential activities will decrease and the starved aphids response to parasite attack may be weakened. There are two reasons: first, growth and development having been delayed, the defense system may also be either delayed or even lacking. An example of a defense system is that of the citrus mealybug, which exudes droplets from the anal region in response to attack by *L. dactylopii* (de Jong and van Alphen, 1989). As in the mealybug and the green peach aphid, *Myzus persicae* (Hågvar and Hôfsvang, 1987), "normal" pea aphids are capable of emitting alarm pheromones (Müller, 1983; Nault *et al.*, 1973). In starved aphids, these pheromones might not be effective against the parasite because the mechanisms for producing such substances are impeded. The second reason for a weakened response to attack is that, due to reduced energy, escape movements such as walking away will be minimized and the aphids' ability to struggle will be decreased, a condition allowing the parasite to overcome the host resistance more easily.

The behaviour of some insects is often dependent on their previous experience. For a parasite, experience can influence host selection. Samson-Boshuizen *et al.*, (1974) showed that the rate of successful attacks on larvae of *Drosophila melanogaster* by *Pseudeucoila bochei* (Cynipidae) depends on prior exposure of the parasite to the host: female parasites which had been exposed previously to the hosts laid more eggs than those that had not been exposed. This has also been reported for many other species of Hymenoptera, including *Coccygomimus turionellae* (Ichneumonidae) (Sandlan, 1979), and *Exeristes roborator* (Ichneumonidae) (Wardle and Borden, 1985). It is assumed that some female parasites require trials and time to co-ordinate effective attack and oviposition movements, i.e. host handling, inserting the ovipositor and pushing eggs through the ovipositor. One can argue in the same way that the host also may gain some experience. For a slow parasite, such as *E. californicus*, which needs 6 sec or more for oviposition, it is unlikely that the first attempt will be successful. Failure of one or two attacks from the parasite may alarm the aphids and give them the opportunity to learn to escape better during the subsequent attacks. In starved aphids, it is possible that the learning process was much slower than in control aphids because learning may depend on age and development. Wardle and Borden (1985) observed that female *E. roborator* conditioned immediately after eclosion learned faster than those conditioned 5 to 10 days after eclosion. The authors argued that this indicated that development constrains learning ability.

The fact that *E. californicus* did not show any preference when hosts of equal size were offered, indicates that in this parasite host size is the determining factor for oviposition decisions; the parasite "preferred" to lay most of its eggs in small hosts, an observation that was confirmed by the trials with anesthetized aphids.

At first, it appears that these findings contradict classical optimal foraging theory, which suggests that a larger host is more suitable than a small one for the development of immature parasites; hence, the parasite ought to discriminate against small hosts. In fact, the difference is not fundamental because suitability is not always dependent on size. Mackauer (1973) found that second instar pea aphids were more suitable for immature *A. smithi* than first, third, and fourth instars. The physiological state of the host may be of prime importance. *E. californicus* is known to have one of the longest developmental times amongst Aphidiidae (Cohen, 1985). It follows that the eggs must be laid in hosts in which their development can be completed before the host dies. Therefore, it appears that the small hosts, owing to the delay in development caused by starvation, were more acceptable than the larger, non-starved hosts at the time of the attack.

The fact that a parasite will oviposit preferentially in small hosts might be expected to influence its fitness. This aspect will be examined in the next section of this paper.

CHAPTER IV

EFFECTS OF HOST STARVATION ON EMERGENCE TIME AND SIZE OF *EPHEDRUS CALIFORNICUS*

INTRODUCTION

The importance of size in host-parasite interactions has been recognized by many workers. The size of the host is a rough indicator of the quantity of food available: the larger the host, the more resources are available for the parasite. Size can also strongly influence the behaviour of a predator and its prey as well as that of a parasite and its host and, for this reason, the selection process. In a predator-prey system, for example, size may determine the predator's searching activity and feeding frequency. Thus, the ability of a predator to keep a prey population at a low level may depend on the distribution of prey sizes (Evans, 1976).

For endoparasitic insects, host size is of fundamental importance because the survival, growth and development of the next generation of parasitoids depends entirely on the quantity and quality of nutrients available in the host. Moreover, hosts of different sizes may differ in their metabolic (Thompson, 1986a,b) and endocrine (Lawrence, 1986) physiologies and thus provide different internal environments, which can be modified under stress (Weseloh, 1984). It has been shown that starvation changes the nutrient composition of insect haemolymph (Hill and Goldsworthy, 1970; Mwangi and Goldsworthy, 1977; Lim and Lee, 1981). Because starved insects tend to be smaller than normally fed insects, it is to be expected that starvation will also affect the emerging parasite's size, survival, and fitness (Salt, 1940, 1941; Smith and Pimentel, 1969; Dransfield, 1979; Wallner and Grinberg, 1984). Gutierrez (1968) and Cohen (1985) showed that the pea aphid is a suitable host for *E. californicus*.

In the previous section, I have shown that *E. californicus* attacked small, starved pea aphids most frequently and laid more eggs in them than in relatively larger, well-fed hosts. The purpose of this chapter is to investigate the effects of the size of the pea aphid on development time and size of *E. californicus*.

MATERIALS AND METHODS

Cultures of the pea aphid, *Acyrthosiphon pisum*, and its solitary endoparasite, *Ephedrus californicus*, were maintained in the laboratory under the conditions described earlier.

Aphids for use in these experiments were obtained by starving two groups of 24h-old (±2.5h) nymphs every day for 4h (4H) and 6h (6H), respectively. A control group was allowed to feed continuously (CF).

Aphids aged 5 days (± 2.5h) were parasitized by confining a 4- to 5-day-old female parasite with a single aphid in a gelatine capsule (size 00). Parasite and aphid were kept together until the parasite attacked the aphid once. The aphid was then replaced by a nonparasitized one. To ensure adequate parasitization, I considered that an aphid was attacked only if the parasite inserted her ovipositor into the aphid for 6 sec or longer (Chow and Mackauer, 1986). Attacked aphids were transferred to rearing cages (5.5 cm diam x 4 cm high), in groups of 30-35 individuals per cage. The cages, which contained a plant growing in water, were kept in a controlled environment chamber at 21±1°C, 75±5% RH and under continuous light. The starvation treatments continued for parasitized aphids in the 4H and 6H groups until they mummified, while aphids in the CF group were kept on plants in the growth chamber. The mummies were collected and placed separately in numbered gelatine capsules. The emergence times of the parasites from the mummies were recorded with a video camera and reported every 30 min. The emerged parasites were sexed and were kept in capsules until they died. Dead wasps were dried for 48h at 100°C in a PS Thelco dryer and weighed on a Mettler UM3 microbalance. Hosts from which no parasites emerged were counted and recorded in each group, and the mummies were dissected to determine the stages of development of the parasites. The unemerged adult parasites could be distinguished from the pupae by differences in colour: adults were black whereas pupae were whitish.

RESULTS

The results of the experiments are summarized in Table 4.1. The data show that male and female parasites emerging from starved hosts required significantly less time than those from the non-starved hosts (Oneway ANOVA; males: df=2,325; F=392.11; P≤0.001; females: df=2,123; F=102.96; P≤0.001). Wasps from 6h-starved aphids emerged on average in about 334.62 h after parasitization, a significantly longer period than that of wasps from 4h-starved aphids (mean=322.13±0.81h, n=131). The chronology of parasitoid emergence can be summarized as follows:

$$4H < 6H < CF$$

Male and female parasites emerging from the CF group were significantly larger and heavier than those from starved aphids (Oneway ANOVA; males: df=2,325; F=644.90; P≤0.001; females: df=2,123; F=377.80; P≤0.001). A Student-Newman-Keuls (SNK) multiple range test indicated a significant difference between the dry weights of parasites emerging from starved hosts: 6h-parasites were smaller and lighter (4h: mean=0.123±0.002mg; 6h: mean=0.102±0.001mg). The data suggest a negative correlation between the length of host starvation and the weight of the parasite emerging from this host, and a positive correlation between host size at parasitization and parasite weight at emergence.

In all three treatments, more males than females emerged (Table 4.1). Although the parasite sex ratio seemed to decline

Sex ratio:	0.308	0.290	0.261
(95% CI)	(0.229-0.394)	(0.216-0.370	(0.203-0.324)
males/females	2.24	2.58	2.83
No. males	83	95	150
No. females	37	36	53

[1]: CF = continuous feeding; 4H=aphids starved 4h/day; 6H=aphids starved 6h/day;

[2]:Differences between males and females were significantl in all treatments: CF: df = 1,118 F = 9.880, P = 0.002; 4H: df = 1,129 F = 9.033 P =0.003; 6H: df = 1,201; F = 57.57; P = 0.001

[3]: Means showing the same letter(s) were not significantly different within rows (P > 0.05).

Table 4.1. Effects of aphid host starvation on developmental time and size of males and females of *E. californicus*.

	TREATMENT			ANOVA		
	CF^1	4H^1	6H^1			
	(n=120)	(n=131)	(n=203)	DF	F	P
VARIABLE						
Emergence time^2 (h)						
(mean±SE)						
males	363.47±1.172a^3	320.73±0.940c^3	331.29±0.927b	2,325	392.112	0.000
females	356.99±1.624a^3	325.84±1.209c^3	344.80±1.397b	2,123	102.985	0.000
Dry weight (mg)						
(mean±SE)						
males	0.178±0.002a^3	0.115±0.002b^3	0.097±0.001b	2,325	644.902	0.000
females	0.207±0.002a^3	0.148±0.003b^3	0.115±0.002b	2,123	377.807	0.000

with host size (i.e. length of starvation), the means overlapped within their 95% confidence intervals. Therefore, I concluded that there were no consistent differences in the sex ratio between the groups. Dissections showed a high proportion of non-emerged parasites in the starved hosts: 8.33% in CF, 11.11% in 4H and 13.65% in 6H starved hosts. All the non-emerged parasites were in the adult or pupal stages.

DISCUSSION

Salt (1941) was among the first to demonstrate that the size of an endoparasite is influenced by the size of its host. He showed also that host size is associated with differences in various parasite attributes, such as morphology, rate of development, fecundity, and sex ratio. Various authors have evaluated aspects of metabolism (Thompson, 1986a,b), endocrine physiology (Fisher, 1971; Lawrence, 1986), and nutritional ecology (Beckage, 1985; Slansky and Scriber, 1985; Slansky, 1986) and have demonstrated that a host parasitized by an endoparasite represents an integrated biological system which generally responds to the parasite's requirements (Read, 1970; Mackauer, 1986, Slansky, 1986; Thompson, 1986b).

My experiments showed that eggs of *E. californicus* grew and developed in all three aphid groups, but that the rates of development varied considerably. *E. californicus* from starved pea aphids emerged earlier than those reared on aphids fed *ad libidum*, with '6H' parasites requiring longer to develop than their counterparts reared in 4H aphids. Parasites from the CF group were larger and weighed more than those from 4H hosts which, in turn, were larger than those from 6H hosts. These findings show that, in *E. californicus*, host starvation does not prevent parasite development but affects the rate of development.

Most of the reported effects of host size on parasite growth and development are based on the assumption that a large host represents a greater quantity of resources that are available to the host in order to meet both its own energy requirements and those of the parasite. Living inside the host, the immature parasites' needs inevitably must be satisfied by the host. In particular, nutrient availability depends on the efficiency of the host's food consumption and allocation. In pea aphids, assimilation efficiency is high. Because under normal conditions, the amounts of energy expended on growth, reproduction, maintenance, and excretion vary with age (Randolph *et al.*, 1975), it can be predicted that much of the energy flow will indeed depend on aphid size.

A correlation between the sizes of hosts and their parasites has been noted in many relationships (Jackson, 1937; Arthur and Wylie, 1959; Smilowitz and Iwantsch, 1973; Miles and King, 1975; Lawrence *et al.*, 1976; Jowik and Smilowitz, 1978; Weseloh, 1984; Liu and Hughes, 1984; Liu, 1985; Opp and Luck, 1986; de Jong and van Alphen, 1989). Almost all of these studies showed that limited reserves in hosts are also limiting to parasite growth.

The development of a parasite appears to be a non-linear function of host size. In some insect parasites, development was negatively correlated with the age or size of their hosts, that is, the development time is short in large, old hosts and long in small, young ones. *Anagyrus indicus* (Encyrtidae) developed faster when growing in third-instar nymphs and older individuals of the spherical mealybug, *Nipaecoccus vastator*, than when growing in first and second instars (Nechols and Kikuchi, 1985). This was also the case in *Hyposoter exiguae* (Ichneumonidae) developing in the noctuid cabbage looper, *Trichoplusia ni*, (Smilowitz and Iwantsch, 1973), and in *Meteorus trachynotus* (Braconidae) growing in the spruce budworm, *Choristoneura fumiferana* (Hébert and Cloutier, 1990).

In other cases, the parasite developed faster in small than in large hosts. Arthur and Wylie (1959) observed that development of the ichneumonid *Pimpla turionellae* (=*P. examinator*) was delayed longer in large pupae of many species of Lepidoptera than it was in small and medium-sized pupae; but the reason for this prolonged development was not investigated. Lawrence *et al.* (1976) observed similar patterns in the development of *Biosteres (=Opius) longicaudatus* parasitizing the Caribbean fruit fly, *Anastrepha suspensa*; braconids which developed in 5-day-old larvae emerged in 19 days whereas those developing in 7-day-old hosts required 20 days to do so. Salt (1940, 1941) showed that development of *Trichogramma evanescens* was delayed in both small (*Sitotroga cerealla*) and large hosts

(*Agrotis c-nigrum*) but required least time in medium-sized hosts (*Agrotis kuehniella*). He suggested that medium-sized hosts contained the optimum quantity of food for rapid development of the parasite.

Results of the present study agree with those reported above: the parasite developed faster in small hosts. The short development time of *E. californicus* reared in starved hosts may be explained by the different nutritional potentials of starved *versus* non-starved aphids. The fact that most of the eggs laid in starved aphids developed suggests that, in general, these aphids are suitable. They contained sufficient food to complete their own growth and development and support the minimum requirements of the immature parasites. However, the lack of food in starved hosts limited further parasite growth. By comparison, control aphids (CF) continued to grow and accumulate additional nutrients. As a consequence, parasites emerging from CF aphids were larger and weighed more than those from starved aphids.

The larger quantity of food, or the extra time necessary to consume the additional host contents, may explain the delayed emergence of parasites from CF aphids. Regardless of its nutritional potential, the size of any host must eventually present a physical barrier to parasite growth. In small aphids, this barrier was rapidly reached; thus, parasites were possibly prevented from growing further, and hence may have emerged earlier, even though they were smaller, had a short survival time (de Jong and van Alphen, 1989; Nechols and Tauber, 1977) and low fecundity (Liu, 1985).

The difference in developmental time may also be due to metabolic or physiological changes both in the immature parasites and in their hosts. It is known that, under certain circumstances, parasitism can affect host performance (Vinson and Iwantsch, 1980; Vinson, 1986; Mackauer, 1986), particularly feeding and assimilation (Slansky and Scriber, 1985; Slansky, 1986). Generally, gregarious parasites have stimulatory effects on their hosts whereas solitary parasites have inhibitory effects (Thompson, 1982a,b). However, it should be noted that these effects are highly variable in solitary species and may be stimulatory under certain conditions. For example, when parasitized by two larvae of *Aphidius smithi*, the pea aphid showed a higher feeding rate than when it was parasitized by one larva (Cloutier and Mackauer, 1979, 1980). Thompson (1982a) found that, in *Trichoplusia ni*, glycogen and lipid contents were similarly reduced in individuals starved and parasitized by *Hyposoter exiguae*. Therefore, it is possible that, under starvation coupled with parasitization, pea aphids modify their food utilization and assimilation in response to parasite needs.

The changes mentioned above might have contributed to a more rapid development of larvae in starved aphids. Brodeur and McNeil (1989) observed that a higher proportion of *Aphidius nigripes* (Aphidiidae) that had developed in small, first nymphal instars entered diapause than larvae developing in large, fourth instars. The importance of these mechanisms remains to be investigated.

No obvious reason is available to explain why the emergence time of parasites from 4H aphids was shorter than that from 6H aphids (Table 4.1). It is possible that excessive host starvation can be detrimental to parasite development, as shown by the fact that a high proportion of parasites did not survive in such hosts. There appears to be, therefore, a minimum amount of nutrients needed to sustain growth and successful development of parasites. Below this limit, development is not only delayed, but can be arrested due to lack of reserves.

CHAPTER V

GENERAL DISCUSSION AND CONCLUSIONS

For living organisms, food is an essential factor because the quantity and quality of nutrients are important regulators of energy flow at all levels of development (Waldbauer, 1968; Gordon, 1972; van Emden, 1977). The amount of food ingested, digested, and excreted, metabolized and converted into biomass has a major influence on physiology and behaviour and consequently, on performance (Gordon, 1972; McGinnis and Kasting, 1972; Beck and Reese, 1976).

Results in the present study show that constraints on the length of feeding time had a number of negative effects on growth and development rates, and on the reproductive potentials and survival of the pea aphid. When nymphs were starved for a certain period each day, they grew more slowly and, in the adult stage, were smaller than their counterparts that had fed normally; reproduction was delayed and fecundity was reduced. The slow growth observed in starved aphids suggested that their energy requirements for the basic metabolic functions were only partially satisfied, that is, there was an imbalance between gain and utilization of energy. This imbalance might be due to an inadequacy in the quantity and the quality of the food consumed and, possibly, to an increase in energy requirements.

Although my experiments were not concerned specifically with aphid nutrition, the observations indicated that pea aphids subjected to interrupted feeding consumed proportionately less food than those that fed continuously. Therefore, less energy was available for normal activities. Further, it appeared that aphids did not store nutrients or compensate for energy lost during starvation by increased feeding rates or, alternatively, that any compensation was not sufficient to meet all the energy requirements. An imbalance between energy gained and used might result also from the fact that during starvation, the aphids were searching for food and hence were more active than when they were feeding on the plants. Thus, the aphids had increased energy requirements, as their respiration and overall maintenance costs increased.

In the pea aphid, reduced energy might also result from reduced efficiency of nutrient assimilation or from the conversion of these nutrients into body weight, as observed in the grasshopper *P. pictus* and the cherry scallop moth (Muthukrishnan and Delvi, 1974; Schroeder, 1976).

Starving pea aphid nymphs for 4 h or 6 h per day did not prevent them from reaching maturity, but it did prolong their developmental time and delayed their maturation, as shown by an increase in the prereproductive period. The longer reproductive period of starved pea aphids indicated that, in this species, the development of the reproductive system lags behind that of the somatic tissues. When nutrients are scarce, aphids allocate the available energy to ensure maintenance at the expense of reproduction. Reduction of aphid fecundity under starvation might have been caused by the arrestment of the development of the reproductive system or by the resorption of embryos or by both (Brough and Dixon, 1990; Bell and Bohm, 1975; Trepte and Trepte-Feuerborn, 1980; Ward and Dixon, 1982).

Experimental results presented in Chapter III show that *E. californicus* exhibited a distinct preference for attack and oviposition in small, starved aphids rather than in non-starved hosts. The high rate of parasite attacks on, and oviposition in, small aphids can be explained by the absence of proper host defensive mechanism. In Chapter II, I showed that starvation reduced the rate of growth, prolonged development and delayed maturation. These delays might have been accompanied by a delay in the development of the aphid's defensive system, in such a way that the aphids were unable to defend themselves efficiently against parasite attacks. The lack of proper defensive behaviour might have been caused also by inadequate energy. In either case, the handling time by the wasps appeared to be longer and parasitization more difficult in non-starved, large aphids than in small ones. When aphids were of equal size, starved aphids were more often attacked than non-starved ones, but each aphid group was accepted equally for oviposition. These observations indicate that host size was the determining factor in oviposition decisions by *E. californicus*. The choice of small hosts for oviposition may suggest that small hosts are more suitable than large ones because parasitoids are better able to complete their development before the host dies.

E. californicus' preferential oviposition in small pea aphids affected several life history and offspring fitness components. Parasite eggs developed in all three host groups, a fact indicating that limiting host resources did not prevent growth. This was because aphids in all three groups contained sufficient resources to complete their own growth and support the minimum requirements of the parasites' development. However, non-starved hosts had additional resources which allowed immature parasites to feed longer and accumulate more nutrients for further growth. The extra feeding explained why parasites in non-starved hosts emerged later and were heavier than those from starved aphids.

The short developmental time of parasites from starved hosts can also be attributed to the fact that both starvation and parasitization affect host physiology. It is thus possible that under starvation coupled with parasitization, modifications of food consumption and utilization and changes in the metabolism and physiology of the pea aphid occurred to contribute to a rapid development of *E. californicus*

These results show that a lack of food influences pest population size by reducing pest fecundity. This effect has been shown in laboratory studies by many authors, including Trepte (1980), Slansky (1980), Weaver and Pratt (1981), Gunn and

Gatehouse (1985), Juliano (1986), Grüber and Dixon (1988), and Brough and Dixon (1990). Problems of food shortage may occur in the field through seasonal changes and agricultural activities. Seasonal changes can render host-plants scarce either because these plants have been partly consumed or must be shared with populations of other insect species. Seasonal variations may also cause changes in food quality because host-plant nutrients can decline with age as non-digestive plant components accumulate. An example of the consequence of host-plant sharing on an aphid populations was reported by Andrewartha and Birch (1984). The introduction of the blue alfalfa aphid, *Acyrthosiphon kondoi*, into California limited the numbers of pea aphids in the fall. The authors argued that, at low temperatures, populations of the blue alfalfa aphid increase faster than those of the pea aphid. Therefore, they pre-empt the growing tips so that pea aphids are denied access to the most nutritive parts of the plants. Similarly, in areas where alfalfa is harvested regularly, pea aphids can be starved when they have less access to suitable host-plant following each cut (Campbell, R.E., 1926; Campbell, A., 1974).

Lack of food may also affect pest populations through host-parasite relationships, particularly by influencing host size, defensive behaviour and parasite oviposition decisions and development. This is an important area for future studies.

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