NUTRITIONAL AND PHYSIOLOGICAL ECOLOGY OF INSECT HOST - PARASITOID ASSOCIATIONS: THE PEA APHID - *APHIDIUS ERVI* SYSTEM

by

Richard Vincent Sequeira

B.Sc. (Agric.), Mahatma Phule Agricultural University, 1982

M.P.M., Simon Fraser University, 1987

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in the Department

of

Biological Sciences

SIMON FRASER UNIVERSITY

April, 1991.

APPROVAL

Name: Richard Vincent Sequeira

Degree: Doctor of Philosophy

Title of Thesis:

NUTRITIONAL AND PHYSIOLOGICAL ECOLOGY OF INSECT HOST - PARASITOID ASSOCIATIONS: THE PEA APHID - *APHIDIUS ERVI* SYSTEM

Examining Committee:

Chairman: Dr. E. B. Hartwick

Dr. M. Mackauer, Professor, Senior Supervisor,
Dept. of Biological Sciences, SFU

Dr. M.L. Winston, Professor,
Dept. of Biological Sciences, SFU

Dr. A.S. Harestad, Associate Professor,
Dept. of Biological Sciences, SFU

Dr. K.K. Nair, Professor,
Dept. of Biological Sciences, SFU
Public Examiner

Dr. R.C. Ydenberg, Associate Professor,
Dept. of Biological Sciences, SFU
Public Examiner

Dr. S.N. Thompson, Professor, Dept. Entomology,
University of California, Riverside,
External Examiner

Date Approved 11 April 991

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

NUTRITIONAL AND PHYSIOLOGICAL ECOLOGY OF INSECT HOST - PARASITOID ASSOCIATIONS: THE PEA APHID - APHIDIUS ERVI SYSTEM

Author: _____
(signature)

Richard Vincent Sequeira
(name)

April 15, 1991.
(date)

ABSTRACT

Aphidius ervi Haliday (Hymenoptera: Aphidiidae) is a primary parasitoid of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae). Parasitism of pea aphids representing different age/instar groups, and its impact on the life history parameters of juvenile and adult parasitoids, were examined under laboratory conditions. Host size at parasitization is not always a good indicator of the amount of resources available to the developing parasitoid larvae. Parasitoid larvae grow along different trajectories in hosts parasitized at different ages. These differences indicate that host quality is a nonlinear function of host size.

Body size (dry weight) and developmental time of adult parasitoids are influenced by host size and growth potential at parasitization; they covary positively when host size is a limiting factor for parasitoid growth, but vary independently in hosts above a threshold size. Parasitoid larvae utilize host resources first to maximize body size before minimizing developmental time. Age-specific fecundity and survivorship of parasitoids reared from different host instars vary nonlinearly with parasitoid body size and host size at parasitization.

Parasitoid body size, often considered an index of fecundity, has higher heritability, and is more plastic in its response to variability in host size than developmental time. These observations suggest that, in the field, developmental time may be more important in determining the parasitoid's reproductive success than fecundity.

Patterns of covariation in body size and developmental time in another species of aphidiid wasp, *Ephedrus californicus* Baker, are similar to those found in *A. ervi*, indicating that the observed epigenetic structure and control of some life history parameters may be typical of aphidiid parasitoids. Growth rate responses and inter-sexual differences in growth rate may be unique to each parasitoid species. Life history strategies of parasitoids appear to be moulded by trade-offs operating at several physiological and behavioural levels. To make realistic predictions theoretical approaches to the analyses of life history problems concerning host-parasitoid associations must account for the complexity of interactions and phenotypic plasticity of characters.

ACKNOWLEDGMENTS

To Dr. Manfred Mackauer, mentor and friend, I express my deepest gratitude for the enjoyable and rewarding years spent in his lab. His support, patience and constructive criticisms over the years contributed not only to the successful completion of this project but also to my self-confidence as a biologist.

I thank Drs. Mark Winston and Alton Harestad for their advice and excellent editing of previous drafts of this thesis.

I thank my collegues, B. Bai, A. Chow, T. Danyk, K. Kouame, H. McBrien and J. P. Michaud for invaluable discussions on my work and for their assistance in the maintenance of insect colonies. It has been a pleasure knowing and working with them.

I am deeply indebted to Peter and Clara D'Mello for their unfailing support and help throughout my stay in Canada.

Financial support provided by the Department of Biological Sciences, Simon Fraser University, and a grant from the Natural Sciences and Engineering Research Council of Canada to Dr. Manfred Mackauer is gratefully acknowledged.

DEDICATION

To Jules and Mary, for believing in me

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The problem

It has long been recognized that the link between life history phenomena and patterns of development is of great importance to the processes of adaptive evolution (Schmalhausen 1949; Waddington 1957). Free-living organisms that experience nutritional and/or physiological forms of developmental stress resulting from fluctuations in the "quality" of their environment have evolved elaborate escape mechanisms such as hibernation or diapause (Pond 1981; Pianka 1983). For insect parasitoids, the host represents the complete nutritional and physiological environment during larval development. Therefore, variation in host quality is a principal source of developmental stress for insect parasitoids. Questions then arise concerning the effects of variation in host quality on parasitoid larval ontogeny, and the influence of the latter on adult life history phenomena.

Hymenopteran parasitoids belonging to the family Aphidiidae are important agents of population regulation specific to aphids (Hagen and van den Bosch 1968; Mackauer and Chow 1986). The aphidiids, although a relatively small group of parasitoids, exhibit considerable diversity in the degree of host-related adaptations and host specificity (Starý 1970). Most aphid populations are characterized by the overlapping of generations, which results in several developmental stages of the aphid being present in the population at any time (Dixon 1985). Aphid size is not critical for host acceptance and oviposition by the Aphidiidae, but when given a choice of host sizes for oviposition, many parasitoids exhibit distinct preference for one or more host sizes (Starý 1970;

Mackauer 1973; Liu *et al.* 1984; Sequeira and Mackauer 1987).

The endoparasitic larval stages of parasitoids are confined to the nutritional and physiological milieu of the host selected by the ovipositing female. A newborn aphid may be several orders of magnitude smaller than its mother, and yet when parasitized both give rise to viable and functional parasitoids. The effects of size-specific parasitism on the biology and reproduction of hosts are well known (*e.g.*, Cloutier and Mackauer 1979; Mackauer and Kambhampati 1984; Polaszek 1986; Sequeira and Mackauer 1988), but the mechanisms by which parasitoids adapt to nutritional and physiological conditions resulting from the parasitism of hosts of different sizes are poorly understood.

The objectives

To answer the questions posed above, I chose a laboratory host-parasitoid system consisting of the pea aphid, *Acyrthosiphon pisum* (Harris), (Homoptera: Aphididae) and its primary parasitoid, *Aphidius ervi* Haliday. The objectives of my study were:

i) to examine how individual life history characters of parasitoids such as growth rate, adult body size and developmental time respond to parasitism of hosts from different age/size classes and variation in nutrient availability;

ii) to evaluate the impact of larval ontogeny and feeding experiences on adult survivorship and reproductive success of parasitoids; and

iii) to assess the relative ecological importance of variation in different parasitoid life history characters in relation to variability of host size and growth potential.

The experimental work is presented in chapters II-VI. Chapters II and III are concerned with objective (i). In chapter IV, I review and interpret the results of

the preceeding three chapters, and in doing so address objective ii). Chapters V and VI are concerned with objective iii).

General biology of insects and methodology

Detailed accounts of the biology and field ecology of the Aphidiidae were given by Mackauer and Finlayson (1967), Starý (1970), and Mackauer and Chow (1986); aphid biology has been discussed by Blackman (1987) and Dixon (1987). The Aphidiidae are primary parasitoids, most being heterosexual and arrhenotokous (unfertilized eggs develop into males and fertilized eggs into females). A single alecithal egg (without yolk) is laid at each oviposition. Superparasitism and multiparasitism are normally avoided, but are known to occur under field as well as laboratory conditions (Chow and Mackauer 1984). The parasitoid embryo is enclosed by a trophamnion or pseudoserosa. The egg hatches into a first-instar larva, whereupon the trophamnion separates into individual cells or cell complexes that develop into "giant cells" or "teratocytes" (Salt 1968). Just prior to pupation, the final-instar larva begins to feed destructively on aphid embryos and body tissues, until only the hardened aphid integument or "mummy" remains. The parasitoid then pupates within or under the mummified aphid.

A culture of parthenogenetic, viviparous pea aphids was maintained on broad bean, *Vicia faba* L., cultivar 'Broad Windsor', at 20 ± 2 °C, 55-65% r.h., and continuous light. Under these conditions reproduction is exclusively parthenogenetic, and most progeny are apterous. The aphid goes through four nymphal instars, L_1-L_4, before moulting to the adult stage. Aphids of known age for experimental purposes were obtained by confining reproductive adult aphids to potted broad bean sprouts that were approximately 1.5 inches tall, for a period of 4 h. After

that period the adults were removed, and the offspring produced were maintained at 20 ± 0.5 °C, 55–65% r.h., and constant light, until they reached the desired age.

A laboratory culture of *A. ervi* was started in 1986 from a large sample of parastized aphids collected on alfalfa in southwestern British Columbia. The parasitoids are reared, on a continuing basis, on late L_3 or early L_4 aphids. At 20 °C, the larval stage lasts 8–9 days during which the parasitoid goes through three larval instars. At the end of the third instar, the mature larva consumes the host tissues and spins its cocoon inside the mummy. Within 4–6 days of pupation, the mature parasitoid adult emerges from the mummy after cutting a hole with its mandibles. The entire life cycle, from egg to adult, takes approximately two weeks.

CHAPTER II

LARVAL ONTOGENY OF *A. ERVI* INFLUENCED BY HOST SIZE AND GROWTH POTENTIAL AT PARASITIZATION

Introduction

Evolutionary models of host selection and reproductive decisions by parasitoids predict that, when host size varies, parasitoid size, frequently assumed to be an index of fitness, should increase with host size (*e.g.*, van den Assem 1971; Charnov 1979; Charnov *et al.* 1981; Charnov and Skinner 1984, Werren 1984, Werren and Simbolotti 1989). Large hosts are expected to be qualitatively superior for parasitoid growth and development because they contain more resources. Differences in host quality are expected to be evaluated relative to other hosts in the environment (Charnov 1979; Charnov *et al.* 1981). These predictions are based on the largely untested assumption that the quality of a host is a linear function of its size.

Although functionally easy to measure in terms of the outcome, relative host quality is operationally difficult to define. It refers to a diverse set of attributes that are related to parasitoid growth and development (Mackauer 1973, 1986). A working definition of host quality may be based on the observed impact of the host on the parasitoid's larval growth rate. Since the larval stages depend entirely on the host for all their nutritional/energetic requirements, the growth rate represents an appropriate measure of host quality. The parasitoid's growth rate will depend on the dynamics of food consumption and utilization by the host. Non-developing hosts such as insect egg and pupal stages represent a fixed

amount of resources that the parasitoid can potentially exploit, whereas hosts parasitized as larvae generally continue to feed, grow and develop until the parasitoid starts consuming host organs and tissues. The energy/resource budget of growing hosts varies during ontogeny (Klekowski and Duncan 1975; Randolph *et al.* 1975; Howell and Fisher 1977), implying that quality is an age dependent attribute of the host. The above considerations indicate the need for a critical examination of the relationship between parasitoid and host ontogenies, and between host size and host quality.

In this study I examined the dynamics of growth and nutritional integration in the association between the pea aphid and *A. ervi*. First, I describe parasitoid growth and development in different nymphal instars of the host under controlled laboratory conditions. Next, I compare trajectories of larval growth in different host instars by fitting non-linear regression equations to the data. Differences in growth trajectories are discussed in relation to host size and host quality, and their potential impact on parasitoid life history characteristics. I show that host quality is not a linear function of host size in the pea aphid-*A. ervi* association, and furthermore, that this result may be valid for a large class of host-parasitoid associations. I develop a conceptual physiological model that describes the hypothetical energy/resource budget of the host, and the manner in which competing nutritional demands of the host and the parasitoid may be satisfied.

Methods

Parasitoids used in experiments were 2-3 days old. They were individually mated and enclosed for about 2 h with aphids that were identical in age to

those used in the actual experiments. After 24 hours, 30–40 mated parasitoids were used to parasitize 420 aphids of desired age. Hereafter I adopted the experimental procedure of Mackauer (1986). A parasitoid was enclosed with one aphid in a gelatin capsule (size 00) and allowed to strike the aphid only once. All parasitizations were done within a 4–h period.

The stung aphids were separated into groups of about 35. Each group was reared on a single bean plant enclosed in a cylindrical plastic cage, 15.5 x 4 cm in dimension. The roots of the bean plant were washed to remove the soil and immersed in tap water. Under these conditions, the plants were able to sustain the parasitized aphids until the aphids died. At the mid–point of the parasitization interval a group of 20 unparasitized aphids were oven dried to obtain estimates of host dry weight (DW) at the time of attack. Weights of hosts and parasitoid larvae were obtained at 24–hour intervals, at the mid–point of the parasitization interval.

Beginning on the fourth day after parasitization until the emergence of adult parasitoids, one group of parasitized aphids was selected at random. The wet weight (WW) of each aphid was determined on a Mettler UM3 electronic balance. The aphid was then dissected on a numbered, pre–weighed pan, and the parasitoid larva was carefully separated from the aphid remains and transferred to a second pre–weighed pan. The larvae and associated host remains were oven dried at 100 °C for 3 days and then weighed. Because of their small size, parasitoids were weighed in groups of 5 on day 4, but individually on all subsequent days. WWs and DWs were also obtained for 30 unparasitized aphids of identical age that were reared under the same conditions

On the day that adult parasitoids eclosed, WWs of the adults were obtained at the scheduled time after killing them with fumes of ether, and DWs were obtained three days later. The procedure described above was carried out on four age/size classes of the host. These classes correspond approximately to the aphid's nymphal instars, L_1-L_4.

Statistical analysis involved fitting curvelinear regression models to the data with the aid of a least-squares procedure (NLIN) from the SAS library of statistical procedures (SAS 1985).

Results

Aphid and parasitoid growth

Characteristics of pea aphids at the time of parasitization are given in Table 2.1. The growth pattern of unparasitized pea aphids is typically sigmoid, with DW eventually reaching a plateau (Murdie 1969). Under the present rearing conditions, DW reached a plateau at age 9 days (Fig. 2.1). The growth curve in Fig. 2.1 can be described by a logistic equation of the form (regression MS = 34.83; error MS = 0.005):

$$H = 1.06 / (1 + \exp (4.97 - 0.78t_H)), \quad (1)$$

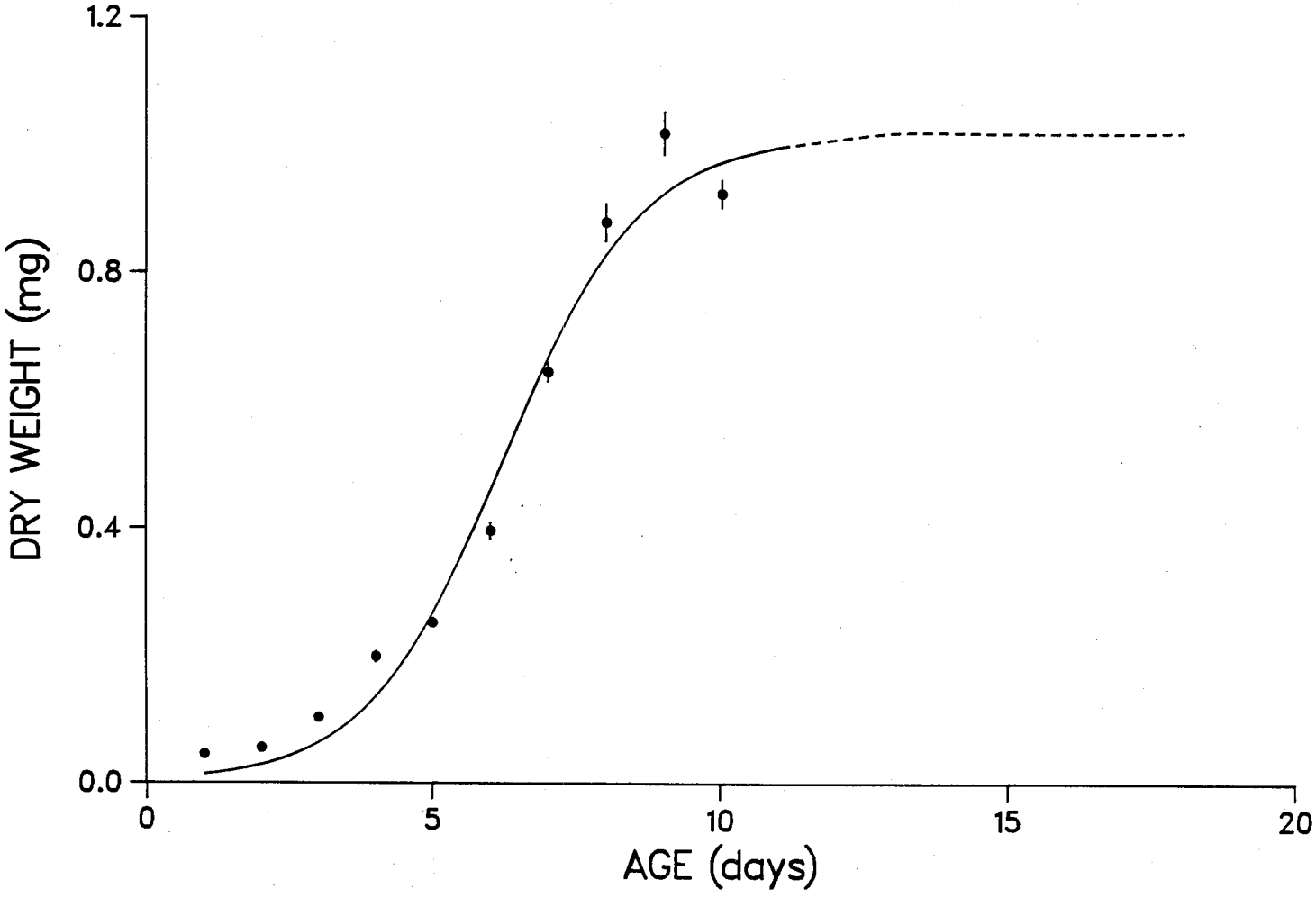
where H is aphid DW in mg and t_H is aphid age in days; the numerator gives the asymptotic host DW at maturity. The sample DW/WW ratio of unparasitized aphids increased from a mean of 0.198 (N = 30) on day 1 to 0.218 (N = 30) on day 10, with an overall mean of 0.203 (SD = 0.019; N = 300). The growth pattern of aphids parasitized at different ages and of the corresponding parasitoid immatures developing in them are shown in Figs. 2.2a-d. Aphids continued to gain

Table 2.1. Growth and developmental statistics of the pea aphid and *A. ervi*.

Pea aphid at parasitization				Parasitoid								
				Immatures				Adults				
N	Instar	Age	DW	N	$\bar{R}$	t_{max}	W_{max}	N	T	SR	DW_m	DW_f
20	1	24 ± 3	42 (4)	30	1.82	8	449 (46)	30	13	0.20	238 (32)	297 (36)
20	2	48 ± 3	71 (8)	30	1.47	8	514 (107)	43	12	0.19	254 (47)	258 (66)
20	3	72 ± 3	103 (10)	30	1.23	8	753 (117)	30	14	0.17	369 (40)	365 (32)
20	4	120 ± 3	285 (42)	20	1.53	8	674 (132)	24	13	0.54	297 (41)	333 (41)

Abbreviations: N = sample size; Age = host age at parasitization, in hours; DW = mean dry weight (± S.E.M.), in micrograms; $\bar{R}$ = mean relative growth rate, in micrograms per microgram.day; t_{max} = time from oviposition to attainment of maximum larval DW, in pivotal days; W_{max} = maximum larval DW (± S.D.), in micrograms; T = time from oviposition to 50% adult eclosion, in days; SR = proportion females among all progeny.

Figure 2.1. Mean daily dry weight (•) of the pea aphid from birth to maturity, measured at 20 °C, 55–65% r.h., and constant light. Vertical bars represent 95% confidence intervals. The smooth curve shows predicted daily dry weight given by Eq. (1) in the text.


1.2
0.8
0.4
0.0
DRY WEIGHT (mg)
0
5
10
15
20
AGE (days)

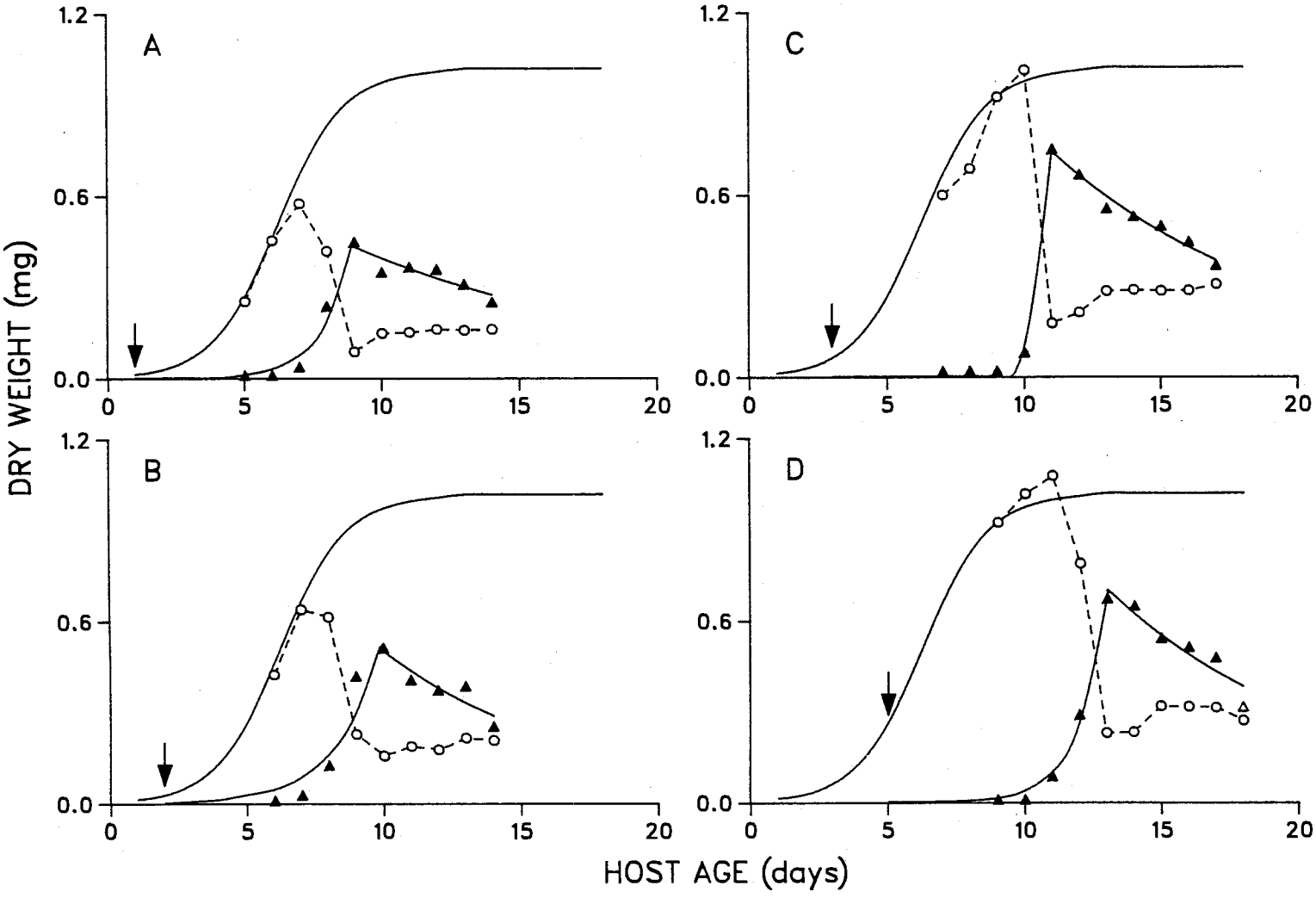
weight after parasitization, with the period of growth varying with host age at parasitization. In all host classes, the maximum DW of parasitized aphids agreed closely with that of their unparasitized counterparts at the same age; however, in parasitized aphids DW declined sharply after reaching a maximum.

The DW/WW ratios of the host+parasitoid complex were higher than those of their unparasitized aphids, increasing from an average, calculated over L_1–L_4, of 0.235 (N = 100; SD = 0.026) on day 4 after parasitization, to 0.371 (N = 110; SD = 0.024) on day 11. The DWs of the host+parasitoid complex were heavier than those of the corresponding unparasitized aphids. It should be noted that the overall weight changes in the host+parasitoid complex cannot be partitioned into host and parasitoid components, except with considerable error.

Parasitoids eclosed to the 1st-instar stage about 4 days after oviposition in all 4 host instars. The mean relative growth rate, $\bar{R}$ (Causton 1977; Causton and Venus 1981), measured over the period from 4–7 days, was lowest in L_3 and highest in L_1 aphids (Table 2.1). Because the observed growth pattern of *A. ervi* in L_3 was so obviously different from that in any other host class, I repeated the DW measurements for days 6 and 7 after parasitization; mean DWs did not differ between the 1st and the 2nd trial (1-way ANOVA, F = 3.24; df = 1, 58; P = 0.08).

In all four host instars, parasitoid larvae began destructive feeding on host tissues and embryos on day 7. At this time the proportion of maximum larval DW (*Wmax*) already achieved by parasitoids in L_1, L_2 and L_4 aphids ranged from 65–90%, whereas the corresponding figure in L_3 aphids was 30% (Fig. 2.2). The increase in DW on days 7 and 8 resulted mostly from the mass of host tissues

Figure 2.2. Mean daily dry weight of immature *A. ervi* (closed triangles) and the corresponding dry weights of parasitized (open circles) and unparasitized (sigmoid curve) aphids. Arrows indicate host age, t_H, at parasitization: A) t_H = 24h; B) t_H = 48h; C) t_H = 72h; D) t_H = 120h. Parasitoid age is obtained by subtracting age indicated by the arrow from host age. The turnover point in the parasitoid growth curves corresponds to parasitoid age 8 days.


A
B
C
D
1.2
0.6
0.0
0
5
10
15
20
DRY WEIGHT (mg)
HOST AGE (days)

and embryos ingested. *Wmax* was achieved in all four host instars at age 8 days (Table 2.2), when the fully grown 3rd instar larvae killed their hosts and spun cocoons inside the mummified aphids. Parasitoids developing in L_3 and L_4 aphids achieved a significantly higher *Wmax* than those that had L_2 and L_1 aphids as hosts, in that order (1-way ANOVA, $F = 50.86$; $df = 3, 116$; $P < 0.000$; SNK test for multiple comparisons, $P < 0.05$). The median developmental time (from oviposition to ≥ 50% eclosion) varied between parasitoids developing in different host classes, with those from L_2 hosts eclosing first from the mummy (Table 2.1).

Analysis of parasitoid growth curves

The increase in dry weight of *A. ervi* in the growth phase (Fig. 2.2) follows a continuously increasing exponential curve with a sharp cut-off (J-curve) characteristic of many invertebrate endoparasitoids (Calow 1981a; Sibly and Calow 1986). The loss of dry weight in the pupation phase follows an exponential decay curve (Fig. 2.2). Because the two phases are physiologically and functionally distinct, I analysed them by fitting a curvelinear function to the logarithmic growth and pupation phases separately. The form of the equation is:

$$P = \exp (\mathbf{A} + \mathbf{B}t_P), \qquad (2)$$

where P is parasitoid DW in mg, t_P is parasitoid age in days, and **A** and **B** are fitted parameters. The form of Eq. 2 was selected for several reasons. First, it reflects the exponential nature of growth and development in *A. ervi*. Taking the logarithm of both sides of Eq. 2 yields the familiar form of the linear regression equation which facilitates a direct comparison of growth curves in different host instars. Second, with only two parameters, the equation is relatively simple and provides a good fit to the exponential-growth and pupation phases in all four

host instars. Estimated parameter values for Eq. 2 and goodness-of-fit statistics are given in Table 2.2.

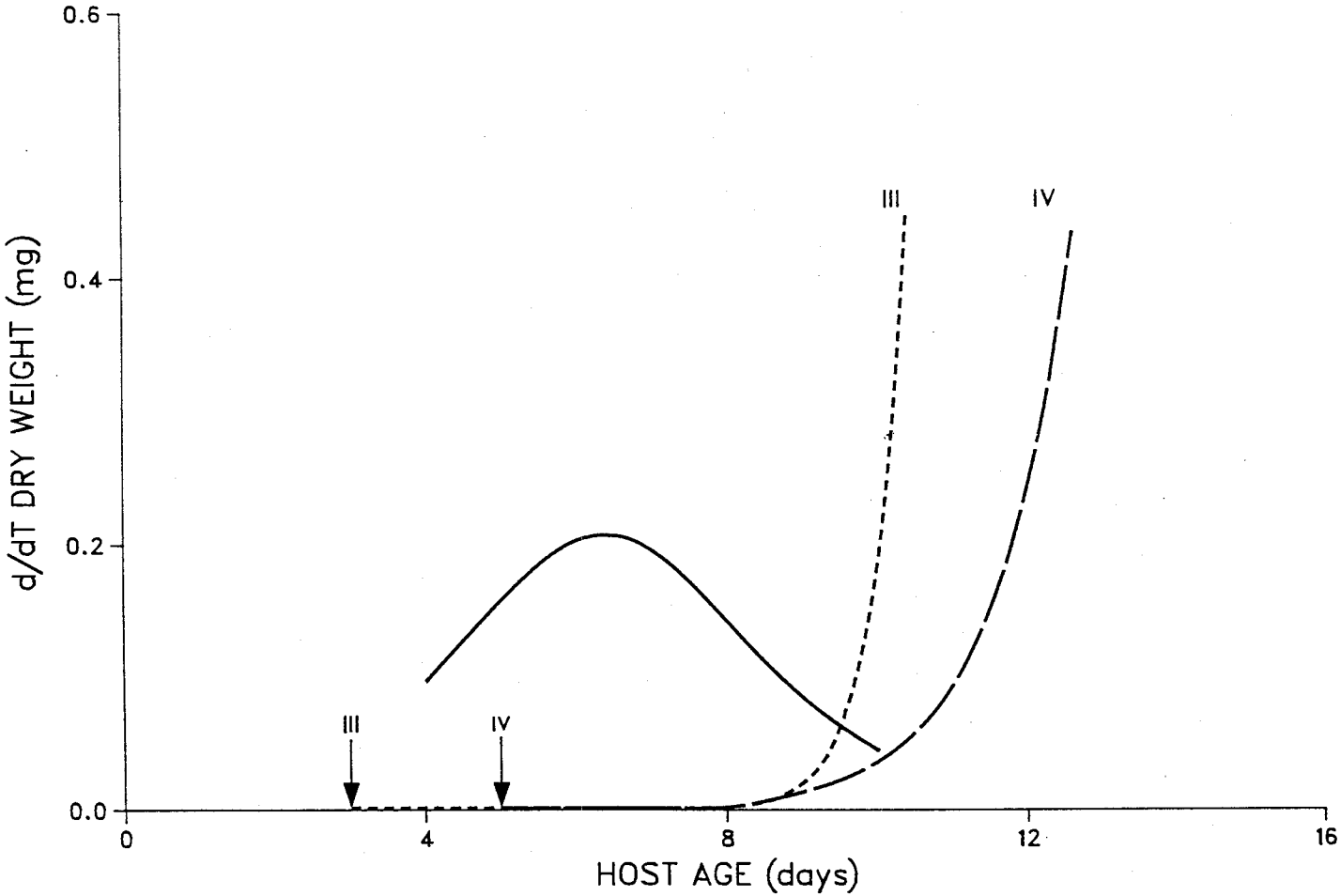
In the growth phase, the parameters **A** and **B** of Eq. 2 characterize the dynamic nature of the growth trajectory. The relative influence of each parameter on the growth trajectory depends upon the age of the parasitoid larva. **A**, analogous to the y-intercept, has a relatively greater influence on the parasitoid's growth rate in the embryonic stages of growth. This is clearly evident from the right hand side of Eq. 2, which tends to $exp(\mathbf{A})$ for values of t_P close to 0. The shape to the growth trajectory in the post-embryonic stages, *i.e.*, the rate of increase in weight during the last 2-3 days of growth, is determined mainly by the value of **B**. When Eq. 2 is fitted to the pupation phase, the interpretation of the parameters is the same as above, except that the equation now describes the rate of weight loss during pupation. From Table 2.2 it can be seen that parasitoid larvae in L_2 aphids started off with the highest initial growth rate in the embryonic stages but achieved the lowest growth rate in the post-embryonic stages. By comparison, parasitoids from L_3 showed exactly the opposite pattern, growing at the lowest and highest rates in the embryonic and post-embryonic stages, respectively. The growth trajectories in L_1 and L_4 were not significantly different, with growth rates that were intermediate in magnitude, despite considerable differences in aphid size at parasitization (Table 2.1).

The derivatives of Eqs. 1 and 2 with respect to time give the instantaneous rates of growth for host and parasitoid, respectively (Fig. 2.3). As can be seen, parasitoids developing in L_3 aphids hatched to the first instar while the host was still growing at a high rate, t_H = 6-6.5 days. However, quantitatively detectable logarithmic growth was delayed until about day 8, a time when host growth had

Table 2.2. Estimates of parameters **A** and **B** and goodness-of-fit statistics for Eq. (2) describing the growth of *Aphidius ervi* in four age groups of the pea aphid (see text for details).

Host age (h)	Parasitoid growth parameters				Reg. MS	Error MS
	A	(95% C.I.)	B	(95% C.I.)		
		Logarithmic growth phase				
24	-7.92	(-8.44; -7.39)	0.89	(0.83; 0.96)	3.82	0.002
48	-5.47	(-6.05; -4.89)	0.61	(0.53; 0.69)	6.54	0.010
72	-17.94	(-20.03;-15.84)	2.21	(1.94; 2.47)	8.61	0.004
120	-8.00	(-8.76; -7.24)	0.95	(0.85; 1.05)	5.48	0.006
		Pupation phase				
24	-0.11	(-0.23; 0.02)	-0.09	(-0.10;-0.08)	11.08	0.002
48	0.48	(0.25; 0.71)	-0.15	(-0.17;-0.12)	12.14	0.007
72	0.58	(0.48; 0.68)	-0.11	(-0.12;-0.10)	32.68	0.006
120	0.65	(0.45; 0.84)	-0.12	(-0.14;-0.11)	17.75	0.009

Figure 2.3. Rate of change of parasitoid dry weight in parasitized L_3 and L_4 aphids in relation to that of unparasitized (solid curve) aphids. Arrows indicate host age at parasitization.


0.6
0.4
0.2
0.0
d/dT DRY WEIGHT (mg)
III
IV
III
IV
0
4
8
12
16
HOST AGE (days)

declined appreciably. By comparison, parasitoids developing in L_4 aphids hatched to the first instar at about t_H = 8–8.5 days and began logarithmic growth immediately.

Discussion

Nutritional ecology of host-parasitoid interactions

The availability of nutrients for parasitoid growth and development is the basic determinant of host quality, whereas host size (dry weight) is a measure of the total biomass present at a given time. The availability of nutrients can vary independently of host size if the parasitoid competes with the actively growing somatic tissues and embryos of the host for nutrients from the haemolymph. An evaluation of several indices of host quality based on quantitative interactions between *A. ervi* and the pea aphid indicates that host quality is not a linear function of host size throughout the range of observed sizes.

Parasitoid size increases as host size increases from L_1 to L_3, but parasitoids from L_4 aphids are smaller than those from L_3 (Table 2.1). However, the dry weights given in Table 2.1 were obtained soon after eclosion from the mummy, and are only approximate indicators of size. Starved adult parasitoids lose a considerable proportion of their dry weight between eclosion and death (Henkelman 1979), with the highest rate of weight loss observed soon after eclosion. Under the present experimental conditions, the time interval between parasitoid eclosion and weighing varied within and between cohorts of parasitoids from different host instars because the weights were obtained at fixed daily intervals, whereas parasitoids eclosed over a period of 36–48 hours. When the

bias resulting from differential weight loss was eliminated, the dry weights of parasitoids from L_3 and L_4 aphids were not significantly different (see Chapter III).

Using adult parasitoid size as an index of fecundity and of host quality for growth and development, it can be concluded that host quality increases linearly with host size only up to the third aphid instar. Since parasitoids reared from third and fourth instar aphids do not differ in size, the relative quality of these two aphid instars must be evaluated using other criteria.

The commencement of destructive feeding by the parasitoid larva marks a change in its mode of nutrient acquisition, from surface absorption and ingestion of haemolymph material to consumption of undigested host tissues and embryos (Cloutier 1978, 1986; Polaszek 1986). At the beginning of destructive feeding on day 7, quality differences between the four aphid instars could be described based on the DWs of parasitoid larvae growing within them (Fig. 2.2) as $L_2 > L_4 > L_1 > L_3$. This rank order indicates the cumulative effect of growth conditions in the different aphid instars during embryonic and early larval development of the parasitoid. On the assumption that larval DW is an adequate indicator of nutrient reserves accumulated, L_2 and L_3 represent the extremes in host quality for the parasitoid in the early stages of parasitism.

In the later stages, the above rank order changes because L_1 and L_2 aphids, due to their limited growth potential, do not permit the parasitoids to achieve their maximum potential size. Thus, at the commencement of pupation, on day 8, the rank order of larval DWs is $L_3 > L_4 > L_2 > L_1$. This order, however, may not reflect differences in host quality because dry weight gain by parasitoid larvae

between days 7 and 8 is mostly due to their gut contents, *i.e.*, host tissues and embryos consumed. On day 7, parasitoids in L_3 aphids were, on average, 3.6 times smaller than their counterparts in L_4 aphids (Fig. 2.2). As a result, the former presumably ingested a significantly larger mass of host tissues and embryos than the latter to begin pupation on day 8. This would explain the longer total developmental time (Table 2.1) and the sudden jump in larval dry weight between days 7 and 8 in L_3 aphids.

The observed sex ratio differences between host instars are probably due to host quality differences. The fact that more female *A. ervi* emerged from L_4 aphids than any other host instar (Table 2.1) is consistent with the interpretation that L_4 aphids support the optimal growth trajectory, but due to small sample sizes sex ratio differences must be interpreted cautiously. It is also possible that sex ratio differences (Table 2.1) may have biased the differences between growth trajectories in the four aphid instars. However, any such bias is unlikely to account for the differences, particularly because the ratio of female to male dry weight is only 1.10 (see Chapter III).

Evidence from the published literature on a wide range of host parasitoid associations supports the hypothesis of a nonlinear relationship between the size of a host at a given time and its quality for parasitoid growth and development. Salt (1940) found that adult size of the egg parasitoid *Trichogramma evanescens* increased with host size (species) but developmental time varied non-linearly, being longer in the largest and smallest hosts than in the medium sized hosts. However, Salt's results should be interpreted cautiously because his comparisons were interspecific. Jones and Lewis (1971) measured the size and developmental time of *Microplitis croceipes* developing in all larval stages of the corn earworm,

Heliothis zea. Parasitoid size was positively correlated with host size, but developmental time was longer in the smallest and biggest hosts than in the medium sized hosts.

Miles and King (1975) evaluated the quality of all instars of the sugarcane borer, *Diatraea saccharalis*, for the tachinid parasitoid, *Lixophaga diatraeae*, based on successful completion of parasitoid larval and pupal stages, and developmental time. Again, the smallest and biggest host instars were least suitable for the parasitoid. The highest percentage emergence of flies and the shortest developmental times were observed in the middle host instars. In the interactions between *Encarsia formosa* and the greenhouse whitefly, *Trialeurodes vaporariorum* (Nechols and Tauber 1977), parasitoid survival was higher and total developmental time shorter in third, fourth and transitional sub-stage whiteflies than in the first and second instars, and pharate adults.

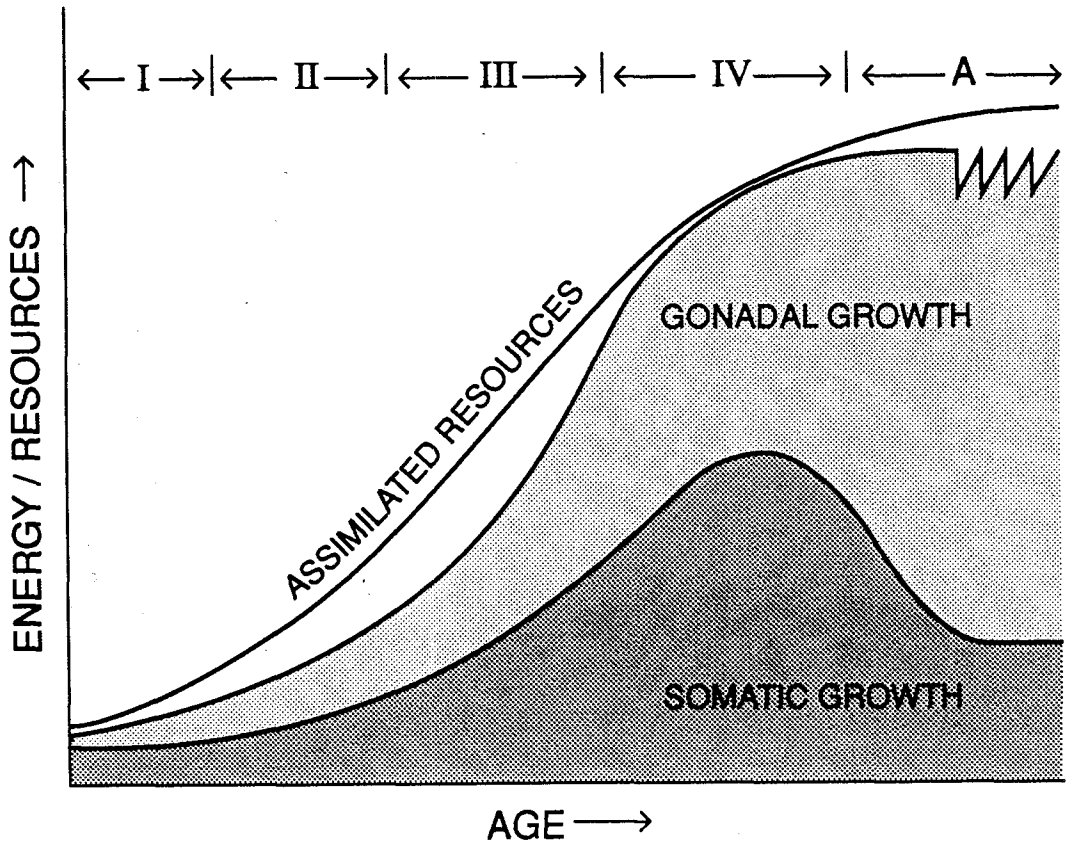
In all the studies cited above, parasitoid size is generally positively correlated with host size but developmental time clearly varies non-linearly. Differences in developmental time imply differences in parasitoid growth rates, and thereby provide an index of relative host quality. In other host-parasitoid associations, the positive correlation between host size and parasitoid size is confirmed, but developmental time increases with host size in some associations (*e.g.*, Arthur and Wylie 1959; Vinson 1972; Lawrence *et al*. 1976) and decreases in others (Smilowitz and Iwantsch 1973; Nechols and Kikuchi 1985). These findings indicate that host quality is a highly variable attribute during ontogeny.

Physiological aspects of host and parasitoid growth

The interactions between *A. ervi* and the pea aphid in the early stages of parasitism can be viewed as a struggle for control over a pool of resources. The presence of a parasitoid egg within the aphid can be expected to invoke competition between "host" and "parasitoid" tissues for resources. In this competitive situation, the growth of host and parasitoid tissues will depend upon the interaction of the respective resource utilization profiles and competitive abilities at any given time. A hypothetical model representing the relationship between assimilated and utilized resources, and the partitioning of utilized resources between the subsystems of aphids is shown in Fig. 2.4. The model combines age specific energetics of aphids (Llewellyn 1972; Randolph *et al.* 1975; Cloutier 1978) with energy changes in aphids during reproduction (Kindlmann and Dixon 1989). Cumulative change in assimilated resources is assumed to follow a sigmoid curve over time. The proportion of assimilated resources utilized varies with growth rate during development (Waldbauer 1968; Duncan and Klekowski 1975; Randolph *et al.* 1975), always being less than one (Waldbauer 1968; Grodzinski 1975; Duncan and Klekowski 1975; Calow 1977b; Kováč 1987). For simplicity, the utilized resources are assumed to be partitioned between the functions (*i.e.*, growth, development and maintenance) of embryos and somatic tissues of the host.

Early in aphid development most of the utilized resources are allocated to somatic growth (Fig. 2.4). From the fourth instar onward, allocation to the gonads increases exponentially. At maturity allocation to somatic growth peaks and begins to decline, whereas allocation to the gonads continues to increase (Fig. 2.4). Aphids go through a pre-reproductive period after the final moult to adulthood

Figure 2.4. A hypothetical model of resource assimilation and utilization in aphids. Assimilated resources are assumed to be utilized for gonadal growth and somatic growth. For simplicity, resources utilized for "growth" include those needed for maintenance and respiration. Roman numerals represent nymphal instars. Vertical bars indicate approximate time of moult. See text for explanation.


← I →|← II →|← III →|← IV →|← A →
ENERGY / RESOURCES →
ASSIMILATED RESOURCES
GONADAL GROWTH
SOMATIC GROWTH
AGE →

during which somatic growth ceases and resources are used mainly for maintenance. Consequently, allocation to the soma declines and levels off. A large proportion of utilized resources is now allocated to growth and maintenance of embryos (Fig. 2.4).

Gonadal growth of aphids is maximized throughout their development (Kindlmann and Dixon 1989) but the volume of the haemocoel may represent a potential constraint on the size of the gonads and the amount of resources they can utilize. Offspring production will reduce the size of the gonads, allowing the excess energy to be utilized for ovulation or growth of immature embryos. As aphids reproduce singly, the pattern of resource utilization during reproduction will resemble a saw-tooth graph (Fig. 2.4; see also Kindlmann and Dixon 1989).

Fig. 2.4 shows two bottlenecks in the volume of available (= assimilated - utilized) resources; during the early first- and fourth-instar stages. Newborn aphids are presumably more susceptible to dessication, and may also be constrained by feeding rate. In the fourth instar, the aphid has to support exponential growth in its own soma, that of its embryos, and the gonads of the embryos. During this period the aphid achieves the highest instantaneous rate of weight gain. This is clearly seen in the growth rate achieved between days 6-8 (Fig. 2.1).

There is some empirical evidence to support the hypothetical model shown in Fig. 2.4. Brough *et al.* (1990) quantified the relationship between somatic and gonadal growth during larval development in the vetch aphid, *Megoura viciae* Buckton. The change in gross dry weight follows a sigmoid curve. Somatic growth is also sigmoid. The ratio of gonadal to somatic dry weights increases exponentially with age. The English grain aphid, *Sitobion avenae* (Fab.) shows a

similar pattern of somatic and embryonic growth (Newton and Dixon 1990). The overall growth of the pea aphid is also logistic (Fig. 2.1), suggesting that the relationship between somatic and gonadal growth will be similar to that seen in *M. viciae* and *S. avenae*. The similarity of the general growth pattern in these three aphid species suggests that it may be common to most parthenogenetically reproducing species.

Observational reports on the embryogenesis of other aphid species, for example, *Macrosiphum tanaceti* (Uichanco 1924), *Brevicoryne brassicae* (Bruslé 1962), *Aphis fabae* (Banks 1964; Tsitsipis and Mittler 1976) suggest a pattern of embryo growth and development similar to that described by Brough *et al.* (1990). Embryos are derived from successively ovulated eggs. One egg is ovulated in each instar. Development of same-aged embryos in different ovarioles is simultaneous. The most developed embryos start ovulating when their mother is approximately in the fourth-instar stage. Pre-reproductive adult virginoparae contain a large number of differentiated embryos. For instance, *M. viciae* contained an average of 108 embryos (Lees 1959) and *A. fabae* contained 72 embryos (Tsitsipis and Mittler 1976).

Evidence to support the existence of a resource availability bottleneck in aphids between the third instar and adulthood comes from studies on comparative embryogenesis in apterous and alate virginoparae. Tsitsipis and Mittler (1976) found that in *Aphis fabae* reared under short and long day length conditions, alate virginoparae contained fewer and considerably smaller embryos under both conditions. There was a delay in embryogenesis in third-instar alatiforms during the initiation of wing buds. Embryogenesis ceased completely in the fourth instar during the development of wings. Tsitsipis and Mittler (1976) attribute this to

channelling of resources toward developing wings rather than to formation and development of embryos. These findings support the observations of Johnson (1957, 1959) on several aphid species. He found that ovulation and development of embryos ceased during wing development, but resumed following autolysis of the flight muscles.

Growth trajectories of *A. ervi* in response to host size/age at parasitization can now be evaluated within the conceptual framework provided by Fig. 2.4. Soon after the parasitization of the host, the nutritional requirements of the parasitoid can be considered negligible due to its extremely small size, and resources are expected to be acquired passively from the haemolymph. This is reflected in host growth, which is close to normal in all host classes (Fig. 2.2; see also Cloutier 1978; Cloutier and Mackauer 1979). The nutritional requirements of the parasitoid increase with its size, particularly following hatching of the egg to the first instar larval (Cloutier and Mackauer 1979). Exponential growth begins in the first instar stage but a critical size must be achieved before the larva can effectively compete with the host and embryos for nutrients. Upon achieving critical size, the parasitoid assumes control over the assimilated resources by virtue of its superior competitive ability, resulting in negative growth of the host (Fig. 2.2).

The hypothetical scenario presented above and in Fig. 2.4 provides a good explanation for the results obtained in this and other studies. When the aphid is parasitized at age 3 day, the egg hatches between days 6 and 6.5, a period when the host is growing at the maximum rate (Fig. 2.3). The resultant bottleneck in resource availability (Fig. 2.4) delays parasitoid growth until the host moults to the adult stage, when competition for resources from the somatic tissues decreases. By contrast, in a host parasitized at age 5 days, the parasitoid egg

hatches between days 8 and 8.5, by which time the host has completed most of its growth (Fig. 2.3). In this case the larva achieves a high growth rate early in the first instar, and maintains it until pupation.

At critical size, the parasitoid larva is large enough to prevent resource bottlenecks by suppressing the nutritional requirements of either the host or the embryos within it. The gross internal morphology of the pea aphid parasitized by *A. ervi* reveals that somatic tissues remain unaffected whereas embryos degenerate considerably prior to the beginning of destructive feeding by the parasitoid (Soldan and Starý 1981; Polaszek 1986). Therefore, prevention of resource bottlenecks is probably through physiological suppression of the embryos. Suppression of embryo growth, resulting in their degeneration, is thought to be caused mainly by a nutrient deficiency due to competition with the parasitoid larva (Corbet 1968; Soldan and Starý 1981; Thompson 1983b; Polaszek 1986).

The foregoing discussion leads to the conclusion that the ontogeny of immature *A. ervi* may be characterized by a passive (non-destructive) mode of resource acquisition until just prior to the commencement of destructive feeding. Early in the association, availability of nutrients for the parasitoid depends upon the resource budget of the host. In the advanced stages, the parasitoid competes for resources with the embryos, leaving the soma more or less unaffected. This differential effect may be achieved if the embryo and the soma have different nutritional requirements. Competition for certain elements of the nutrient composition (*e.g.*, amino acids) may affect embryo growth more than somatic growth. Extra-embryonic factors such as teratocytes (Salt 1968) may effectively increase the mass of "parasitoid tissue" competing for resources and provide the parasitoid larva with food (Polaszek 1986). In doing so, two purposes would be

served. First, a direct onslaught on host tissues would be avoided and second, nutrients could be effectively diverted from a specific subsystem of the host, *e.g.*, embryos. The trophic role of teratocytes postulated here in no way denies other possible functions they may have in different systems. For example, their role in hosts such as lepidopteran larvae and eggs may be secretory as well as trophic (Strand 1986).

CHAPTER III

THE COVARIANCE OF ADULT SIZE AND DEVELOPMENTAL TIME IN RELATION TO JUVENILE ONTOGENY AND HOST SIZE IN *A. ERVI*

Introduction

Adult size at maturity, often considered an index of fecundity, and developmental time influence lifetime reproductive success in different ways; the benefits of increased fecundity may be offset if developmental time increases concommitantly (Lewontin 1965; Roff 1981). By varying size and developmental time, organisms may be able to maximize lifetime reproductive success in different environments. When the growth rate is constant, an increase in body size can be achieved only at the expense of an increase in developmental time. Alternatively, an increase in size with a concommitant decrease in developmental time could be achieved by increasing the growth rate (Sibly *et al.* 1985; Sibly and Calow 1986; Stearns and Koella 1986).

Growth rates and the resulting phenotypes produced in response to environmental heterogeneity can vary only within limits imposed by developmental and genetic constraints (Ricklefs 1979, Stearns 1980). Within these bounds, variability in phenotypic traits is ultimately the result of resource partitioning between competing functions such as cellular growth and differentiation rates, fecundity and survivorship (Murdoch 1966; Law 1979; Ricklefs 1979; Boggs 1981). Developmental patterns and genetic connections between traits can result in correlated responses or tradeoffs in different environments (Schaffer 1974; Rose 1982; Murphy *et al.* 1983; Stearns 1983b; Bell 1984a, b). Thus, patterns of

covariation between fitness-related traits of adult parasitoids may be indicative of the mechanism(s) by which life history is adjusted in response to developmental stress and/or variation in resource availability.

In this chapter, I examined variation in adult size (dry weight) and developmental time of *A. ervi* in relation to amount and availability of food resources (host size). I show that a distinct pattern of covariation between traits emerges in response to increasing host size. Parasitoids utilize resources to maximize size before minimizing developmental time. Parasitoid size and developmental time are positively correlated only when host size is a limiting factor for parasitoid growth and development. The results could be explained on the basis of constraints imposed by the size and growth pattern of the host on the immature parasitoid (Chapter II), and the epigenetic structure of body size and developmental time. The pattern of covariation between the traits suggests that adult size and developmental time may be structurally independent and result from sequentially expressed (genetic) developmental subprograms.

Methods

Cohorts of uniform-aged aphids from each of the four nymphal instars of the pea aphid, L_1-L_4, were produced by following the procedure given in Chapter I (Table 3.1). From each cohort, 120 aphids were randomly selected and separated into groups of 30. Mated 2-3-day-old *A. ervi* females were used to parasitize the aphids singly, in capsules (size 00). To gain experience in handling aphids, parasitoids were enclosed for 2 hours with aphids that were similar in age and size to the experimental aphids. In the experiments, parasitoids were allowed to

strike each aphid only once to avoid superparasitism. Each group of 30 aphids was parasitized by 3 females used in sequence. Females used to parasitize one group of aphids were not used again. All parasitizations were done within a period of one hour. At the mid-point of the parasitization interval, 20 experimental aphids were oven dried to obtain their dry weight (DW) at the time of parasitization. The entire experimental procedure was replicated 3 times for each aphid instar.

After parasitization, groups of 30 aphids were confined to individual broad bean stalks that were enclosed in circular plastic cages of dimension 15.5 x 4 cms, and immersed in tap water. The aphids were reared in a growth chamber at 20 ± 0.2 °C, 65% r.h., and constant light. On the 12th day after parasitization, aphids that had mummified (contained a parasitoid pupa) were enclosed singly in gelatin capsules arranged in a grid. The capsules were placed under a video camera for continuous observation to obtain precise (± 45 min) estimates of individual parasitoid developmental time, T_P. Upon eclosion, the parasitoids were allowed to die in the capsules, oven-dried for 3 days, and weighed on a Mettler UM3 electronic balance.

The data were analysed by analysis of variance and multivariate discriminant analyses using the SPSS^X library of statistical programs (SPSS^X 1983).

Results

Within instars, aphid DW at the time of parasitization increased with replication number because aphids continued to grow between replication intervals (Table 3.1). Aphids parasitized in the L_1 stage died in the fourth instar, whereas

Table 3.1. Oviposition success and F_1 sex-ratio[1] of *A. ervi* in relation to aphid instar, age[2] and weight[3] at the time of parasitization.

	Aphid Instar			
	L_1	L_2	L_3	L_4
Replicate 1				
Host age	22	46	70	118
weight	39 (6)	64 (9)	93 (7)	284 (47)
Replicate 2				
Host age	24	48	72	120
weight	42 (4)	68 (8)	104 (9)	247 (19)
Replicate 3				
Host age	26	50	74	122
weight	44 (5)	75 (6)	111 (9)	262 (45)
Mummies monitored	283	266	254	258
Mummies emerged	278	259	244	255
Sex-ratio	0.17	0.21	0.14	0.44

[1] number of females as a proportion of the total number of parasitoid offspring.
[2] in hours (± 2).
[3] in micrograms, mean (S.D.).

when parasitized in the L_2 stage, some died in the fourth instar (45%) and the remainder died as adults (55%). Aphids parasitized in the L_3 and L_4 stages died as adults. In all four aphid instars, parasitoids completed larval development within 8–8.5 days after parasitization. The emerging adult parasitoids were assigned to one of 5 classification groups, *viz.*, L_1, L_2(IV), L_2(A), L_3 and L_4, on the basis of the host instar at the time of parasitization and the host stage at the time of death (Table 3.2).

Statistical differences in parasitoid DW and T_P between different categorical levels were tested by a nested analysis of variance (Table 3.3). DW was significantly different among groups, replicates within groups and sexes within replicates. T_P differed significantly among groups and replicates within groups, but not between the sexes (Table 3.3). The F_1 sex-ratio varied non-linearly with host instar (Table 3.1). Aphids parasitized as L_4 produced the most female parasitoids whereas L_3 produced the least.

DW and T_P of individual parasitoids increased as host size at parasitization increased from L_1 to L_3 (Fig. 3.1a). Parasitoids reared from L_4 did not increase further in size than their counterparts from L_3 aphids, but emerged significantly earlier (For DW: ANOVA df = 1, 351; F = 2.636; P = 0.105; For T_P: ANOVA df = 1, 351; F = 28.612; P < 0.000). Aphids parasitized as L_2 produced parasitoids that fell into two distinct clusters (Fig. 3.1b); those emerging from fourth-instar mummies (L_2 IV) had the characteristics of group 1, whereas those from adult mummies had the characteristics of group 3. Female parasitoids were generally larger than males, but total developmental time appeared to be similar in both sexes, regardless of differences in host size at the time of parasitization (Figs. 3.2a–b).

Table 3.2. Total developmental time (T_P) and dry weight (DW) of *A. ervi* reared in the four nymphal instars of the pea aphid.

Variable label			T_P (hours)			DW (micrograms)			
			mean	S.D.	C.V.	mean	S.D.	C.V.	N
L_1: M		rep 1	319.13	(8.21)	2.57	155	(11)	7.10	76
		2	316.22	(7.78)	2.47	155	(10)	6.45	72
		3	321.12	(11.57)	3.61	158	(13)	8.23	84
	F	rep 1	323.86	(6.91)	2.13	166	(10)	6.02	11
		2	319.46	(7.49)	2.35	174	(10)	5.75	25
		3	325.95	(8.49)	2.61	173	(13)	7.51	10
L_2: M	IV	rep 1	316.43	(7.56)	2.40	164	(15)	9.15	44
		2	315.57	(10.89)	3.45	159	(14)	8.81	37
		3	331.33	(14.51)	4.38	158	(11)	6.96	6
	A	rep 1	326.96	(10.39)	3.18	194	(15)	7.73	26
		2	325.09	(12.94)	3.97	207	(20)	9.66	27
		3	328.86	(9.96)	3.04	202	(20)	9.90	65
	F IV	rep 1	323.67	(8.04)	2.47	180	(13)	7.22	14
		2	318.50	(9.83)	3.08	186	(16)	8.60	12
		3	327.88	(4.64)	1.40	176	(7)	3.98	4
	A	rep 1	328.42	(8.39)	2.56	215	(10)	4.65	6
		2	326.00	(12.64)	3.87	219	(12)	5.48	9
		3	335.06	(8.20)	2.45	213	(13)	6.10	9
L_3: M		rep 1	333.88	(8.27)	2.49	220	(23)	10.95	70
		2	339.44	(12.62)	3.71	221	(23)	10.41	56
		3	333.29	(11.12)	3.33	218	(22)	10.09	85
	F	rep 1	337.20	(7.37)	2.19	236	(15)	6.36	15
		2	335.37	(9.52)	2.83	231	(21)	9.09	12
		3	333.08	(9.98)	3.00	238	(11)	4.62	6
L_4: M		rep 1	311.09	(8.52)	2.76	234	(25)	10.68	49
		2	312.54	(12.21)	3.90	219	(19)	8.68	48
		3	316.23	(10.85)	3.45	217	(19)	8.76	45
	F	rep 1	312.57	(4.56)	1.47	247	(17)	7.29	43
		2	315.21	(6.53)	2.06	246	(13)	5.28	34
		3	320.15	(10.27)	3.22	244	(23)	9.43	36

Abbreviations: C.V. = Coefficient of Variation; L_1–L_4 = aphid instar at the time of parasitization; M, F = male and female parasitoids, respectively; rep = replication number; IV, A = fourth-instar and adult mummy, respectively; N = sample size.

Table 3.3. Nested analysis of variance on parasitoid DW and T_P. Parasitoids were classified by host group, replicates† (rep) within groups and sex within replicates. All classification factors were treated as fixed. Tests of all hypotheses are based on Type III sums-of-squares (SAS 1985).

Dependent variable: DW

source	df	SS	MS	F	Pr > F
Group	4	5.60×10^{-1}	1.40×10^{-1}	442.93	0.0001
Rep(Group)	10	6.70×10^{-3}	6.70×10^{-4}	2.12	0.0205
Sex(Group(Rep))	15	6.40×10^{-2}	4.27×10^{-3}	13.50	0.0001
Error	1006	3.18×10^{-1}	3.16×10^{-4}		

Dependent variable: T_P

source	df	SS	MS	F	Pr > F
Group	4	34628.59	8657.15	90.71	0.0001
Rep(Group)	10	4733.19	473.19	4.96	0.0001
Sex(Group(Rep))	15	2399.13	159.94	1.68	0.0501
Error	1006	96009.94	95.44		

† replication was treated as a fixed effect because aphids continued to grow between parasitization intervals, resulting in *a priori* differences between replicates.

Figure 3.1. Developmental time and dry weight of male *A. ervi*: A) Parasitoids reared from pea aphids parasitized as L_1 (Δ), L_3 (O) and L_4 (X). B) Parasitoids reared from L_2 aphids that mummified in the fourth-instar stage (inscribed squares) and in the adult stage (open squares).

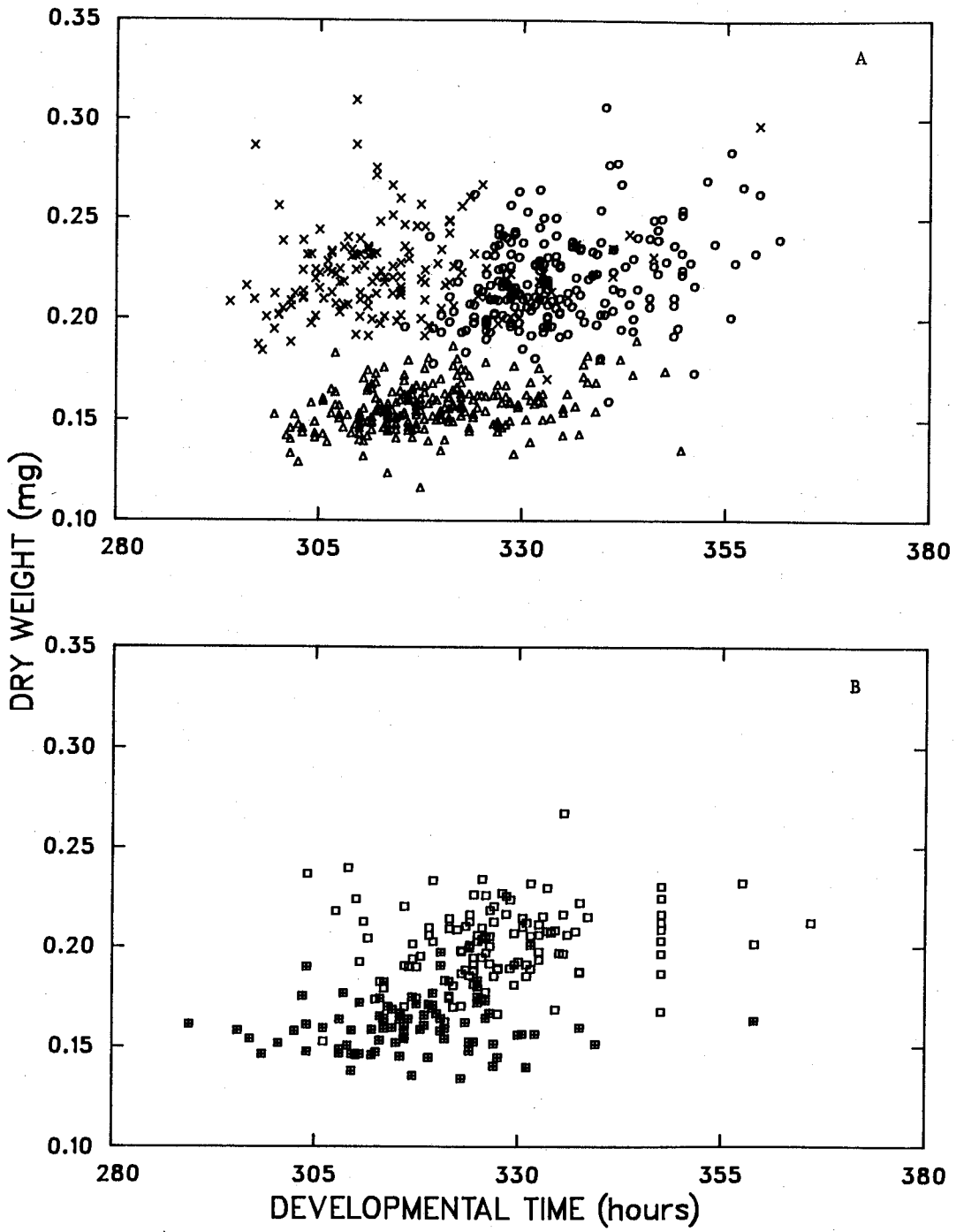
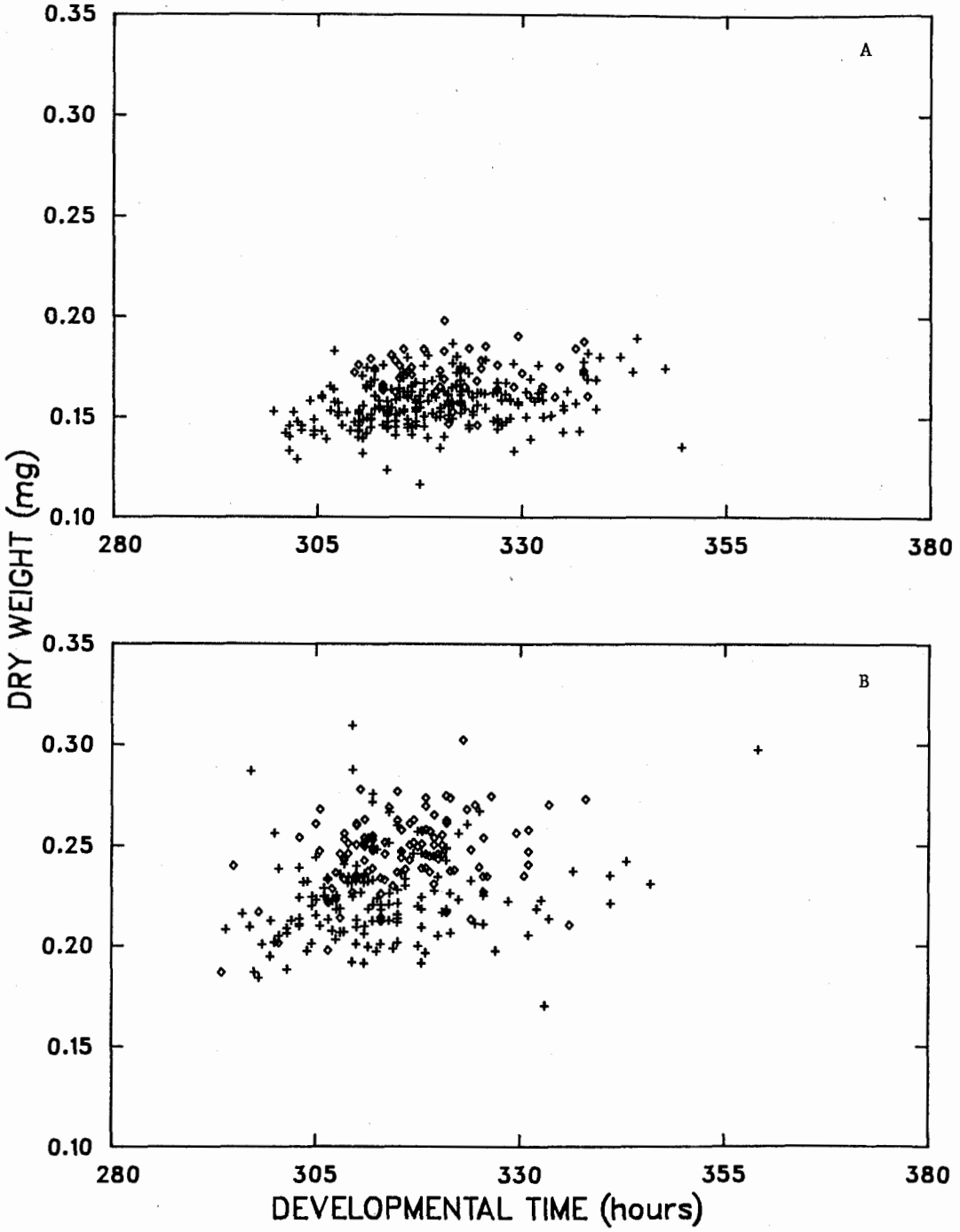

A
B
0.35
0.30
0.25
0.20
0.15
0.10
280
305
330
355
380
DRY WEIGHT (mg)
DEVELOPMENTAL TIME (hours)

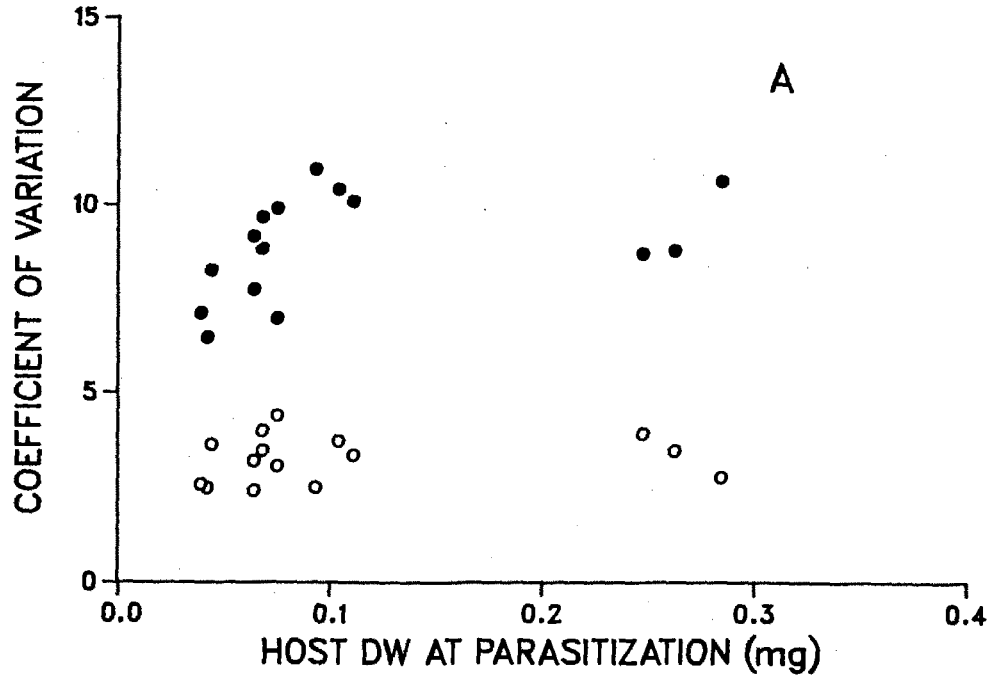
Figure 3.2. Developmental time and dry weight of *A. ervi* males (crosses) and females (diamonds) emerging from aphids parasitized as A) L_1 and B) L_4.

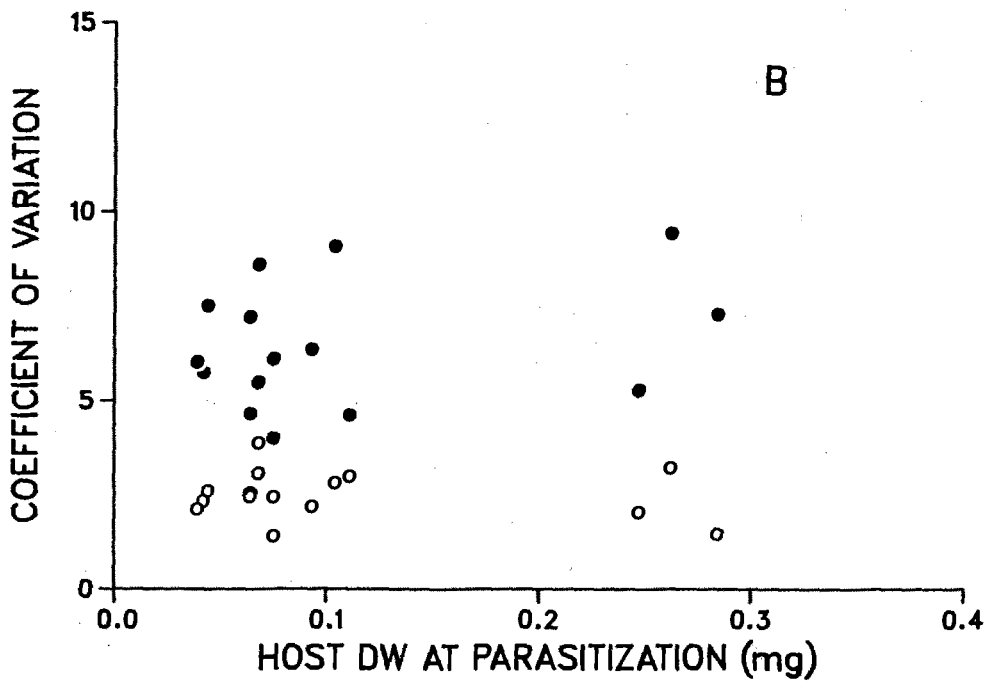

A
B
0.35
0.30
0.25
0.20
0.15
0.10
280
305
330
355
380
DRY WEIGHT (mg)
DEVELOPMENTAL TIME (hours)

Within groups, differences between replicates were analysed separately for males and females using analysis of variance. The results given below are for males only; the pattern of statistical significance was the same for females. Parasitoids within L_1, L_2(IV) and L_3 differed in T_P between replicates (ANOVA 5.21 $\leq F \leq$ 7.13; 0.001 $\leq P \leq$ 0.006) but not in DW (ANOVA 0.27 $\leq F \leq$ 1.75; 0.18 $\leq P \leq$ 0.76). Within L_2(A), the pattern of significance was reversed, showing significant differences in DW (ANOVA df = 2, 115; F = 3.32; P = 0.04) but not in T_P (ANOVA df = 2, 115; F = 1.22; P = 0.30). Within L_4, DW differed significantly between replicates (ANOVA df = 2, 139; F = 8.99; P = 0.0002) but T_P did not (ANOVA df = 2, 139; F = 2.89; P = 0.05).

Figs. 3.3a–b show coefficients of variation (C.V.) for parasitoid DW and T_P at each level of classification (Table 3.2) plotted against the average host dry weight at the time of parasitization. DW is inherently more variable than T_P in both sexes than T_P. The C.V. for DW of male parasitoids (Fig. 3.3a) shows an increasing trend with increasing host size (Spearman rank correlation r_s = 0.6321; P = 0.006); a third-order polynomial model provides a significant fit to the data (regression r^2 = 0.6177; df = 3, 11; MS = 5.68; F = 5.93; P = 0.01). The variability of T_P in males (Fig. 3.3a) does not change appreciably as host size increases. Among female parasitoids (Fig. 3.3b), the C.V. of DW shows less stability than that of T_P; there does not appear to be a correlation between the C.V. of either variable with host size at parasitization. Females show consistently less variability than males across all categories (Wilcoxon matched-pairs signed rank test, N = 15; Z_{T_P} = −3.351; 2-tailed P = 0.001; Z_{DW} = −3.294; 2-tailed P = 0.001; see Table 3.3).

Figure 3.3. Coefficients of variation for parasitoid DW (closed circles) and T_P (open circles) in A) males and B) females plotted against host dry weight at the time of parasitization.


A
COEFFICIENT OF VARIATION
15
10
5
0
0.0
0.1
0.2
0.3
0.4
HOST DW AT PARASITIZATION (mg)


B
COEFFICIENT OF VARIATION
15
10
5
0
0.0
0.1
0.2
0.3
0.4
HOST DW AT PARASITIZATION (mg)

The statistical relationship between DW and T_P was examined using Multivariate Discriminant Analysis. In addition, a discriminant function was used to statistically separate males from females. The results are shown in Table 3.4 and Figs. 3.4a, b. Analysis 1 (Table 3.4) shows that male parasitoids from group 1 are tightly clustered, resulting in a perfect separation from groups 3 and 4. Parasitoids from L_2 are clearly separated into two groups with the characteristics of L_1 (42.4%) and L_3 (43.4%). Approximately 90% of L_3 and L_4 are correctly classified. Canonical function 1 separates parasitoids from L_1 and L_2(IV) from the other groups based on differences in mummy size and DW. Because mummy size and DW are positively correlated (Henkelman 1979; Liu 1985), these two factors can be amalgamated into one common factor, *i.e.*, DW. Canonical function 2 separates parasitoids from L_2(A) and L_3 from L_4 based on differences in T_P. A discriminant analysis on females yields similar results. Analysis 2 (Table 3.4) shows that weight is the principal discriminator between males and females followed by mummy size.

Females are, on average, 1.10 times heavier than males (One way ANOVA, df = 1, 1034; F = 115.3; P = 0.000), and represent the upper tail of a unimodal continuous distribution. There is an aproximately 25% overlap in weight between males and females. The dry weight ratio (females:males) is constant across host instars. More females emerged from aphids that died as adults rather than in the fourth-instar stage. Although males generally began emerging a little earlier than females, the difference in T_P over all groups was not statistically significant (One-way ANOVA df = 1, 1034, F = 2.73, P = 0.099). Analysis 2 (Table 3.4) shows that T_P contributed little to the discriminant function separating males from females.

Figure 3.4. Classification of *A. ervi* males by discriminant analysis: A) Parasitoids from L_1 (open triangles), L_3 (X) and L_4 (open circles); B) Parasitoids from L_2 are sepatated into two subgroups on the basis of the mummy size from which they emerged.

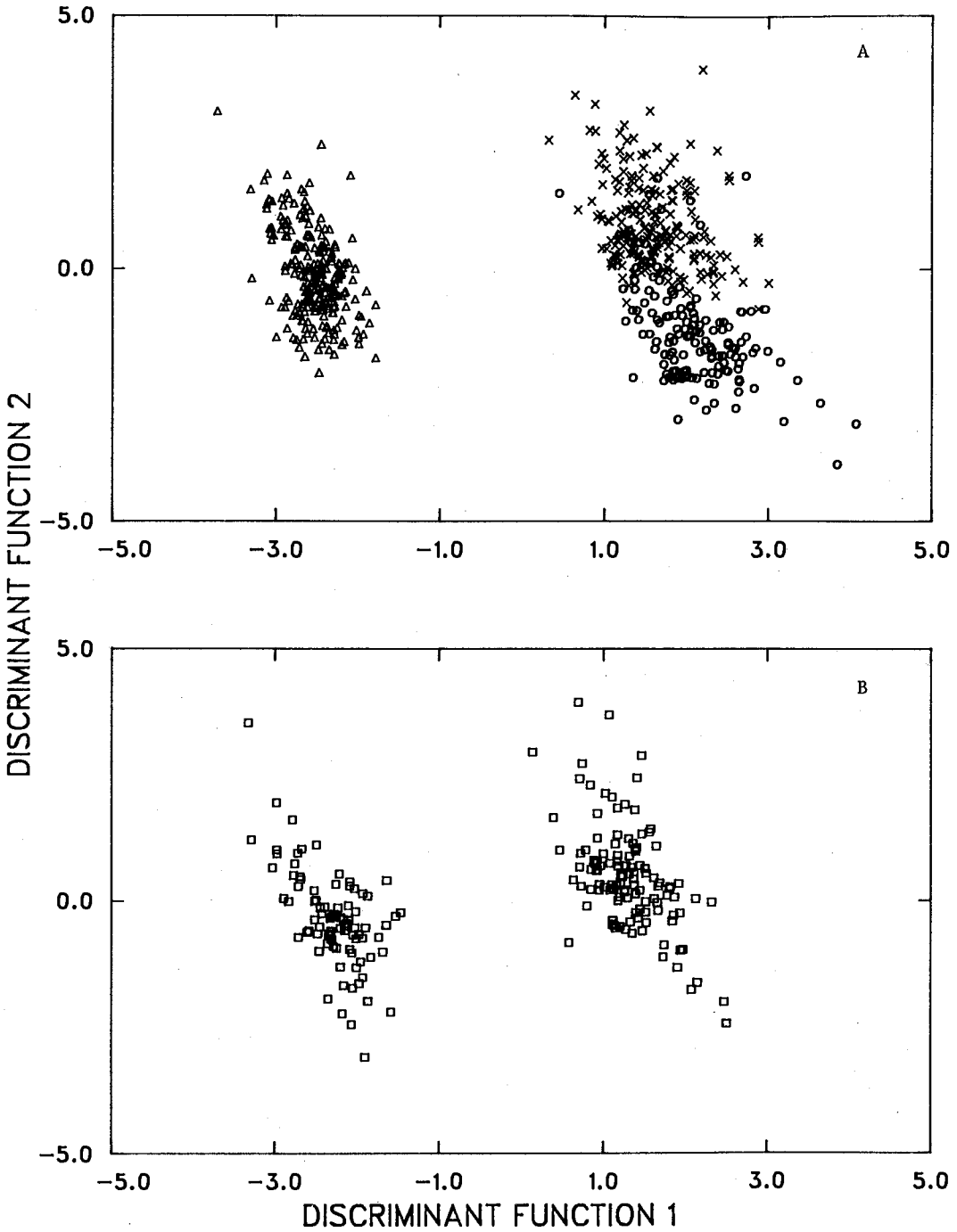

5.0
0.0
−5.0
−5.0
−3.0
−1.0
1.0
3.0
5.0
A
B
DISCRIMINANT FUNCTION 2
DISCRIMINANT FUNCTION 1

Table 3.4. Standardized coefficients of canonical discriminant functions for separating *A. ervi* reared from the four nymphal instars (L_1-L_4) of the pea aphid, on the basis of host instar, replicate number, mummy size, developmental time (T_P) and size (DW).

ANALYSIS 1: Classification of male parasitoids from L_1-L_4

	func 1	func 2
REPLICATE	-0.19096	-0.10084
MUMMY SIZE	0.80012	0.15625
T_P	-0.19205	1.05205
DW	0.41650	-0.38073

classification results:

host instar	N	predicted instar membership 1	2	3	4
L_1	232	232	0	0	0
L_2	205	87	5	89	24
L_3	211	0	0	192	19
L_4	142	0	0	18	124

ANALYSIS 2: Classification of parasitoids by sex

	func 1
INSTAR	0.07647
REPLICATE	-0.02921
MUMMY SIZE	-1.25965
T_P	-0.21558
DW	1.71247

classification results:

sex	N	predicted sex 1	2
M	790	615	175
F	246	72	174

Discussion

In holometabolous insects such as *A. ervi*, with complex life cycles involving metamorphosis, the adult phenotype is the aggregate result of several developmental stages. The transition between life cycle stages is rather abrupt; the larval stages are programmed mainly for growth resulting in an increase in biomass, whereas in the pupal stage growth and differentiation are involved in replacing larval tissue with adult biomass. Adult size is a function of maximum larval biomass, *Wmax*, which is converted into adult biomass in the pupal stage (Ochieng'-Odero 1990), whereas total developmental time, *T*, includes the duration of the embryonic, larval and pupal stages.

There appears to be a threshold size of the host at the time of parasitization below which parasitoid size is nutritionally constrained. Aphids parasitized in the L_1 and part of the L_2 stage die as fourth instars, giving rise to considerably smaller parasitoids, than those that die as adults (Figs. 3.1a, b). There is also an upper limit for parasitoid size which is rapidly attained in aphids parasitized as L_3. Although aphids parasitized as L_4 are 2.4–3.1 times heavier than L_3 aphids (Table 3.1), the parasitoids developing in these two groups do not differ significantly in size. This may be the result of constraints imposed by the determinate growth form of aphids and/or genetic constraints on parasitoid size.

A. ervi achieves *Wmax* upon the death of the host; this is seen within 8 days after parasitization, irrespective of host size at parasitization (Chapter II). Because adult DW at eclosion is proportional to *Wmax*, the variance in DW may be attributed to differences in individual growth rates. The response of parasitoid

DW to an increase in host size at parasitization appears to be different in males and females. Although average size increases with host size in both sexes, the C.V. of DW appears to increase in males but not in females (Fig. 3.3). This result, combined with the overall lower variability of females, suggests that males may have less developmental homeostasis than females.

Developmental time, T_P, increases for parasitoids reared from host instars L_1-L_3 (Figs. 3.1a, b). This increase can be explained on the basis of developmental constraints imposed by the host on the immature parasitoid. Parasitization of aphids in the L_3 stage (and presumably some in the late L_2 stage) results in a depressed growth trajectory of parasitoid immatures during their early stages (Chapter II). The delay in the beginning of exponential parasitoid growth appears to last until the parasitized aphids have completed the developmental phase involving exponential growth of their soma and gonads (see Chapter II, Fig. 2.2). The depressed early growth rate of parasitoids prolongs the length of their pupation phase and thereby extends overall developmental time, T_P, in L_3 (and some L_2) aphids. Once parasitoid DW is at or near the upper limit, and host growth is no longer a limiting factor, *i.e.*, in aphids parasitized as L_4, the additional resources available to the parasitoid are apparently utilized to minimize developmental time (Fig. 3.1).

T_P is less than half as variable as DW (Tables 3.2, 3.3). The C.V. of T_P remains constant in both sexes regardless of host size at parasitization (Fig. 3.3). This indicates that developmental time is tightly controlled so as to minimize variation. Such a response is characteristic of developmental canalization (Waddington 1957), whereby different genotypes give rise to the same phenotype. Thus, size and developmental time appear to respond in an uncorrelated manner

as host size at parasitization increases. In addition, males and females appear to respond differently to variation in host size.

Discriminant analysis serves to characterize the relative contributions of DW and T_P to the overall pattern of variation (Fig. 3.4, Table 3.4). The results of the analysis suggest that DW and T_P may be genetically uncoupled. This would not be surprising in holometabolous insects because traits expressed in the larval and pupal stages are controlled by different sets of imaginal discs (Gehring and Nothiger 1973; Postlethwait and Schneiderman 1973; Crick and Lawrence 1975; Yund and Germeraad 1980). Within the bounds of physiological and genetic constraints, traits controlled by different imaginal discs that do not overlap in their growth and development may be somewhat autonomous (Cowley and Atchley 1990).

The literature on host-parasitoid associations reveals several patterns of covariation between size and age at maturity. In a numer of studies, DW is positively correlated with host size but T_P varies nonlinearly (*e.g.*, Salt 1940; Jones and Lewis 1971; Miles and King 1975; Nechols and Tauber 1977). The covariance between DW and T_P has also been reported as positive in some cases (*e.g.*, Arthur and Wylie 1959; Vinson 1972; Lawrence *et al.* 1976) and negative in others (*e.g.*, Smilowitz and Iwantsch 1973; Nechols and Kikuchi 1985). The reasons for this are not clear. The strength of the correlation between traits may be influenced by the scale of measurement. For example, the pattern of covariation shown in Figs. 3.1a, b would not be discernible if developmental time had been measured in days rather than in hours. Differences in the sign of the correlation between characters may also be the result of association-specific nutritional and physiological interactions of parasitoids and their hosts.

Roff (1981) examined the potential for the evolution of body size in natural populations of *Drosophila melanogaster*. On the assumptions that resources are unlimited, and inter- and intra-specific competition are absent, Roff showed that variation in body size can be explained on the basis of trade-offs between life history parameters that are correlated with body size. Roff's study, although useful as a framework for testing evolutionary hypotheses, has limited applicability to those systems where the assumptions concerning resource availability and competition may not be valid. A comprehensive life history model must include genetic and environmental factors and their influence on overall phenotypic variability in life history traits. Also, the role of developmental plasticity, a factor that Roff (1981) ignored in his analysis, and the effect of larval ontogeny on demographic characteristics must be addressed in any comprehensive life history model.

The results of this study show that when nutritional constraints on parasitoid growth and development are removed, phenotypic traits closely related to fitness can vary somewhat autonomously. One possible implication of this finding is that selection could operate on individual traits without a significant correlated response from other traits when environmental conditions are favourable, *i.e.*, when host size at parasitization exceeds a certain threshold. Thus, the distribution of host sizes in the environment could profoundly influence the observed correlational structure between phenotypic traits and their relative contributions to parasitoid reproductive success.

CHAPTER IV

THE EFFECTS OF HOST SIZE AND LARVAL ONTOGENY ON SELECTED LIFE HISTORY PARAMETERS OF *A. ERVI*

Introduction

Age-specific fecundity and survivorship are two of the principal determinants of reproductive success and population growth rates (Lotka 1925; Fisher 1930). Fecundity and survivorship are often observed to be negatively correlated (Snell and King 1977; Calow 1979; Law 1979; Bell 1984a, b; Reznick 1985; Sutherland *et al.* 1986), possibly as a result of resource allocation trade-offs at the physiological level (Calow 1979). The above studies indicate that resource acquisition and allocation are basic to life history phenomena. Patterns of covariation between age-specific fecundity and survivorship that emerge in response to resource limitations may be used to evaluate the scope for adaptive adjustments to life history phenomena in variable environments.

Among aphidiid wasps, the nature and scope of resource limitations are likely to be stage-specific. For the endoparasitic larval stages that rely exclusively on the host for nutrition, variation in host size and growth potential at parasitization are the only sources of resource limitations. The free living adult parasitoids do not host-feed, but obtain nutrients mainly from plant nectar and honeydew secretions of the host (Mackauer and Kambhampati 1988b). These differences between larval and adult modes of nutrition suggest that nutrients obtained in the larval stages may be different from those obtained in the adult stages. Furthermore, the functions of larval-derived nutrients may be different

from those obtained by adults. Variation in nutrient availability in the larval stages is likely to influence the amount of larval-derived nutrient reserves and their subsequent allocation to adult functions. Thus, an important and seldom addressed issue in the analysis of parasitoid life history phenomena is the impact of variability in host size and growth potential at parasitization on patterns of variation in adult life history parameters.

In this study, I quantified the relationship between body size and life history parameters of adult parasitoids and examined the possible influences of larval growth history and feeding experiences on patterns of age-specific fecundity and longevity. I show that life history parameters of *A. ervi* do not vary linearly with body size throughout its range. Differences in adult fecundity and survivorship curves appear to correspond closely to differences in larval ontogenies of immature parasitoids in relation to host age/instar at parasitization. The results indicate the possibility of resource allocation trade-offs between life history parameters at several physiological levels.

Methods

Eight female *A. ervi* were randomly selected from a laboratory maintained population and allowed to parasitize 60 aphids of uniform age, enclosed singly in gelatin capsules (size 00). The parasitoids were allowed to strike each aphid only once to avoid superparasitism. In this manner, four age classes of aphids, *viz.*, 24 ± 2, 48 ± 2, 72 ± 2 and 120 ± 2 hours, corresponding to the four nymphal instars, L_1-L_4, were parasitized. Parasitoids used to parasitize one host class were not used again. Parasitized aphids were separated into groups of 30 and each

group was transfered to an individual broad bean plant enclosed in a cylindrical plastic rearing cage (15.5 x 4 cm) with its roots immersed in tap water. The caged aphids were reared at 20 ± 0.5 °C, 55-65% R. H., and constant light until the parasitoids developing within them reached maturity.

On the day of adult eclosion, 15 female parasitoids were randomly selected from each host class and transfered to fresh rearing cages for the measurement of daily fecundity (M_x) and survivorship (l_x). Beginning on the first day of adult life, each parasitoid female was enclosed with 40 2-3-day old aphids every day, throughout her life. M_x values were then estimated by dissecting half the number of aphids provided to each female for every day of life, and counting the number of eggs and/or larvae present. At the end of their life span, when death occurred due to natural causes, the parasitoids were oven dried at 100°C for 3 days and weighed on a Mettler UM3 balance.

The data were analysed in two stages using the $SPSS_x$ library of statistical computer programs ($SPSS_x$ 1983). In the first stage, M_x schedules of parasitoids from the four host classes were compared using profile analysis (Morrison 1976; $SPSS_x$ 1983, p. 535) to identify linear segments and test for parallelism of segment slopes. The MANOVA subroutine was used to execute a profile analysis. The program computes, among other statistics, univariate F-statistics for differences between adjacent days of the fecundity schedule, compared across host classes. In the second stage of analysis, linear segments of the fecundity schedules identified by profile analysis were compared across host classes using ANOVA and Kruskal-Wallis nonparametric ANOVA (wherever appropriate).

The intrinsic population growth rate, r_m (Southwood 1966), was used as a measure of physiological performance under ideal conditions, to compare parasitoids reared from the four host classes. r_m was calculated iteratively, assuming a 1:1 sex ratio, using a Fortran computer program, from the Euler-Lotka equation:

$$1 = \int e^{-r_m x} L_x M_x.$$

Variability among parasitoid females from each host class was estimated by employing Tukey's jackknife technique (Efron 1982). The pseudovalues of r_m were generated by omitting a different female each time and recalculating r_m (Lenski and Service 1982).

Results

Parasitoids reared from L_1, L_2 and L_4 eclosed 12 days after parasitism, whereas those from L_3 eclosed a day later. L_x curves for the duration of adult life and M_x curves for the first 8 days of adult life are shown in Figs. 4.1a-d. Under the present experimental conditions, the survivorship plateau (period of zero mortality) of *A. ervi* was longest in L_4 (Fig. 4.1d), shortest in L_3 (Fig. 4.1c) and intermediate in L_1 and L_2 (Figs. 4.1a and b, respectively). Median cohort survivorship followed the same pattern (Table 4.1). Peak M_x was achieved on different days (Figs. 4.1a, d), and differed significantly among the four parasitoid classes (ANOVA df = 3, 54; Error MS = 595.516; F = 16.033; P = 0.000), with the exception of parasitoids from L_3 and L_4, which were not significantly different (SNK range test, $P > 0.05$). M_x values increased linearly in parasitoids from L_2 and L_4 before declining, whereas in parasitoids from L_3 M_x declined sharply after the first day of adult life (Fig. 4.1c).

Figure 4.1. L_X (solid) and M_X (dashed) curves of *A. ervi* in relation to pea aphid nymphal instar and age at parasitization: A) L_1 (24 ± 2 h), B) L_2 (48 ± 2 h), C) L_3 (72 ± 2 h), D) L_4 (120 ± 2 h). Bars on the M_X curve represent 95% confidence intervals.

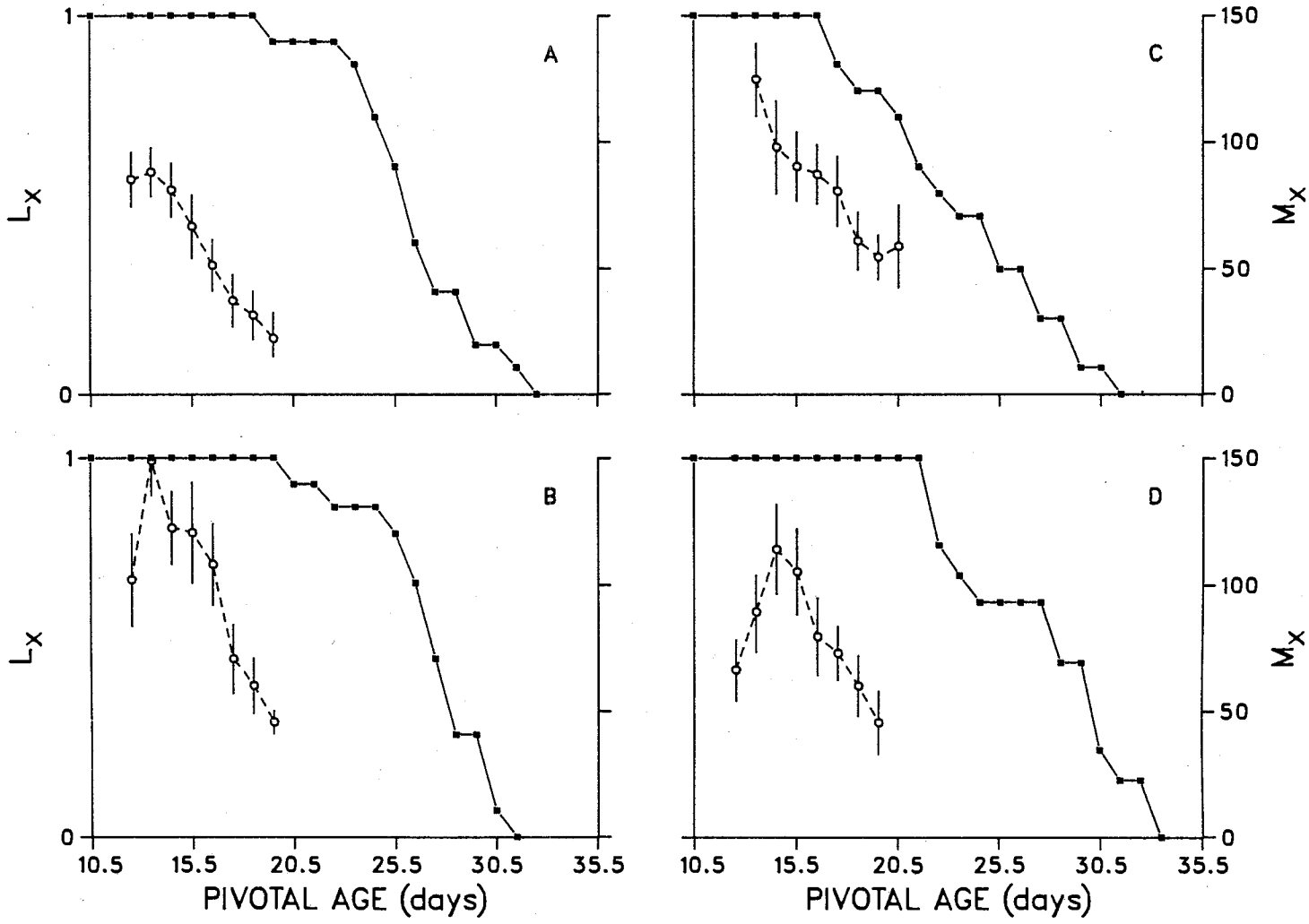

A
B
C
D
L_X
M_X
1
0
150
100
50
0
10.5
15.5
20.5
25.5
30.5
35.5
PIVOTAL AGE (days)

Table 4.1. A summary of life history parameters for *A. ervi* females in relation to pea aphid age and instar at parasitization.

Aphid		Parasitoid life history traits						
				fecundity				
Instar	t_H	N	Dry weight† mean	S.D.	1-3-day‡ mean	S.D.	total	S	r_m mean	S.D.
L_1	24	15	1538	(110)c	254	(29)c	463	24.50	0.372	(.010)c
L_2	48	15	1809	(227)b	373	(60)a	777	25.33	0.407	(.010)a
L_3	72	15	1901	(159)b	312	(49)b	654	20.50	0.349	(.012)d
L_4	120	13	2118	(377)a	269	(51)c	631	26.00	0.390	(.016)b

Symbols: t_H = median age of cohort at the time of parasitization, in hours (± 2 h); S = median cohort survivorship, in days; r_m = jackknifed intrinsic population growth rate, in females/female/unit time.
† in micrograms.
‡ Number of eggs laid, estimated by dissecting 20/40 hosts provided to each female each day.
Means that share the same letter are not significantly different (SNK range test, $P < 0.05$).

Profile analysis indicated that M_x profiles for the first 3 days were dissimilar in the direction of change across host classes (Univariate F-tests on differences between adjacent days; df = 3, 50; $F \geq 5.742$; $\alpha = 0.05$; $P \leq 0.002$), whereas M_x profiles for the last 5 days were generally similar in direction (Univariate F-tests on differences between adjacent days; df = 3, 50; $F \leq 4.223$; $\alpha = 0.05$; $P \geq 0.094$) with one exception (Day 5 - Day 6: $F = 4.223$; $P = 0.01$). Thus, profile analysis identified two distinct linear phases within each fecundity schedule, *viz.*, an early phase that includes M_x values for the first 3 days and a late phase that includes the remainder of the M_x curves.

The early and late phases of the fecundity schedules were further analysed separately. M_x values in the early phase were summed for each parasitoid, after verifying homoscedasticity between measurements on different days, and the totals analysed by ANOVA. Total early-phase fecundity was significantly different between parasitoid classes (ANOVA df = 3, 54; Error MS = 2351.939; $F = 17.912$; $P = 0.000$). Total fecundity during this period increased as host age at parasitization increased from 24 ± 2 to 48 ± 2 hours but declined with further increases in host age (Table 4.1). The variance in total fecundity was not significantly different between host classes (Cochran's $C = 0.3856$; $P = 0.230$).

Late-phase fecundity was analysed using the Kruskal-Wallis nonparametric ANOVA to avoid difficulties arising from heteroscedasticity and empty cells caused by declining parasitoid survivorship. Total late-phase fecundity did not differ between parasitoids from L_2, L_3 and L_4 ($N = 206$; $\chi = 2.192$; $P = 0.334$), whereas parasitoids from L_1 layed considerably fewer eggs ($N = 280$; $\chi = 55.546$; $P = 0.000$).

Average size (dry weight) of parasitoids from the four host classes was significantly different (ANOVA df = 3, 54; Error MS = 0.001; F = 14.872; P = 0.000). Host classes L_1 and L_4 produced the smallest and largest parasitoids, respectively (Table 4.1), however, there was no correlation between individual parasitoid size and total fecundity in the early phase as well as the lifetime (8 days) total ($r^2 \leq 0.044$; df = 1, 52; Regression MS $\leq$ 45713.859; Residual MS $\leq$ 18895.275; F $\leq$ 2.419; P $\geq$ 0.126). Total early-phase fecundity showed no correlation with survivorship within any of the four parasitoid classes ($r^2 \leq 0.551$; F $\leq$ 0.760; P $\geq$ 0.399).

r_m was significantly different between parasitoid classes (ANOVA df = 3, 54; Error MS = 0.0002; F = 58.360; P = 0.000), and varied nonlinearly with body size (Table 4.1). The small standard deviations associated with the jackknifed estimates of r_m (Table 4.1) indicate that the variance in fecundity and survivorship was larger between groups than within groups.

Discussion

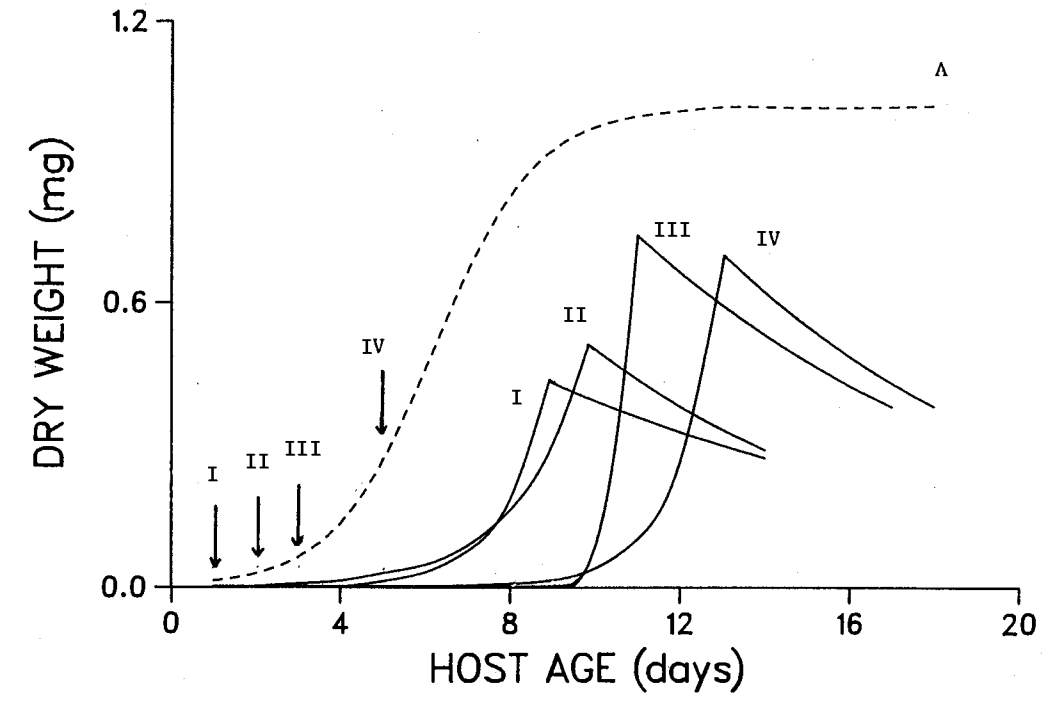
In insects with complete metamorphosis, adult life history functions are fuelled by some combination of larval-derived and adult-derived nutrients (Boggs 1981). The allocation of larval-derived nutrient reserves to adult functions is determined during the transition from the larval to the adult stage. Factors that influence larval feeding and growth history are therefore likely to indirectly influence adult functions. In the experiments reported here, *A. ervi* females from all four host classes were exposed to similar environments; each female was provided with the same number of hosts on each day of life, and maintained

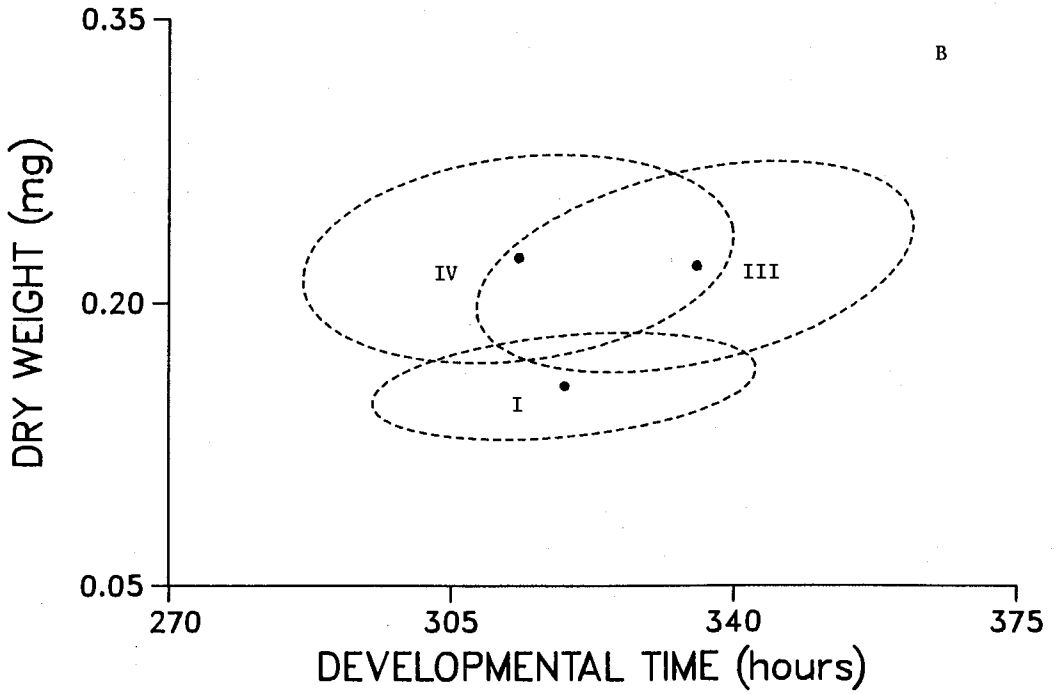
under standardized abiotic conditions. Under this scenario, differences in life history parameters possibly reflect differences in larval environments and growth history.

The ontogenies of immature parasitoids in relation to host age at parasitization, examined in Chapter II, are summarized in Fig. 4.2a. The quality of the pea aphid as a host for immature *A. ervi*, measured by parasitoid growth rate, varies with aphid age/instar at the time of parasitization. Using parasitoid larval dry weight on day 7 after parasitization as an index of host quality, the four aphid instars could be ranked in the order $L_2 > L_4 > L_1 > L_3$. This rank order is identical to the ranking of adult parasitoids reared from the four host instars on the basis of overall reproductive success, *i.e.*, r_m (Table 4.1).

The lowest median survivorship (Table 4.1) and the smallest survival plateau (Fig. 4.1c) of parasitoids reared from L_3 aphids corresponds to a delay in achieving exponential growth in early larval life (Fig. 4.2a). By comparison, the ontogeny of parasitoids reared in L_4 hosts is characterized by an intermediate growth rate in the early phase of development and corresponds with the highest adult survivorship (Table 4.1). Changes in fecundity and longevity of parasitoids reared from L_1 and L_2 are in the same direction as the change in adult size (Table 4.1). Thus, the close correspondence between juvenile ontogeny and adult life history characteristics demonstrated above suggests that larval growth history, through its influence on the accumulation of larval reserves, may be an important factor in determining the pattern of resource allocation between life history functions.

Figure 4.2. Larval ontogeny and adult characteristics of *A. ervi* in relation to host age and instar at parasitization. A) Predicted parasitoid growth curves (solid lines) in aphid instars L_1 (I), L_2 (II), L_3 (III) and L_4 (IV). The dashed curve represents growth of unparasitized aphids. Arrows indicate aphid age at parasitization. B) 95% confidence ellipsoids for developmental time and adult weight of parasitoids reared from aphid instars L_1 (I), L_3 (III) and L_4 (IV). (•) indicates group centroid.


A
1.2
0.6
0.0
DRY WEIGHT (mg)
I
II
III
IV
0
4
8
12
16
20
HOST AGE (days)


B
0.35
0.20
0.05
DRY WEIGHT (mg)
IV
III
I
270
305
340
375
DEVELOPMENTAL TIME (hours)

Based on differences in shape, the M_x curves in Fig. 4.1 could be assigned to one of three distinct categories. In the first category are parasitoids reared on L_1 (Fig. 4.1a) that achieve similar M_x values in the early phase of the fecundity schedule. Their size, lowest total early-phase fecundity and constant M_x values suggest that mobilization of stored resources for reproductive functions is at or near the upper limit. In the second category, M_x values increase significantly before declining (Figs. 1b, d), which may be interpreted as increased mobilization of stored resources following the onset of egg laying on the first day. In this category, allocation to reproductive functions may be maximized independently of maintenance (longevity) functions. In the third category (Fig. 4.1c), parasitoids achieved the highest M_x value on the first day of egg laying relative to the other parasitoid classes, followed by a sharp decline. Survivorship in this group of parasitoids is significantly less than that of all other groups, which suggests the hypothesis that survivorship is compromised to maintain a high fecundity in early life.

In the literature on host-parasitoid associations, parasitoid size and fecundity are generally found to be positively correlated (Cloutier *et al.* 1981; Mackauer 1983; Nealis *et al.* 1984; Waage and Ng 1984; Liu 1985; Opp and Luck 1986). A positive correlation may be expected *a priori* if larval feeding experiences are similar, and parasitoids differ only in adult size. However, the life history parameters of *A. ervi* clearly vary nonlinearly with body size. The relationship between body size and developmental time in *A. ervi* (Chapter III) is summarized in Fig. 4.2b. Parasitoids reared from L_4 aphids achieve the same body size, eclose much earlier but initially lay fewer eggs than their counterparts from L_3 aphids (Fig. 4.2b, Table 4.1). This result indicates the possibility of a trade-off between

developmental time and fecundity, once a threshold body size has been achieved.

Age at first reproduction may, in some circumstances, be more important than fecundity for maximizing life-time reproductive success (Lewontin 1965; Roff 1981) so that the potential may exist for additional trade-offs in resource allocation to minimizing developmental time versus maximizing fecundity, independent of survivorship. With the exception of Hopper (1986), no previous studies on insect parasitoids have addressed this issue. Hopper (1986) demonstrated a clear trade-off between development rate and the egg complement of newly eclosed adults of the Braconid, *Microplitis croceipes* (Cresson), a parasitoid of *Heliothis virescens* (F.). He found that adults reared from the most preferred host instars achieved the highest rate of development but possessed the smallest number of oocytes at maturity.

The relationships among life history parameters are likely to be complex and intricately dependent on larval ontogeny and feeding experiences. The narrow range of body sizes within which a positive linear relationship between body size and fecundity is found in *A. ervi* suggests that fecundity, *per se*, may be less important than developmental time and other size-related attributes in an ecological context. The nature and sources of variability in body size itself, and size-related characteristics in natural populations of *A. ervi* must be understood to assess the relative importance of various life history parameters.

CHAPTER V

THE QUANTITATIVE GENETICS OF BODY SIZE AND DEVELOPMENTAL TIME IN *A. ERVI*

Introduction

The heritability of a quantitative character is a biometrical description of variability at the population level, in terms of an average genotypic value and an environmental deviation (Bulmer 1980, Falconer 1989). Adaptive evolution in the phenotype is thought to proceed through modifications of the average genotypic value by natural selection. Fisher's (1930) fundamental theorem of natural selection provided the framework for examining the evolution of metric characters in panmictic populations by equating the rate of increase in fitness at any time to the additive genetic variance at that time. Phenotypic traits closely and consistently related to fitness are expected to exhibit low additive genetic variance (Fisher 1930, Ewens 1976, Falconer 1989). Heritability estimates for numerous characters in a wide range of animal and plant taxa generally support this hypothesis; life history traits tend to have lower heritabilities than, for example, morphological traits (Mousseau and Roff 1987; Roff and Mousseau 1987; Falconer 1989).

Among insect parasitoids, reproductive success is centered on body size because it is correlated with female fecundity (Cloutier *et al.* 1981; Mackauer 1983; Nealis *et al.* 1984; Waage and Ng 1984; Opp and Luck 1986), longevity (Wylie 1966; Sandlan 1979; Charnov *et al.* 1981; Waage and Ng 1984), oviposition success (van den Assem 1971; Rotheray *et al.* 1984) and male mating success

(van den Assem 1976; Grant *et al.* 1980), among other traits. Developmental time influences reproductive success differently than body size; a small increase in developmental time can offset a relatively large increase in fecundity (Lewontin 1965; Roff 1981). The above studies indicate that, under controlled laboratory conditions, body size and developmental time are key determinants of survival and population growth, and should therefore be constantly under selection pressure in the direction that leads to maximum fitness. Heritabilities of characters in natural populations of parasitoids may be conveniently used to assess their relative influence on fitness under field conditions.

However, a majority of the heritability estimates found in the literature may be considered incomplete descriptions of adaptive evolutionary potential because organisms must deal with spatial and temporal heterogeneity in the environment under natural conditions. There may not always be a one-to-one correspondence between a genotype and the phenotype produced in different environments. Environmental heterogeneity may result in phenotypic plasticity in some traits whereby a given genotype produces different phenotypes under different conditions (Bradshaw 1965, Lewontin 1974, Schlichting 1986, Sultan 1987), or canalization in others whereby a constant phenotype is produced under different environmental conditions (Waddington 1957). Thus, heritability estimates may be largely uninformative when considered in isolation from their corresponding environmental components (Falconer 1989).

In this study, I examined the basis of variability in body size and developmental time of the aphid parasitoid, *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). I present the first heritability estimates for an insect parasitoid, and identify the factors that may influence the variability of fitness parameters of

parasitoids. I analysed the sensitivities of body size and developmental time to the main source of environmental heterogeneity for parasitoids, *viz.*, host size. The results show that the trait that is more heritable is also more plastic in its response to variability in host size. I argue that, under certain conditions, developmental time may be more important than body size to the demography and evolution of *A. ervi*. The relative ecological importance of genetic variability versus phenotypic plasticity will be discussed.

Methods

Estimation of heritability

In June 1989, a sample in excess of 500 mummified pea aphids containing the immature stages of *A. ervi* was collected from different alfalfa fields near Salmon Arm, British Columbia. Adult parasitoids eclosing from the mummified aphids were separated by sex, provided with a solution of honey and water as food, and maintained at 20 ± 2 °C, 55-65% r.h., and constant light.

The laboratory F_1 population was propagated by selecting a group of 25 randomly paired male and female parasitoids from the field collected sample. Once mated, the female parasitoids were allowed to parasitize approximately 500 L_3 and L_4 pea aphids. A second group of 20 virgin females was selected to produce male full-sib families, and each female was allowed to oviposit into 8 L_3 aphids, which were then reared together. Aphids parasitized by different virgin females were reared separately. The F_1 from both groups of parasitoids were used in experimental crosses.

One sire was selected randomly from each male full-sib family and mated to 2-3 dams resulting in the production of full- and half-sib families. Parasitoids were mated individually in gelatin capsules (size 00) to ensure uninterrupted mating. For oviposition, a mated parasitoid was enclosed with a single aphid in a gelatin capsule and permitted to strike the aphid only once to avoid superparasitism. Aphid age (and implicitly size) at parasitization was standardized to 120 ± 2 h, and temperature was controlled to within ± 0.2 °C. Each dam parasitized 20 L_4 aphids, producing 16-20 offspring. Parasitized aphids were reared in cylindrical plexiglass cages (15.5 x 4 cm) enclosing a single broad bean plant with the roots immersed in tap water.

Pea aphids parasitized at age ≥ 4 days (at 20 °C) reproduce before death occurs. The progeny of parasitized aphids were removed with minimum disturbance of the adults to sustain the quality of the bean plant and prevent overcrowding within the cage. On the 12th day after parasitization, the mummified aphids were collected and placed singly in capsules. Precise estimates of parasitoid developmental times from oviposition to adult emergence (in hours, ± 0.75 h) were obtained using a video camera; upto 275 mummified aphids, placed singly in capsules, were monitored continuously for 96 hours beginning with the first parasitoid eclosion. For the measurement of size, adult parasitoids were allowed to die in their eclosion capsules, oven dried for 3 days at 100 °C and weighed on a Mettler UM3 electronic balance.

The analysis of genetic variability in *A. ervi* was based on the model of polygenic inheritance in bees (*e.g.*, Polhemus *et al.* 1950; Eickwort 1969; Kerr 1974; Rinderer 1977; Collins *et al.* 1984; Owen 1989). As a result of haplodiploidy, the entire males (haploid) genome can be considered sex-linked (Crozier 1977). In

hymenopterous insects there is no evidence for the formation of bivalents and meiotic reduction division during spermatogenesis (White 1973). Consequently, males can be expected to produce genetically homogeneous sperm (Polhemus *et al.* 1950; Rinderer 1977). Thus the coefficient of relatedness among siblings is 0.75 for full-sisters and 0.5 for half-sisters. Male half-sib families cannot be produced because males are produced from haploid eggs. The coefficient of relatedness among brothers is 0.5 (Bulmer 1980, p. 99).

Due to the asymmetrical relatedness among sibs between sexes, heritability must be analysed separately for male and female offspring (Bulmer 1980, p. 97). The degree of resemblance among female sibs was estimated by the intraclass correlation coefficient, r_A, defined as the ratio of the additive genetic variance, V_A^2, to the total phenotypic variance, V_P^2 (Falconer 1989):

$$r_A = V_A^2 / V_P^2.$$

Variance components were estimated under a random effects ANOVA model, with Dams nested within Sire. The covariance of male sibs was estimated by the intraclass correlation from a full-sib design and a weighted parent-offspring (P-O) regression (Falconer 1989, p. 182). Variance components were estimated using Type IV sums of squares computed by procedure GLM and by Maximum Likelihood using VARCOMP from the SAS package of computer programs (SAS 1985).

Non-parametric 95% confidence intervals for the intraclass correlation coefficient were calculated by employing Tukey's jackknife technique on the *z*-transformed pseudovalues (Efron 1982; Sokal and Rohlf 1981 p. 795). In the half-sib design, the pseudovalues were generated by omitting one sire (and the associated dams) each time and recalculating the variance components (Knapps *et*

al. 1989). The pseudovalues for the full-sib design (male progeny) were calculated by the deletion of dams, one-at-a-time. In each case heritability in the narrow sense was calculated using the jackknifed estimate of the intraclass correlation. For the female progeny, heritability was calculated as:

$$\text{sire component } h^2 = 2\, r_A^*,$$

$$\text{dam component } h^2 = 4/3\, r_A^*.$$

For the male progeny, heritability was calculated as:

$$h^2 = 2\, r_A^*.$$

Analysis of Reaction norms for size and developmental time

Fifteen randomly paired male and female parasitoids were selected from the F_1 population. Each mated female was allowed to oviposit once into 15 each of L_1 and L_4 aphids. The parasitized aphids from both instars were reared together on a broad bean plant enclosed in a circular plexiglass cage. Aphids that mummified were then separated on the basis of mummy size. Parasitized L_1 die in the fourth-instar stage whereas the L_4 die as adults (Chapter III). The mummies were enclosed in gelatin capsules and adult eclosion was monitored using a video camera.

A complication in the analysis of inter-environmental correlations for sexually reproducing species is that a given genotype can develop in only one environment. To circumvent this difficulty, inter-environment responses can be analysed by correlating the means of sib families across environments (Via 1984). The average response of *A. ervi* genotypes to different host sizes was evaluated by estimating the Spearman rank correlation between corresponding family means. The significance of the correlation was examined by employing the bootstrap

technique (Efron 1982). The sampling variance of the correlation coefficient was estimated based on N = 50 random samples drawn with replacement.

Results

Mean adult size (dry weight) for families of female and male progeny are given in Tables 5.1 and 5.2, respectively. Females are heavier and, on average, less variable than males. Female developmental times for each family are given in Table 5.3. Due to inadequate sample sizes, developmental time of male progeny was not analysed. The regression of family standard deviations on corresponding means was not significant, a fact indicating the absence of significant scale effects (Wright 1968, Chapter 10). The ANOVA assumption of homogeneity of variances was satisfied for the half-sib design (females) but not for the full-sib design (males). A suitable transformation to stabilize the variance of male full-sib families could not be found, partly because heterogeneity of variances was due to large differences in family sizes. In the calculation of heritability for males, therefore, full-sib families consisting of 1 and 2 offspring were omitted from the analysis to make the sample sizes more equitable. This resulted in the omission of 3 families (5 variates) from the analysis.

Heritability of size and developmental time

Table 5.4 gives the summary of Sum-of-squares (SSE) and Maximum Likelihood (MLE) estimators of the resemblance between sibs for body size and developmental time. Jackknifing influences the two estimators in different ways. The SSE sire component is biased upward but the dam component is unaffected. MLE sire and dam components are biased in opposite directions. Although the

Table 5.1. Experimental design[1] used in the estimation of heritability and summary of the observational component of body size (dry weight, in micrograms) in female *A. ervi*.

	Dam 1			Dam 2			Dam 3		
Sire	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
1	6	242	(12)	6	255	(15)			
2	14	247	(17)	7	242	(14)	11	236	(9)
3	12	241	(10)	7	229	(11)			
4	13	245	(21)	15	245	(20)	7	216	(5)
5	10	237	(10)	15	227	(16)	7	229	(21)
6	15	235	(13)	8	214	(10)			
7	14	217	(13)	6	256	(15)			
8	10	224	(9)	14	261	(9)			
9	4	248	(20)	11	232	(13)	14	232	(14)
10	11	222	(15)	6	224	(6)			
11	12	258	(16)	7	266	(8)	8	255	(14)
12	10	237	(19)	15	216	(12)	4	199	(23)
13	6	234	(21)	16	220	(21)	14	246	(10)
14	5	198	(21)	9	225	(25)	19	219	(13)
15	15	218	(15)	7	215	(8)			
16	7	223	(19)	11	228	(16)	9	223	(21)
17	7	253	(14)	7	230	(6)	10	245	(17)
18	14	234	(11)	18	233	(16)			

[1] Each sire was mated to 2-3 randomly selected females. The sequence of dams does not correspond to the mating sequence. N is sample size.

Table 5.2. Summary of the observational component of body size (dry weight, in micrograms) in male[1] *A. ervi*.

	Dam 1			Dam 2			Dam 3		
Sire	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
1	12	232	(32)	11	242	(39)			
2	4	219	(10)	7	214	(14)	8	205	(24)
3	1	267	(0)	9	206	(29)			
4	6	245	(25)	2	210	(28)	3	175	(32)
5	8	211	(18)	3	208	(27)	12	201	(20)
6	3	209	(19)	5	184	(18)			
7	5	181	(14)	7	230	(19)			
8	9	190	(15)	4	214	(44)			
9	13	207	(18)	6	221	(31)	2	212	(18)
10	3	182	(6)	10	183	(13)			
11	8	222	(21)	10	249	(15)	12	219	(14)
12	9	210	(21)	3	197	(46)	11	173	(13)
13	13	212	(35)	3	189	(10)	6	220	(15)
14	7	202	(21)	6	178	(14)	0		
15	3	195	(8)	6	205	(14)			
16	6	195	(26)	5	200	(5)	7	208	(19)
17	9	209	(13)	7	189	(8)	9	223	(19)
18	0			0					

[1] Males arise from unfertilized eggs. Dams are nested within Sires only to maintain correspondance with Table 5.1.

Table 5.3. Summary of the observational component of developmental time (in hours ± 0.75 h) in female *A. ervi*.

	Dam 1			Dam 2			Dam 3		
Sire	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
1	6	324.6	(3.7)	6	312.3	(12.6)			
5	10	314.6	(5.3)	15	322.0	(7.3)	7	305.4	(5.6)
9	4	308.6	(1.8)	11	321.2	(6.7)	14	326.3	(6.6)
11	12	319.1	(4.1)	7	313.8	(3.7)	8	297.1	(6.6)
13	6	331.4	(5.2)	16	320.1	(6.0)	14	324.4	(6.2)

Table 5.4. Sum-of-Squares (SSE) and Maximum Likelihood (MLE) estimates of variance components for body size (dry weight) and developmental time (age) in *A. ervi*. See text for explanation.

source	d.f.	MS	component estimated	variance component V_A^2	intraclass correlation r_A	jackknifed estimates r_A^* SSE	r_A^* MLE	S.E. (r_A^*) SSE	S.E. (r_A^*) MLE
A) Weight: female offspring									
Sire	17	3.076×10^{-3}	$1/2\ V_A^2$	0.074×10^{-3}	0.175	0.188	0.196	0.128	0.120
Dam (Sire)	28	1.411×10^{-3}	$3/4\ V_A^2 + 1/2\ V_D^2$	0.124×10^{-3}	0.293	0.293	0.283	0.106	0.102
Error	427	0.225×10^{-3}	$1/4\ V_A^2 + 1/2\ V_D^2$	0.225×10^{-3}					
Total	472	4.712×10^{-3}	V_P^2						
B) Weight: male offspring									
Dam	39	0.102	$1/2\ V_A^2 + 1/4\ V_D^2$	0.299×10^{-3}	0.382	0.386	0.370	0.098	0.089
Error	248	0.120	$1/2\ V_A^2 + 3/4\ V_D^2$	0.483×10^{-3}					
Total	287	0.222	V_P^2						
C) Developmental time: female offspring									
Sire	4	9.183×10^2	$1/2\ V_A^2$	1.520×10	0.128				
Dam (Sire)	9	6.360×10^2	$3/4\ V_A^2 + 1/2\ V_D^2$	6.407×10	0.539				
Error	122	0.396×10^2	$1/4\ V_A^2 + 1/2\ V_D^2$	3.957×10					
Total	135	15.939×10^2	V_P^2						

standard error of the Maximum Likelihood estimator is smaller than the corresponding Sum-of-squares estimator, point estimates of the latter, being closer to the original estimates, were used to calculate heritability.

Body size is moderately heritable in female *A. ervi*. Sire component heritability, h^2 = 0.3752, is not statistically significant (95% C.I., $0 \leq h^2 \leq 0.8640$) whereas dam component heritability, h^2 = 0.3903 is statistically significant (95% C.I., $0.1029 \leq h^2 \leq 0.6427$). The lack of significance for the sire component is a consequence of small sample size (N = 18 sires). The proportion of additive (V_A^2) and dominance (V_D^2) variance estimated by each term in the ANOVA model are shown in Table 5.4. Effects of epistatic interactions and environmental variance due to maternal effects were assumed to be negligible. However, since each full-sib family was reared in the same cage, on the same bean plant, the effect of common environment cannot be discounted.

The dam component includes non-additive genetic variance (dominance and epistasis) as well as variance due to common environment (Falconer 1989). The similarity of sire and dam components indicates that the variance is mainly additive in nature, with negligible contributions from dominance interactions and common environment. Heritability of adult size in females averaged over sire and dam components is 0.3828. The covariance of male sibs includes dominance, epistasis and common environment (Falconer 1989). Heritability of size in males, under the ANOVA model, is 0.7710 (95% C.I., $0.4078 \leq h^2 \leq 1$) whereas the weighted regression of offspring mean character value on female parent (= midparent) value gave $h^2 = b_{OP}$ = 0.2342 (S.E. b_{OP} = 0.1914, N = 37).

Heritability of developmental time could not be reliably estimated due to difficulties in monitoring sufficient numbers of parasitoids. Due to this and the asymmetry between sample sizes for body size and developmental time, the genetic correlation between traits was not estimated. The estimates of r_A for developmental time given in Table 5.4c are useful only in that they indicate the relative magnitude of sire and dam components of variance. Assuming that the trend is indicative of the true difference between sire and dam components, the additive genetic variance (sire component) is small, probably close to zero, indicating that the much larger dam component constitutes mainly non-additive genetic and environmental variance.

Reaction norms of size and developmental time

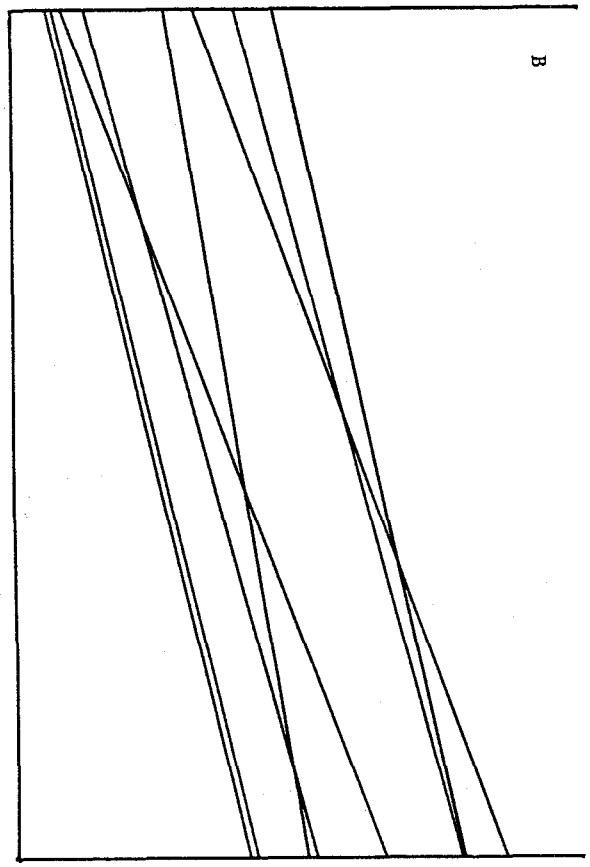
The mean phenotypic responses of the male progeny of individual genotypes to small (L_1) and large (L_4) host sizes are given in Table 5.5. Only three female parasitoids produced female offspring in both host size classes. Therefore, the analysis was restricted to the male offspring. Developmental time is clearly less variable than body size (Table 5.5). Reaction norms for developmental time (Figure 5.1b) show that genotypes developing faster in small hosts are equally likely to do so in large hosts as well (Bootstrapped Spearman rank correlation, $r_{S(B)}$ = 0.80; 95% C.I., 0.46 $\leq r_{S(B)} \leq$ 1). The response of parasitoid size (Fig. 5.1a) is less predictable, indicating that a given genotype is less likely to maintain its relative rank in both host sizes ($r_{S(B)}$ = 0.43; 95% C.I., -0.10 $\leq r_{S(B)} \leq$ 0.96).

Table 5.5. Developmental time (in hours ± 45 min) and dry weight (in micrograms) of the male offspring of *A. ervi* genotypes reared in pea aphid instars L_1 and L_4.

Genotype Number	L_1			L_4		
	N	Mean	C.V.	N	Mean	C.V.
			developmental time			
1	9	293.50	2.00	9	316.10	2.55
2	9	300.78	3.21	9	310.56	1.52
3	8	292.44	2.07	15	306.47	2.75
4	12	292.88	1.19	13	307.00	1.51
5	7	295.14	2.28	5	311.20	2.09
6	8	308.50	3.02	3	321.67	3.19
7	7	302.86	2.48	3	324.67	2.39
8	6	305.75	1.98	3	321.50	2.35
			dry weight			
1	9	126	6.68	9	210	8.15
2	9	138	11.51	9	212	16.41
3	8	148	6.17	15	223	10.45
4	12	153	10.87	13	227	7.92
5	7	132	6.57	5	230	12.35
6	8	129	18.50	3	203	12.89
7	7	131	12.30	3	164	26.64
8	6	124	10.96	3	214	14.24

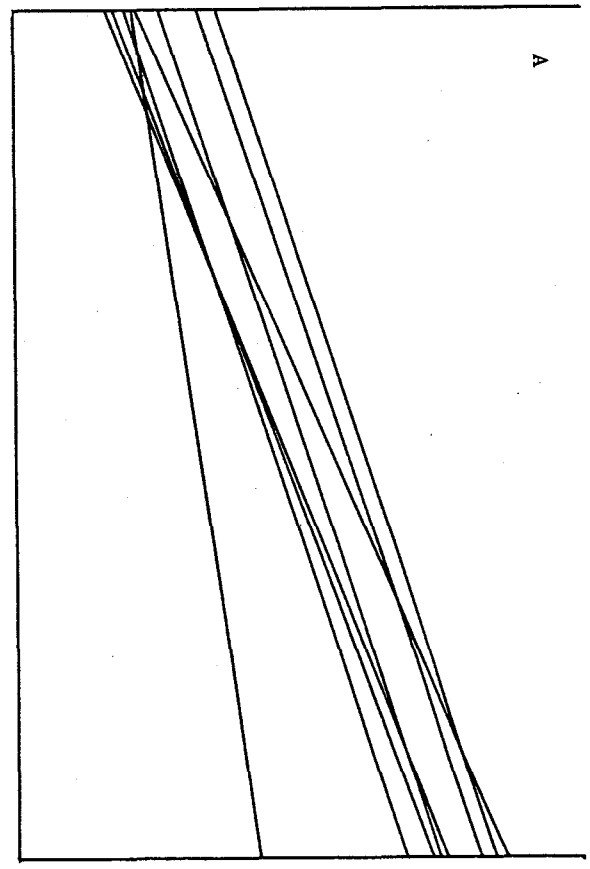
Figure 5.1. Average phenotypic responses of individual *A. ervi* genotypes to differences in host size at the time of parasitization: Parasitoid dry weight (A) and developmental time (B) in L_1 and L_4 aphids.

T_P OF PARASITOIDS FROM L_1



T_P OF PARASITOIDS FROM L_4

DW OF PARASITOIDS FROM L_1



DW OF PARASITOIDS FROM L_4

Discussion

Quantitative genetics of A. ervi

The sex-linked mode of inheritance, characteristic of the Hymenoptera, results in a higher degree of resemblance among sibs of the same sex, as compared to diploid-diploid species (Rinderer 1977; Bulmer 1980). A larger coefficient of relatedness facilitates more accurate estimates of the covariance between relatives by increasing the genetic effects relative to the environmental effects in the estimated variance component. In the present study, I was able to further minimize the environmental effects in the variance components by standardizing host size/age at parasitization, as parasitoid life-history characteristics (*e.g.*, size, developmental time, sex-ratio, longevity) are correlated with host size (Salt 1938; Arthur and Wylie 1959; Lawrence *et al.* 1976; Jowyk and Smilowitz 1978; Cloutier *et al.* 1981; Liu 1985). Parasitoid size increases at a decreasing rate with host size and eventually reaches a maximum (Henkelman 1979; Opp and Luck 1986). The threshold host size at which stability is achieved is most likely association specific. When *A. ervi* is reared at 20 °C, adult parasitoid size does not continue to increase in hosts that are larger than L_3 (Chapter III).

One of the main results of this study, that body size shows greater heritability than developmental time (Table 5.4), is consistent with the results of Chapter III where it was demonstrated that parasitoid size is more phenotypically variable than developmental time. Other species that are typically found in ephemeral and/or unpredictable habitats, *e. g.*, *Drosophila* (Birch *et al.* 1963; Dobzhansky *et al.* 1964) and *Tribolium* (Dawson 1977) show a similar pattern. The moderately high heritability of 38.28% for adult size in female *A. ervi*, averaged

over sire and dam components, lies between the mean heritability value for morphological characters in *Drosophila* (32 ± 2%) and animals in general (46 ± 0.4%) (Mousseau and Roff 1987; Roff and Mousseau 1987).

Significant genetic variability in body size in *A. ervi* is difficult to explain. One possible explanation, based on Fisher's (1930) theorem, is that fecundity is not under strong selection. Although fecundity in parasitoids is positively correlated with body size (Cloutier *et al.* 1981; Mackauer 1983; Liu 1985; Kambhampati 1987), with lifetime egg production capacities reported as high as 1800 (Mackauer and Chow 1986), it appears unlikely that more than a small fraction of the full potential fecundity is realized under field conditions (Gilbert and Gutierrez 1973; Mackauer 1983). Therefore, selection for increased fecundity is unlikely in *A. ervi*. If this is true then other correlates of size, such as mating ability, oviposition success and metabolic cost of maintenance, to name a few, may be more relevant in determining the ecological significance of body size.

An alternative explanation for moderately high heritability of size is that genetic variability may be maintained by selection acting simultaneously on traits that are genetically correlated with each other and with body size (pleiotropy). In a number of insects, moderately high heritabilities have been reported even in those traits believed to be under strong selection (Mukai *et al.* 1974; Istock *et al.* 1975; Dingle *et al.* 1977; Derr 1980; Rose and Charlesworth 1980a, b). As the genetic correlation structure of life history traits in *A. ervi* was not examined, antagonistic pleiotropy as a mechanism partly responsible for the maintenance of variation in body size remains a possibility.

In another aphid parasitoid, *Aphidius smithi* Sharma and Subba Rao, Henkelman (1979) found little genetic variability for adult size. After 9 generations of artificial selection for light and heavy populations, mummy (pupal) weight divergence between the two populations was 5.2% and 3.6% for males and females, respectively. Differences in the estimates of genetic variability between *A. ervi* and *A. smithi* can be explained on the basis of methodological differences. At 20 °C, the phenology of development is similar for both parasitoid species when reared on the pea aphid; the parasitized host mummifies within 8 days and adult parasitoids emerge within 14–15 days (Henkelman 1979). However, Henkelman reared *A. smithi* on 2-day-old (L_2) aphids which give rise to smaller parasitoids whereas, in this study, *A. ervi* was reared in 5-day-old (L_4) aphids which do not impose nutritional constraints on the growth and development of immature parasitoids.

The estimation of genetic variability in developmental time is beset with logistical problems which severely limit sample sizes, especially for half-sib designs. Parasitoid eclosion can be spread out over 2–4 days, making continuous observation of all but a small number of mummified aphids difficult. In the present study, sample sizes could have been increased by compromising the accuracy of individual developmental time estimates, but this would have resulted in severely biased variance components. Although estimates of r_A for developmental time (Table 5.4) cannot be considered precise because of small sample sizes, the direction of the deviation between sire and dam components is indicative of low additive genetic variance. The theory of quantitative genetics predicts that a trait under selection and closely related to fitness should have low additive genetic variance (Fisher 1930; Falconer 1989). Dominance genetic and

environmental variances are expected to increase as the trait in question becomes increasingly correlated with fitness (Travis *et al.* 1987; Falconer 1989).

The low additive genetic variance in developmental time could be attributed to selection for rapid development. Under field conditions the size of aphid populations can fluctuate considerably between and within growing seasons in response to environmental fluctuations (van den Bosch *et al.* 1966; van den Bosch *et al.* 1967; Dixon 1985). In addition, frequent alfalfa harvesting reduces aphid populations to very low levels (Campbell 1974), further increasing the stochasticity in population size and age structure. A rapid buildup of several hyperparasitoid populations over the growing season can result in rates of hyperparasitism as high as 80% (Campbell 1974; Mertins 1985). Thus, frequent and unpredictable fluctuations in the host population size and a high degree of hyperparasitism could result in strong selection for rapid development.

Another interesting aspect of the results presented here is that heritability of size estimated by sib analysis is greater in males than in females (Table 4). However, the genetic covariance for males estimated by P-O regression is not significantly different from zero. A higher full-sib estimate of heritability normally indicates the presence of dominance and environmental effects (Owen 1989). In *A. ervi*, the hemizygous nature of males precludes any contribution of dominance effects to the covariance of full sibs. Therefore, the inflated covariance of full sibs may be attributed, in part, to environmental effects. Haploid males may have less developmental homeostasis, which would produce greater and more phenotypically distinct responses to small environmental differences, *e.g.*, between rearing cages, compared to diploid females. Also, the possibility that small sample sizes and a violation of one or more of the model's statistical

assumptions contributed to the inflation of heritability in males cannot be ruled out.

The conflicting heritability estimates of body size in males obtained from sib analysis and P-O regression preclude any definitive conclusions regarding intersexual differences in genetic variability of *A. ervi*. It is plausible, however, that the pattern of quantitative inheritance between the sexes is asymmetrical. Evidence from studies on several species of bees and wasps (Eickwort 1969; Brückner 1976; Tepedino *et al*. 1984; Owen 1989) provides some support for this hypothesis. Owen (1989) found a two-fold intersexual difference in heritablity of radial cell length (a wing measure) in the bumblebee, *Bombus rufocinctus*, and suggested that the differences were the result of differing levels of homeostasis between the sexes. Brückner (1976) came to a similar conclusion with regard to the greater inter- and intra-individual variability of (haploid) drones compared to (diploid) workers in honey bees, *Apis mellifera*. Eickwort (1969) analysed variability in several morphological characters of the wasp, *Polistes exclamans* Viereck, and found that males were significantly more variable than queens and workers.

Genotype-environment (G-E) interactions

Theoretically, species occurring in environments with predictable long-term fluctuations should be selected for genetic variability and phenotypic inflexibility in fitness related traits, whereas in environments with random short-term fluctuations, fitness traits should have low genetic variability and high levels of phenotypic plasticity (Thoday 1953; Levins 1963; Bradshaw 1965; Marshall and Jain 1968; Hume and Cavers 1982). Thus, phenotypic plasticity and genetic variability

are expected to be negatively correlated. Contrary to these predictions, the trait with the greater genetic variability, *i.e.*, body size, is also more phenotypically plastic. The crossing of reaction norms, resulting in a low correlation coefficient (Fig. 5.1), is indicative of phenotypic plasticity. Developmental time, which is likely to have a low heritability, appears to be canalized, *i.e.*, a phenotype maintains its relative rank with respect to developmental time under different environmental conditions.

The results of several other studies indicate that genetic variability and phenotypic plasticity need not be negatively correlated. Berven and Gill (1983) analysed variability in developmental time and body size in the wood frog, *Rana sylvatica*, from different latitudes and found that greater variability was generally positively correlated with phenotypic plasticity and *vice versa*. Stearns (1983a) estimated the rates of evolution for several life history traits in mosquitofish, *Gambusia affinis*, and concluded that traits that evolved more rapidly were also more phenotypically plastic. Scheiner and Goodnight (1984) found no consistent relationship between phenotypic plasticity and genetic variability in several populations of the grass, *Danthonia spicata*, whereas Hazel *et al.* (1987) found that both components contributed to overall variation in pupal colour of the swallowtail butterfly, *Papilio polyxenes*.

The evidence presented in this chapter suggests that G-E interactions may have a significant role in maintaining genetic variability in populations of *A. ervi*. The observation that genetically variable traits can also be phenotypically plastic implicates G-E interactions in the maintenance of variability. Plasticity is thought to uncouple phenotype from genotype and thus mitigate the force of selection (Wright 1931; Stearns 1980, 1982; Sultan 1987). The apparent paradox, that rapidly

evolving traits can show considerable phenotypic plasticity as well as moderately high levels of additive genetic variance (c.f. Stearns 1983a, p. 72), could be explained, in part, on the basis of a response to selection without any evolutionary consequences, *i.e.*, selection acting only on the environmental component of variance will not erode genetic variability (c.f. van Noordwijk *et al.* 1988; Price *et al.* 1988; Alatalo *et al.* 1990).

Variation in host size at the time of parasitization, a pervasive characteristic of most aphid populations, may be an important factor in preserving genetic variability in parasitoid characteristics, such as size, that are influenced by host size. Under field conditions, aphid size/age class frequency distributions are skewed heavily to the lower end of the scale, with a predominance of first and second instars (Campbell 1974; Gilbert *et al.* 1976; Elliot and Kieckhefer 1989). Parasitoids attack and successfully complete development in all instar/size classes of the aphid but parasitized first- and second-instar aphids produce considerably smaller parasitoids than larger aphids (Liu 1985; Mackauer and Kambhampati 1988). Thus, small hosts may effectively mask genetically determined differences in the size of parasitoids.

CHAPTER VI

THE STRUCTURE OF DEVELOPMENT AND LIFE HISTORY PATTERNS AMONG APHID PARASITOIDS: AN INTERSPECIFIC COMPARISON

Introduction

Variability in the environment and in host characteristics may require adult parasitoids to make a series of decisions, including host selection, progeny allocation and progeny sex allocation (van Alphen and Vet 1986; Waage 1986). Once the parasitoid egg has been deposited within the host haemocoel, the ensuing larva must adapt to the internal host environment or perish. Immature parasitoids developing within the host haemocoel are faced with constantly changing nutritional and physiological environments in hosts that continue to feed and grow after parasitization (Strand 1986).

Parasitoids that are highly host-specific expose their larvae to variability in host size and changes in host quality associated mainly with feeding and growth after parasitization. By comparison, larvae of parasitoids with wide host ranges must be nutritionally as well as developmentally flexible to successfully utilize hosts that may differ widely in their nutritional and physiological characteristics. Quantitative developmental responses provide a convenient way of assessing how parasitoids that differ in their ecological characteristics may adapt to variability in nutritional and physiological host environments.

In this study, I compared host size effects on selected life history parameters of two aphidiid wasps, *A. ervi* and *Ephedrus californicus* Baker. The comparison was intended to identify those aspects of growth and development

that may be common among the aphidiids, and those that may be unique to each host-parasitoid association. First, I describe developmental responses and covariation of adult size (dry weight) and developmental time in *E. californicus* when reared on either the pea aphid or the alfalfa aphid, *Macrosiphum creelii* Davis. Next, I compare the characteristics of *E. californicus* with those of *A. ervi* (Chapter III).

I show that the ontogenies of both parasitoid species are similarly structured with regard to the covariation of body size and developmental time. Immature parasitoids of both species maximize size when host size at parasitization is below a threshold. Above the threshold host size, individuals of both species utilize additional available resources partly or fully for minimizing developmental time independently of body size. These results suggest that the epigenetic structure and control of body size and developmental time may be common to several, if not all, aphidiid wasps. I show that growth rate responses and inter-sexual differences in growth rates of parasitoids may be unique to each species, possibly reflecting bio-ecological differences between the two species.

Methods

Biology and rearing of E. californicus

E. californicus is a solitary internal parasitoid of several aphid species in the genus *Macrosiphum* (Mackauer and Finlayson 1967). Detailed accounts of the biology and field ecology of this parasitoid were given by Mackauer and Finlayson (1967), Starý (1970) and Cohen (1985). At 23 ± 1 °C the entire life cycle from oviposition to the emergence of adult parasitoids takes approximately

2 weeks (Cohen 1985). At 20 ± 0.2 °C the larval stages are completed within 8–10 days and the onset of pupation is marked by the formation of a characteristic black mummy; the entire life cycle requires 15–17 days.

In 1983, a laboratory colony of *E. californicus* was propagated from individuals collected as immatures developing in lupine aphids, *Macrosiphum albifrons* Essig., feeding on large-leaved lupine, *Lupinus polyphyllus* Lindl., in West Vancouver, B. C. The field collected individuals were transferred to the pea aphid reared on broad beans, *Vicia faba* L., c.v. 'Broad Windsor', in the laboratory. *E. californicus* readily attacks and is able to complete development in all stages of the pea aphid. Since its initial establishment in the laboratory, the parasitoid colony has been maintained as a small random breeding population ($N \leq 100$ individuals).

Experimental setup and data analyses

Mated *E. californicus* females were used to parasitize pea and alfalfa aphids of different ages/instars. Groups of same-aged individuals of the two aphid species were obtained by following the procedure described in Chapter I, with one exception; reproductives of the alfalfa aphid were confined to broad bean sprouts for 6 hours. I then followed the procedure described in Chapter II for parasitizing aphids and for measuring parasitoid size (dry weight), DW, and total developmental time from egg to adult, T_P.

Analysis of variance (ANOVA) and multivariate discriminant analysis (MDA) from the SPSSx library of statistical programs (SPSSx 1983) were used to analyze the data. Using MDA, parasitoids were statistically assigned to one of 6 groups in accordance with the host species and instar at parasitization, replicate

number, DW and T_P; males and females were analyzed separately. Only parasitoids reared from the pea aphid were used in computing the coefficients of the variables in discriminant functions (DF) 1 and 2. These coefficients were then used to classify parasitoids reared from the pea as well as alfalfa aphids. Confidence ellipses (95%) for bivariate scatterplots and discriminant function scores were computed according to Cornuet (1982).

Results

The duration of the parasitoid's larval growth phase varied with host instar at the time of parasitization, being shortest in L_1 and L_4, and longest in the intermediate instars (Table 6.1). Pea and alfalfa aphids parasitized as L_1, late L_1 and L_2 died in the fourth-instar stage, whereas when parasitized as L_3 and L_4 they died as adults. Eclosion of adult parasitoids began, in all host instars, within 14 days after oviposition. The proportion of parasitoids eclosing successfully was similar in all host instars (Table 6.1) (Kruskal-Wallis 1-way ANOVA, N = 18, chi-squared = 4.145, P = 0.529).

The sex ratio of adult parasitoids (number of females as a proportion of the total number) varied significantly between host instars (1-way ANOVA, df = 5, 12; F = 4.910; P = 0.01), with pea aphid L_4 producing the most female parasitoids and L_2 the least (Table 6.1). Parasitoids from L_1, late L_1, L_2 and *M. creelii* L_1 (= M.c.L_1 hereafter) showed greater sexual dimorphism in dry weight (measured as the dry weight ratio, DWR) than their counterparts from L_3 and L_4 aphids (1-way ANOVA, df = 5, 12; F = 5.074; P = 0.01; Table 6.1). The average DW and T_P of male and female parasitoids from the different host groups are

Table 6.1. Post eclosion characteristics of *Ephedrus californicus* reared from four instars (L_1-L_4) of the pea aphid, *A. pisum*, and from first-instar alfalfa aphids (M.c.L_1), *M. creelii*.

	Aphid characteristics								Parasitoid characteristics			
	replication											
	1			2			3					
Instar	tH	wH	SD	tH	wH	SD	tH	wH	SD	Tmax	N	ECL	SR†	DWR†
A. pisum:														
L_1	22	041	(5)	24	043	(3)	26	042	(5)	8	266	96.24	0.21b	1.47a
late L_1	28	044	(3)	30	044	(4)	32	047	(4)	10	280	93.57	0.26b	1.42a
L_2	40	049	(4)	42	056	(7)	44	055	(4)	10	280	93.57	0.14b	1.44a
L_3	70	093	(9)	72	099	(8)	74	114	(8)	10	266	95.86	0.44a	1.36ab
L_4	118	232	(32)	120	244	(27)	122	225	(22)	8	247	87.85	0.36a	1.30b
M. creelii:														
L_1	22	049	(9)	24	056	(8)	26	058	(7)	8.5	266	92.48	0.19b	1.43a

Abbreviations: t_H = host age at parasitization, in hours (± 2h); w_H = mean host DW at the time of parasitization, in micrograms; SD = standard deviation in micrograms; Tmax = time from parasitization to 50% mummification; N = number of mummies observed; ECL = % successful eclosion; SR = offspring sex ratio (% females in population); DWR = dry weight ratio (female : male).

† values followed by the same letter are not significantly different (SNK range test; α = 0.05).

Table 6.2. Total developmental time (T_P) and dry weight (DW) of male *E. californicus* reared in the four nymphal instars (L_1 – L_4) of the pea aphid and first-instar alfalfa aphids (M.c.L_1).

Aphid instar		T_P (hours ± 45 min) mean	SD	C.V.	DW (micrograms) mean	SD	C.V.	N
L_1:	rep 1	360.03	(8.60)	2.39	115	(8)	6.96	60
	2	359.48	(7.82)	2.18	113	(8)	7.08	63
	3	363.92	(11.06)	3.04	112	(8)	7.14	80
late L_1:	rep 1	397.62	(8.22)	2.07	113	(12)	10.62	56
	2	391.79	(9.32)	2.38	113	(12)	10.62	63
	3	400.57	(11.74)	2.93	118	(9)	7.63	74
L_2:	rep 1	398.98	(6.45)	1.62	122	(8)	6.56	71
	2	402.39	(9.49)	2.36	119	(10)	8.40	77
	3	399.21	(11.21)	2.81	121	(9)	7.44	78
L_3:	rep 1	389.58	(11.71)	3.01	146	(13)	8.90	31
	2	391.59	(9.71)	2.48	137	(14)	10.22	54
	3	394.73	(10.01)	2.54	144	(15)	10.42	57
L_4:	rep 1	364.27	(11.68)	3.21	172	(16)	9.30	48
	2	369.95	(11.01)	2.98	180	(16)	8.89	44
	3	371.11	(10.43)	2.81	175	(14)	8.00	46
M.c.L_1:	rep 1	370.13	(10.44)	2.82	127	(12)	9.45	80
	2	373.45	(11.08)	2.97	128	(10)	7.81	56
	3	375.84	(13.64)	3.63	127	(13)	10.24	64

Abbreviations: C.V. = Coefficient of Variation; L_1–L_4 = aphid instar at the time of parasitization; M, F = male and female parasitoids, respectively; rep = replication number; IV, A = fourth-instar and adult mummy, respectively; N = sample size.

Table 6.3. Total developmental time (T_P) and dry weight (DW) of female *E. californicus* reared in the four nymphal instars (L_1–L_4) of the pea aphid and first-instar alfalfa aphids (M.c.L_1).

Aphid instar		T_P (hours ± 45 min) mean	SD	C.V.	DW (micrograms) mean	SD	C.V.	N
L_1:	rep 1	382.88	(10.71)	2.80	167	(7)	4.19	26
	2	376.47	(11.93)	3.17	160	(16)	10.00	18
	3	386.94	(14.09)	3.64	171	(8)	4.68	9
late L_1:	rep 1	413.72	(9.47)	2.29	158	(23)	14.56	23
	2	411.45	(7.79)	1.89	170	(11)	6.47	28
	3	410.72	(10.42)	2.54	159	(17)	10.69	18
L_2:	rep 1	415.18	(7.48)	1.89	178	(10)	5.62	14
	2	416.96	(10.18)	2.44	168	(12)	7.14	13
	3	413.61	(11.54)	2.79	176	(15)	8.52	9
L_3:	rep 1	393.75	(10.88)	2.76	201	(18)	8.96	52
	2	395.83	(11.33)	2.86	183	(22)	12.02	32
	3	399.50	(9.24)	2.32	196	(21)	10.71	30
L_4:	rep 1	366.07	(9.90)	2.70	226	(15)	6.64	28
	2	372.11	(10.28)	2.76	232	(15)	6.47	22
	3	372.84	(8.55)	2.29	229	(14)	6.11	29
M.c.L_1:	rep 1	387.95	(14.76)	3.80	188	(18)	9.57	10
	2	390.07	(11.91)	3.05	178	(26)	14.61	21
	3	391.88	(9.47)	2.42	181	(15)	8.29	17

Abbreviations: C.V. = Coefficient of Variation; L_1–L_4 = aphid instar at the time of parasitization; M, F = male and female parasitoids, respectively; rep = replication number; IV, A = fourth-instar and adult mummy, respectively; N = sample size.

given in Tables 6.2 and 6.3, respectively. Male and female parasitoids do not differ significantly with respect to variability in DW and T_P (Wilcoxon sign rank test: Z_{DW} = -0.196; 2-tailed P = 0.845; Z_{T_P} = -0.022, 2-tailed P = 0.983), however, within each sex, T_P is considerably less variable than DW (Tables 6.2, 6.3).

Differences in DW and T_P between parasitoids reared from the various host instars were analysed separately for each variable, using a 2-way fixed-effects ANOVA model, with host instar and sex as main effects and replication number nested within host instar (Table 6.4). The values of both variables were significantly different between host instars, replications within host instars and between the sexes (Table 6.4). The interaction term (sex x host instar) was significant for T_P but not for DW, which indicates that inter-sexual differences with respect to T_P were influenced by differences in host size and, implicitly, future growth potential.

The pattern of covariation of DW and T_P in male parasitoids is shown in Figs. 6.1a-c. A similar pattern was obtained for females but is not shown. Parasitoid DW increases at an increasing rate with host instar at parasitization (Figs. 6.1a, b). T_P covaries positively with DW in parasitoids from pea aphid instars L_1, late L_1 and L_2, and negatively in L_3 and L_4 (Fig. 6.1a). Parasitoids reared from M.c.L_1 were larger than their counterparts from pea aphid L_2 (1-way ANOVA, df = 1, 424; F = 696.42; P < 0.000) and intermediate to L_1 and L_2 in developmental time (Fig. 6.1c) in spite of the fact that M.c.L_1 and L_2 pea aphids had the same dry weight at parasitization (1-way ANOVA, df = 1, 118; F = 1.015; P = 0.316).

Table 6.4. Nested analysis of variance on parasitoid DW and T_P. Parasitoids were classified by host instar, replicates† (rep) within groups and sex within replicates. All classification factors are treated as fixed. Tests of all hypotheses are based on Type III sums-of-squares (SAS 1985).

Dependent variable: DW

source	df	SS	MS	F	Pr > F
Group	5	5.64 x 10-1	1.13 x 10-1	648.30	0.0001
Rep(Group)	12	1.16 x 10-2	9.67 x 10-4	5.57	0.0001
Sex	1	6.94 x 10-1	6.94 x 10-1	3992.93	0.0001
Group x sex	5	1.05 x 10-3	2.10 x 10-4	1.21	0.3001
Error	477	2.57 x 10-1	1.74 x 10-4		

Dependent variable: T_P

source	df	SS	MS	F	Pr > F
Group	5	234479.17	46895.83	441.61	0.0001
Rep(Group)	12	8418.45	701.54	6.61	0.0001
Sex	1	39705.41	39705.41	373.90	0.0001
Group x Sex	5	13475.99	2695.20	25.38	0.0001
Error	1477	156848.13	106.19		

† replication was treated as a fixed effect because aphids continued to grow between parasitization intervals, resulting in *a priori* differences between replicates.

Table 6.5. Standardized coefficients of canonical discriminant functions for separating *E. californicus* reared from pea aphid instars L_1, late L_1, L_2, L_3 and L_4, on the basis of host instar, replicate number, developmental time (T_P) and size (DW).

ANALYSIS 1: Classification of male parasitoids

	func 1	func 2
REPLICATE	0.06807	-0.13121
T_P	-0.72194	0.75590
DW	0.90633	0.49930

classification results:

Group	host instar	N	predicted group membership 1	2	3	4	5
1	L_1	203	192	5	0	5	1
2	late L_1	193	4	123	57	9	0
3	L_2	226	2	93	109	22	0
4	L_3	142	5	6	18	108	5
5	L_4	138	3	0	0	3	132
M.c.	L_1	200	113	19	9	53	6

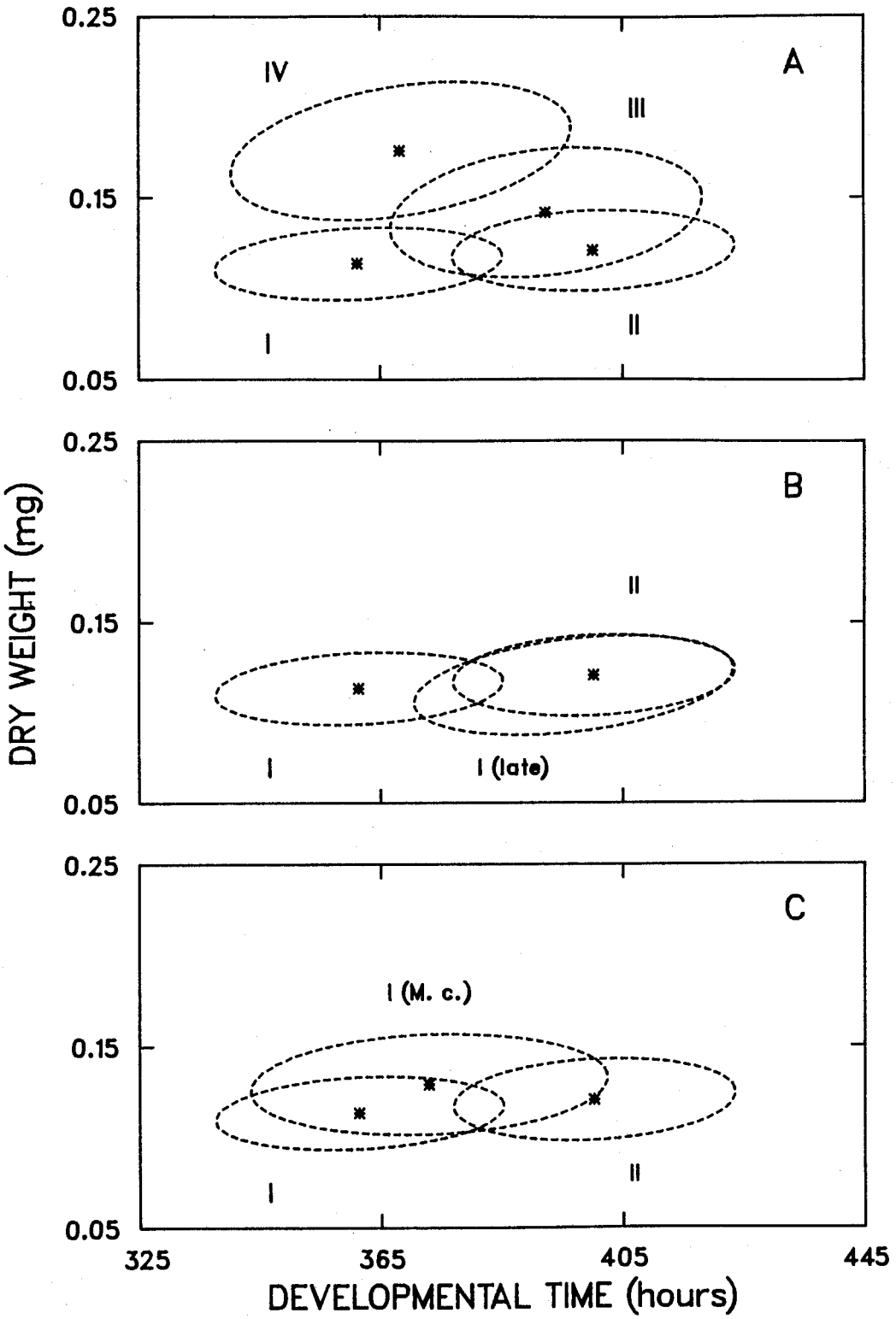
ANALYSIS 2: Classification of parasitoids by sex

	func 1
INSTAR	-0.51392
REPLICATE	-0.10750
T_P	0.35688
DW	1.15782

classification results:

sex	N	predicted sex 1	2
M	1102	1018	84
F	399	33	366

Figure 6.1. 95% confidence ellipses (Cornuet 1982) for developmental time and adult dry weight of *E. californicus* reared from different instars of the pea and alfalfa aphids: A) pea aphid instars L_1 (I), L_2 (II), L_3 (III) and L_4 (IV); B) pea aphid instars L_1 (I), late L_1 (late I) and L_2 (II); C) pea aphid instars L_1 (I) and L_2 (II), and alfalfa aphid (M. c.) instar L_1 (I). The group centroid is indicated by an asterix.


0.25
0.15
0.05
A
IV
III
II
I
B
II
I
I (late)
C
I (M. c.)
II
I
DRY WEIGHT (mg)
325
365
405
445
DEVELOPMENTAL TIME (hours)

The results of MDA indicate that parasitoids are separated by DF 1 (along the X-axis) and DF 2 (along the Y-axis) based on differences in DW and T_P. The coefficients of T_P are roughly similar in both functions, whereas the coefficient of DW is slightly larger in DF 1 (Analysis 1, Table 6.5). MDA correctly classified 73.61% of the total number of cases. Within groups, the highest classification accuracy is seen in pea aphid instars L_1 and L_4; in the intermediate instars the accuracy of prediction is considerably lower (Analysis 1, Table 6.5). Parasitoids reared from M.c.L_1 were classified using DF coefficients calculated for parasitoids reared from the pea aphid. This classification yielded two main groups, with characteristics similar to those of parasitoids reared from L_1 and L_3 (Analysis 1, Table 6.5). MDA used to separate males from females (Analysis 2, Table 6.5) correctly classifies 92.21% of all cases.

Discussion

Observed patterns of covariation among phenotypic traits of adult parasitoids may be attributed, in part, to correlated responses of individual traits, interactions between immature parasitoids and their hosts, or both. Variation in host size at parasitization and the subsequent growth potential of parasitized hosts directly influence variability in phenotypic characteristics and fitness of parasitoids (Salt 1940; Arthur and Wylie 1959; Lewis 1970; Mackauer 1973; Miles and King 1975; Jowyk and Smilowitz 1978; Charnov *et al.*, 1981; Lawrence 1981; Waage and Ng 1984; Liu 1985; Opp and Luck 1986; Mackauer and Kambhampati 1988). The developmental responses of *E. californicus* appear to vary in hosts of different sizes in such a way that resources are utilized first to maximize body size and then to minimize total developmental time. Developmental responses that may

allow immature parasitoids to adapt to host-related physiological and nutritional constraints include the growth rate and the commencement of destructive feeding by the parasitoid.

By comparing body size and total developmental time of parasitoids from different host classes (Figs. 6.1a, b), it can be seen that the growth rate of immature parasitoids appears to be constrained in host instars L_1, late L_1 and L_2. Low growth rates in these instars correspond to an increase in Tmax, which suggests that *E. californicus* delays the onset of the destructive feeding phase, presumably to maximize body size. The response of parasitoid developmental time and body size from L_3 and L_4 indicates that these host instars support higher parasitoid growth rates. Thus, aphids parasitized above the L_2 instar support higher parasitoid growth rates, which permit the maximization of body size as well as the minimization of total developmental time.

E. californicus appears to be unable to fully exploit the growth potential of the pea aphid, especially in the younger host instars (L_1–L_2). This conclusion is supported by several lines of evidence. Firstly, sexual size dimorphism (measured by DWR, Table 6.1) decreases with increasing host size (dry weight) at parasitization, indicating that growth rate differences between males and females become smaller as host size increases. Secondly, parasitoids reared from M.c.L_1 are larger and develop faster than their counterparts from *A. pisum* L_2 (Fig. 6.1c), even though the two classes of hosts do not differ in size at the time of parasitization. Thirdly, host size at parasitization influences the difference in average sex-specific developmental times; females take longer to develop in small hosts as compared to large hosts (Fig. 6.2a, b).

Figure 6.2. 95% confidence ellipses (Cornuet 1982) for sex-specific developmental time and dry weight of parasitoids reared from instars L_1 and L_4 of the pea aphid: *E. californicus* reared from L_1 (A) and L_4 (B); *A. ervi* reared from L_1 (C) and L_4 (D). The group centroid is indicated by an asterix. M and F represent males and females, respectively.

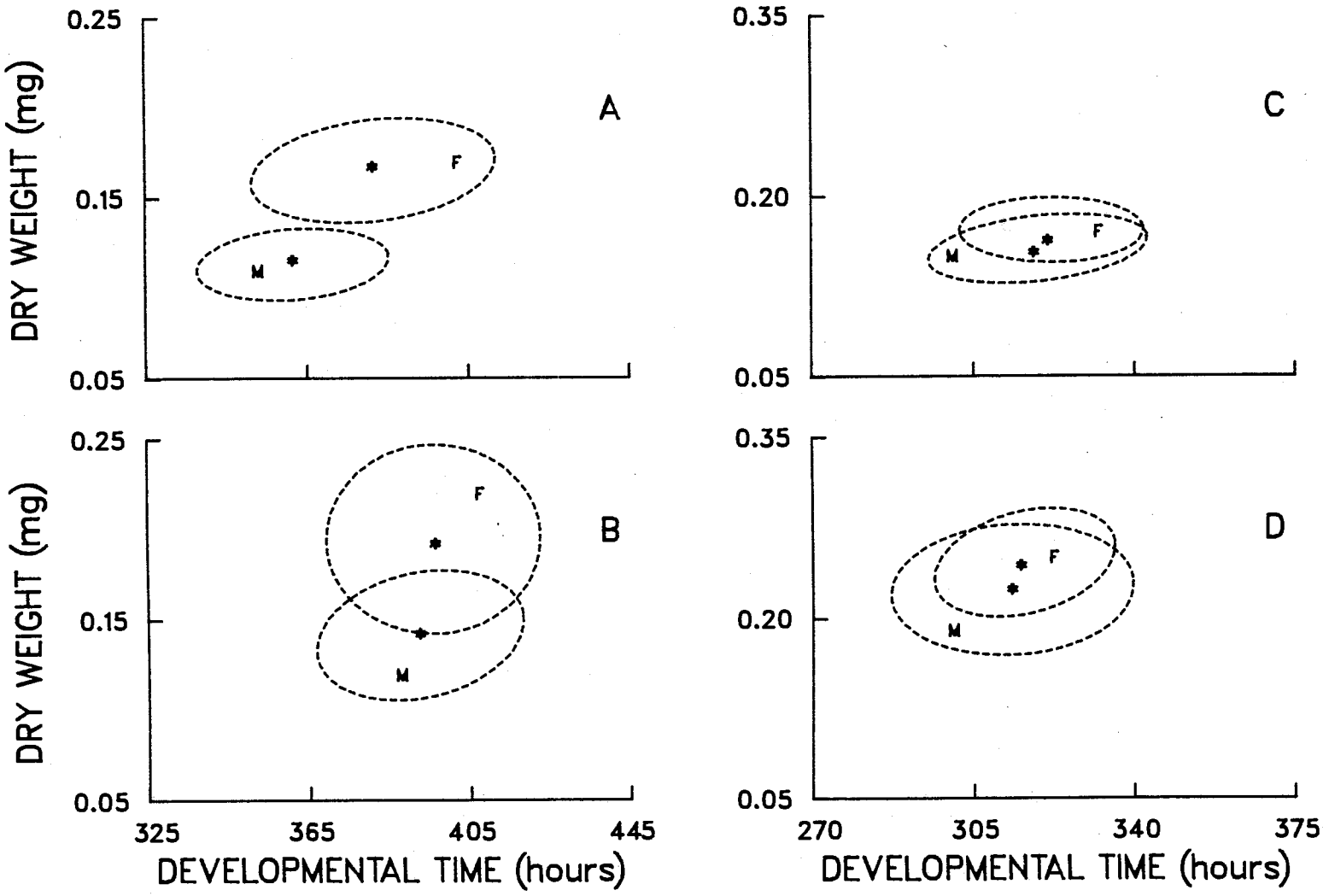
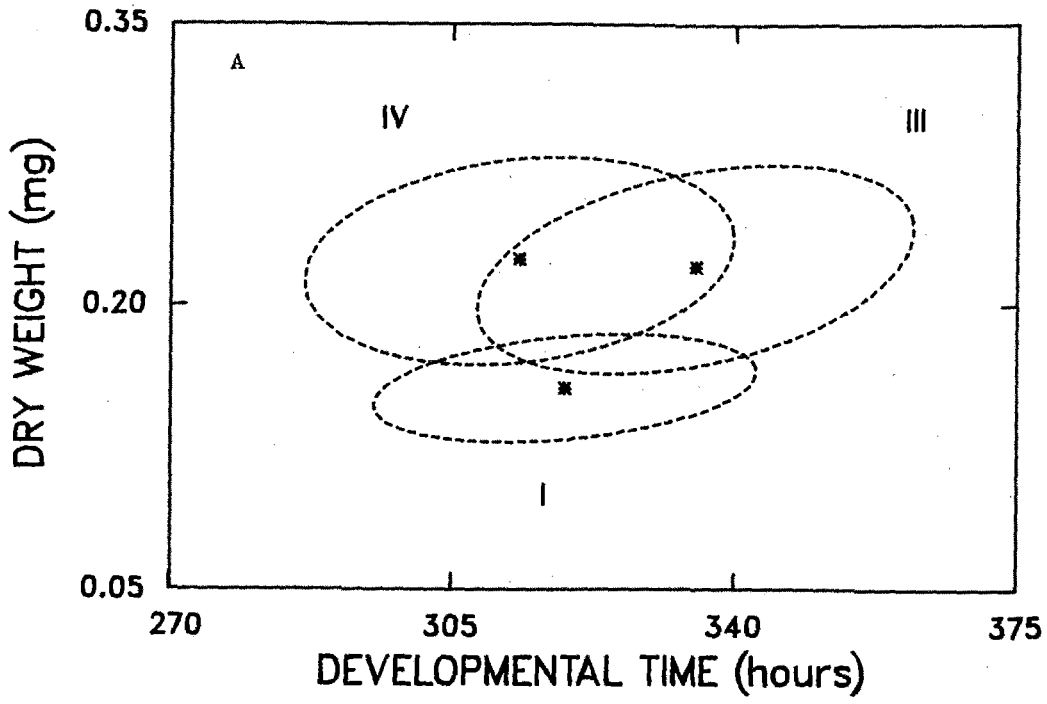
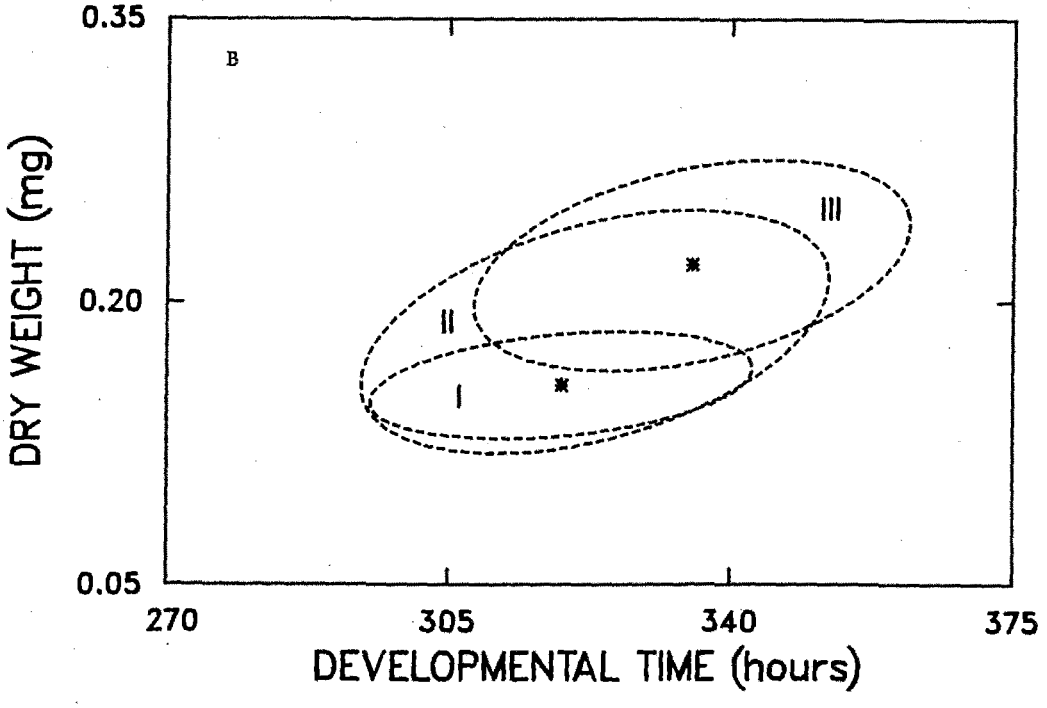

A
B
C
D
F
M
DRY WEIGHT (mg)
0.25
0.15
0.05
0.35
0.20
325
365
405
445
270
305
340
375
DEVELOPMENTAL TIME (hours)

Figure 6.3. 95% confidence ellipses (Cornuet 1982) for developmental time and adult dry weight of *A. ervi* reared from A) pea aphid instars L_1 (I), L_3 (III) and L_4 (IV), and B) instars L_1 (I), L_2 (II) and L_3 (III). The group centroid is indicated by an asterix.


A
IV
III
I
0.35
0.20
0.05
DRY WEIGHT (mg)
270
305
340
375
DEVELOPMENTAL TIME (hours)


B
III
II
I
0.35
0.20
0.05
DRY WEIGHT (mg)
270
305
340
375
DEVELOPMENTAL TIME (hours)

A comparison of developmental characteristics and the pattern of covariation in phenotypic traits between *E. californicus* (Figs. 6.1a-c) and *A. ervi* (Figs. 6.3a,b) reveals that the ontogenies of both parasitoid species are similarly structured; adult body size and total developmental time appear to be under the control of different genetic subprograms, and resources are allocated independently to each trait when host size is not nutritionally or otherwise limiting. Females of both parasitoid species grow faster than males as indicated by final size (dry weight) and developmental time (Fig. 6.2a-d), however, sex specific differences in growth rates are much larger in *E. californicus* (Fig. 6.2a, b) than in *A. ervi* (Fig. 6.2c, d). Sexual size dimorphism, with females being larger than males, has often been explained on the basis of a "fecundity advantage" (Clutton-Brock and Harvey 1978; Berry and Shine 1980; Veuille 1980; Gilbert and Williamson 1983; Hughes and Hughes 1986; Arak 1988; Shine 1988), *i.e.*, an increase in body size of females is correlated with higher fecundity.

At first glance, there is good evidence to support the application of the fecundity-advantage model to parasitoids (Benson 1973; Sandlan 1979; Lawrence 1981; Narasimham 1984; Nealis *et al.* 1984; Waage and Ng 1984; Takagi 1985; Opp and Luck 1986). However, as body size is significantly more variable than developmental time in both parasitoid species, (Tables 6.2, 6.3; see also Chapter III), it could also be argued, on theoretical grounds (Fisher 1930; Lewontin 1965; Roff 1981), that developmental time has a greater influence on parasitoid fitness than fecundity. Thus, the fecundity-advantage model may not fully explain the significance of sexual size dimorphism in parasitoid wasps. It is more likely that sexual dimorphism in parasitoids results from the combined effects of several factors, including sex-specific differences in reproductive success, sexual selection

and haplodiploidy, as noted by Hurlbutt (1987).

Developmental interactions between the host and the parasitoid in the later stages of parasitism may be unique to each association. In the *A. ervi*–pea aphid association, the length of the parasitoids larval phase is independent of host size at the time of parasitization; death of the parasitized host and the formation of the mummy occurs approximately 8 days after parasitization at 20 ± 0.2 °C, 60–65% r.h., and constant light. Under identical environmental conditions, in the *E. californicus*–pea aphid association, the parasitoid's larval period varies with host size at parasitization (Table 6.1). The formation of the mummy is typically observed within 24 hours of the commencement of destructive feeding by the parasitoid larva (Soldan and Starý 1981; Polaszek 1986). Therefore, it can be concluded that the destructive feeding responses of *E. californicus* and *A. ervi* may differ under standardized host size and environmental conditions. This difference suggests that the cues that elicit the destructive feeding response may be different in the two parasitoid species, and furthermore that the parasitoid species may have evolved different mechanisms to cope with host-related constraints on growth and development.

Sex-specific variability in adult size and developmental time also appear to be unique to each parasitoid species. In *A. ervi*, females are significantly less variable than males with respect to both traits. In contrast, there is no difference in variability between the sexes with respect to body size and developmental time in *E. californicus*. The significance of this intersexual difference in variability is open to speculation. In the laboratory, the *A. ervi* population had been maintained under conditions that minimized inbreeding, whereas the *E. californicus* population had experienced several bottlenecks and possibly considerable

inbreeding. Under such conditions, a reduction in genomic heterozygosity expected from inbreeding may have resulted in increased phenotypic variability in female *E. californicus* (see, *e.g.*, Robertson and Reeve 1952; Lerner 1954; Livshits and Kobyliansky 1985; Chakraborty 1987; and review by Mitton and Grant 1984), possibly due to decreased developmental homeostasis. In the haplodiploid Hymenoptera, males, by virtue of their haploid genomes, are often more phenotypically variable than females (Eickwort 1969; Brückner 1976; Owen 1989).

From Figs. 6.1a and 6.3a, it can be seen that parasitoids of both species developing in hosts parasitized above a threshold size will benefit from an increase in body size as well as a shorter developmental time. However, the relative importance of the two traits may be different for each parasitoid species. Body size may be important to *A. ervi* in so far as a minimum body size may be essential for ecological competence; below a certain size threshold survival may be compromised but above the threshold a reduction in developmental time may be vital for maximizing reproductive success. In *E. californicus*, body size may be directly correlated with oviposition success; larger parasitoids may be more successful in overcoming host defenses because oviposition requires, on average, 11 seconds (Chow and Mackauer 1986). By comparison, *A. ervi* requires less than 1 second for oviposition (Starý 1970), which would make the parasitoid's oviposition success less dependent on its body size.

The fact that larval and pupal stages are separated in time and controlled by distinct genetic subprograms (Crick and Lawrence 1975; Yund and Germeraad 1980; Willis 1986; Cowley and Atchley 1990) may allow immature parasitoids to adapt to their internal host environments in different ways. For example, in *A.*

ervi the length of the larval stage is relatively constant whereas in *E. californicus* it varies with host size and species. This difference may reflect differences in the field biology and ecology of the two species. In British Columbia, *E. californicus* may be described as being broadly oligophagous, with a wider host range than *A. ervi* which is found mainly on the pea aphid on alfalfa (Mackauer and Finlayson 1967; Cohen and Mackauer 1986). Thus developmental responses and patterns of covariation between traits may be useful indicators of biological and ecological diversity among parasitoids.

CHAPTER VII

HOST-PARASITOID INTERACTIONS: SOME GENERAL CONSIDERATIONS

This thesis represents the first comprehensive attempt to establish a link between larval growth history, the ensuing adult phenotype and reproductive success. From an ecological perspective, the several aspects of host-parasitoid interactions detailed in this thesis may be viewed as components of a life history strategy, *i.e.*, a series of genetically programmed responses that ensure immature parasitoid survival and the production of functionally competent adults. Relationships between larval ontogenies, the resulting phenotypes and their life history strategies fall within the domain of insect nutritional ecology (Scriber and Slansky 1981; Slansky 1981, 1986). The larval ontogeny of solitary endoparasitic insects, being dependent on nutrition, will be influenced by host quality. In previous studies on host-parasitoid interactions, host quality has been inferred from diverse parasitoid attributes, such as size, weight, growth rate and demography (*e.g.*, Salt 1940; Arthur and Wylie 1959; Lewis 1970; Mackauer 1973; Miles and King 1975; Lawrence *et al*. 1976; Jowyk and Smilowitz 1978; Charnov *et al*. 1981; Liu 1985; Opp and Luck 1986; van Bergeijk *et al*. 1989).

In Chapter II, the trajectory of parasitoid larval growth was selected as an appropriate measure of host quality because it reflects the nutritional interactions between the host and the parasitoid throughout the course of parasitism. Growth is governed by the rate of weight gain, the efficiency of converting food into tissue, and the metabolic cost of maintenance (Calow 1977a). The optimal growth trajectory is therefore one that results in the largest amount of biomass, minimum metabolic cost and the shortest developmental time. The optimality of

different trajectories must be evaluated by their economics of resource/energy acquisition and conversion, rather than by the growth rate, *per se*, which varies with age.

The main function of the larval stages of endoparasitic insects is the acquisition and storage of nutrients. Any factor that influences the parasitoid's growth rate will also influence the amount of nutrient reserves accumulated at the end of the larval stage, and subsequently the life history phenomena of adults. As discussed by Thompson (1982, 1983a, 1983b, 1986), nutritional interactions are determined to a large extent by the level of physiological and metabolic integration which are dynamic processes in host-parasitoid associations. Therefore, host quality, which encompasses all aspects of integration, can be expected to vary with host age/size at parasitization and, as well, during the course of the association.

A. ervi appears to integrate its nutritional requirements with those of the host in a competitive (non-destructive) manner. A competitive mode of resource acquisition requires that *A. ervi* possess a high conversion efficiency, enabling it to compete effectively with the host. Direct estimates of the conversion efficiency are not available, but the evidence presented by Cloutier (1978) suggests that *A. ervi* has a higher conversion efficiency than its host. An unavoidable drawback of passive nutritional interactions would be the necessity of achieving a critical size in order to eventually control host resources. Prior to achieving critical size, the parasitoid would be vulnerable to the effects of fluctuation in available resources.

Studies by Thompson (1982, 1983b) on *Trichoplusia ni* and its parasitoid *Hyposoter exiguae* indicate that nutritional integration in lepidopteran host-parasitoid systems is likely to be based on energy/resource assimilation and utilization profiles, as discussed here, but the mechanisms by which integration is achieved may well be different (Vinson and Iwantsch 1980). Mechanistic differences may be expected purely on the basis of biological differences between the lifestyles of hemi- and holometabolous hosts.

Several different mechanisms of nutritional integration may be possible by adjusting some component of the interaction. Hypothetically, a parasitoid with a low maximum growth rate and conversion efficiency (*i.e.*, wasteful) would require a prolonged developmental time and a greater volume of resources to achieve a given body size than a parasitoid with a higher growth rate and conversion efficiency. One possibe way to increase the volume of available resources would be to inject a toxin or virus particle that specifically inhibits or destroys a certain host sub-system (*e.g.*, reproductive) early in the interaction. This would liberate a considerable volume of resources for use by the parasitoid. Injection of toxins or virus particles is known or suspected for a number of parasitic Hymenoptera, but their definitive functions are, as yet, poorly understood (Strand 1986).

Patterns of covariation in body size and developmental time in *A. ervi* could be interpreted as being the result of adaptive resource allocation responses of immature parasitoids (Chapter III). Correlated responses among characters may be expected because of pleiotropy and other genetic effects (Lande 1980; Rose and Charlesworth 1981a; Rose 1982; Giesel 1986; Scheiner *et al.* 1989). However, host size effects and the epigenetic structure of development could obscure the true

nature of correlations between characters. For example, in holometabolous insects, genetically uncorrelated characters may appear to be correlated at the level of the phenotype if their development is synchronous during ontogeny (Riska 1986; Cowley 1987; Cowley and Atchley 1990), or because immature parasitoids were nutritionally constrained by the host (Chapters II, III and VI).

Inter- and intraspecific variation in size has traditionally been explained mainly on the basis of metabolic efficiencies, predation and competition (Hamilton 1961; Nevo 1973; Sweeney and Vannote 1978; Fenchel 1975; Lynch 1977), whereas variability in developmental time has been examined in relation to reproductive and mortality rates (Sibly and Calow 1986; Stearns and Koella 1986). From a mechanistic viewpoint, patterns of covariation in body size and developmental time of *A. ervi* could be explained on the basis of sequential expression of genetic subprograms controlling different stages of development. Studies on biochemical syntheses during post-embryonic development (*e.g.*, Roberts and Willis 1980; Kafatos 1981; Sheridan 1988; Sternberg 1990) and hormonal control of morphogenesis (Willis 1974; Nijhout 1981) confirm the existence of genetic subprograms that control different phases of development. The timing and level of expression are probably dependent upon changes in the internal physiological environment when the larva stops feeding (Nijhout 1981).

Much of life history theory addresses the central question of how a limited amount of resources may be apportioned between competing life history functions (Tinkle 1969; Stearns 1977; Schaffer 1974; Calow 1981b; Sibly and Calow 1986). Allocation of a limited amount of resource to competing physiological functions is expected to result in trade-offs between somatic growth, reproduction and maintenance requirements (Cody 1966; Calow 1977a; Law 1979; Sibly and Calow

1986). Negative correlations between life history parameters are indicative of resource allocation trade-offs. In *Drosophila* species, some studies report negative correlations between early- and late-life characters (Rose and Charlesworth 1981a, b; Rose 1984) whereas others have found primarily positive correlations (Giesel and Zettler 1980; Giesel *et al.* 1982a, b; Murphy *et al.* 1983).

L_x and M_x schedules of *A. ervi* (Chapter IV) appear to vary independently except when parasitoids experience developmental stress in the form of delayed growth in the larval stages. If this assessment is correct, then it could be argued that some trade-offs between life history parameters will be detectable only when parasitoids are reared under physiologically stressful conditions. This argument has been used by Giesel and co-workers to explain the genetic correlation structure of life history variables in *Drosophila melanogaster* (Giesel and Zettler 1980; Giesel *et al.* 1982a, b; Murphy *et al.* 1983). Using wild and laboratory populations of *D. melanogaster*, Giesel (1986) showed that, when reared at 25 °C (optimal temperature), genetic correlations between early- and late-life characteristics were primarily positive, whereas at 22 °C or 28 °C (sub-optimal temperatures) some negative correlations became evident.

Trade-offs between the fitness consequences of delayed development and increased size (fecundity) could make different combinations of size and developmental time optimal in different environments (Lewontin 1965; Roff 1981). In *A. ervi*, trade-offs may be important only within a limited range of parasitoid sizes, *i.e.*, where fecundity and developmental time increase linearly with size. Such a linear relationship may be expected in parasitoids reared from the first three instars of the pea aphid (Fig. 2.1a), whereas parasitoids reared from L_4 aphids are likely to benefit from a short developmental time as well as a large

body size. On the basis of these differences, two life history strategies are conceivable: one in which parasitoids oviposit in aphids that are below a certain age/size threshold and the optimal combination of life history traits is determined by trade-offs, and the second in which parasitoids oviposit in hosts above the threshold and the maximization of fitness is independent of trade-offs. The evolution of a particular strategy or strategies will be influenced by the phenology and age/size structure of aphid populations, and the relative fitness of parasitoids adopting different strategies.

Under laboratory conditions, the nonlinear relationship between parasitoid body size and r_m indicates that the contributions of developmental time, adult fecundity and survivorship to reproductive success vary with body size and host quality. The relative importance of different life history parameters with regard to host size/quality variation in the field may be evaluated on the basis of heritability and phenotypic plasticity. Genetic variability in body size and developmental time of *A. ervi* discussed in this thesis are valid only for the constant laboratory environment they were obtained in. Body size is moderately heritable whereas developmental time is likely to have low additive genetic variance (Chapter V). The importance of these findings to an understanding of the evolutionary process under field conditions may not be immediately obvious when the relationship between the genotype and the phenotype(s) produced in different environments is ignored (Johannsen 1911; Schmalhausen 1949; Lewontin 1974; Gupta and Lewontin 1982; Stearns and Koella 1986; Gebhardt and Stearns 1988; Barton and Turelli 1989; Gillespie and Turelli 1989).

In view of the heterogeneity in the biotic and abiotic environment, it is likely that different sub-populations of the pea aphid and *A. ervi* are influenced

by different evolutionary forces in space and time. Significant additive genetic variance in fitness related traits cannot be easily explained on the basis of Fisher's (1930) theorem of natural selection. Variability may be maintained by G-E interactions in rapidly fluctuating environments and/or pleiotropic connections with other traits. An understanding of adaptive evolution in life history and morphological traits of parasitic insects will greatly benefit from the incorporation of host size effects and G-E interactions into analyses of evolutionary cause and relationships.

Evolutionary models of host selection and reproductive decisions by parasitoids (*e.g.*, van den Assem 1971; Charnov 1979; Charnov *et al.* 1981; Charnov and Skinner 1984; Werren 1984; Takagi 1985; Werren and Simbolotti 1989) are often based on the assumptions that host size and quality are linearly related to each other and correlate positively with fitness traits of parasitoids. The validity of predictions made by these so called "host size" models rests upon the premise that the ontogenies and feeding experiences of immature parasitoids developing in hosts of different sizes are largely similar and, as a consequence, are irrelevant to life history strategies (*e.g.*, Charnov *et al.* 1981). These assumptions have largely been untested.

The host size models predict female-biased sex ratios in large hosts based on the assumption that females experience greater reduction in fitness in small hosts relative to males. This fundamental assumption of the host size models may not always be valid. In *A. ervi*, sex-specific growth rate differences appear to be constant across host instars, resulting in a constant female:male DW ratio of 1.10 (Chapter III), whereas in *E. californicus* the growth rate of male parasitoids relative to that of females appears to increase with host size at

parasitization (Chapter VI). The prediction that host quality should be evaluated relative to other hosts available in the environment can be falsified. In the experiments reported here, *A. ervi* and *E. californicus* females were not given a choice of host sizes for oviposition, but the resultant sex-ratios are significantly different between small and large hosts for both parasitoid species. This suggests that wasps may be capable of evaluating host quality on an absolute basis.

Differences in life history parameters and their underlying physiological processes are reflected in the intrinsic population growth rate, r_m, at the ecological level. Thus, r_m may be used appropriately as a bio-ecological index as well as a rating of physiological performance (Messenger 1964; Roff 1981; Mackauer 1983). Among insects, r_m scales (usually negatively) with body size across orders (Fenchel 1974; Gaston 1988) but, within species, the relationship has not been closely scrutinized. Indirect evidence from fecundity and longevity data (see King [1987a, b] for reviews) suggests that r_m should scale positively with body size in parasitoid species. In *A. ervi*, r_m is a nonlinear function of body size. Estimates of r_m for *A. ervi* presented in this thesis are valid only as ratings of physiological performance; extrapolation to natural population growth rates is questionable because assumptions concerning population structure may not be valid. The nonlinear relationship between r_m and body size suggests that assumptions of simple linear relationships between parasitoid reproductive success, body size, host quality and host size may not generally be valid. Predictions of models based on assumptions that oversimplify complex ontogenetic interactions between hosts and their parasitoids are likely to suffer from a lack of realism.

Laboratory estimates of a parasitoid's reproductive success cannot be extrapolated to natural environments, but they may be used to scale hosts of

different sizes with regard to their potential ecological impact on parasitoid populations. Aphid populations typically contain several or all immature stages and morphs at any given time (Dixon 1985). Therefore, parasitoids may have several choices of host sizes/instars in which to oviposit. Host size selection is likely to be a compromise between the quality of hosts for the immature progeny and ease of oviposition. Parasitoids may grow faster and attain larger body sizes in bigger hosts, as in L_4 aphids, but younger age/size classes of aphids are more prevalent in natural populations (Campbell 1974; Gilbert *et al.* 1976; Elliot and Kieckhefer 1989) and are easier to attack. The defensive behaviour of large aphids may reduce the oviposition success of parasitoids (Gerling *et al.* 1990). Thus, in addition to physiological trade-offs, life history strategies of aphid parasitoids will also be moulded by the economics of behavioural responses to environmental heterogeneity.

LITERATURE CITED

Alatalo, R. V., Gustaffson, L., and Lundberg, A. 1990. Phenotypic selection on heritable size traits: environmental variance and genetic response. **Am. Nat.** 135: 464-471.

Arak, A. 1988. Sexual dimorphism in body size: a model and a test. **Evolution** 42: 820-825.

Arthur, A. P., and Wylie, H. G. 1959. Effects of host size on sex-ratio, developmental time and size of *Pimpla turionellae* L. **Entomophaga** 4: 297-301.

Banks, C. J. 1964. Aphid nutrition and reproduction. **Rep. Rothamst. Exp. Sta. 1964.** 299-309.

Barton, N. H., and M. Turelli. 1989. Evolutionary quantitative genetics: how little do we know? **Annu. Rev. Genet.** 23: 337-370.

Bell, G. 1984a. Measuring the cost of reproduction. I. The correlation structure of the life table of a plankton rotifer. **Evolution** 38: 300-313.

Bell, G. 1984b. Measuring the cost of reproduction. II. The correlation structure of the life table of five freshwater invertebrates. **Evolution** 38: 314-326.

Benson, J. F. 1973. Intraspecific competition in the population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae). **J. Anim. Ecol.** 42: 105-124.

Berry, J. F., and Shine, R. 1980. Sexual size dimorphism and sexual selection in turtles (Order Chelonia). **Oecologia** 44: 185-191.

Berven, K. A., and Gill, D. E. 1983. Interpreting geographic variation in life-history traits. **Amer. Zool.** 23: 85-97.

Birch, L. C., Dobzhansky, T., Elliot, P., and Lewontin, R. C. 1963. Relative fitness of geographic races of *Drosophila serrate*. **Evolution** 17: 72-83.

Blackman, R. L. 1987. Reproduction, cytogenetics and development. *In* A. K. Minks and P. Harrewijn (eds.), *Aphids, their biology, natural enemies and control*. World Crop Pests, Volume 2A, pp. 163-195, Elsevier, Amsterdam.

Boggs, C. L. 1981. Nutritional and life-history determinants of resource allocation in holometabolous insects. **Am. Nat.** 117: 692-709.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. **Adv. Genet.** 13: 115-155.

Brough, C. N., Dixon, A. F. G., and Kindlmann, P. 1990. Pattern of growth and fat content of somatic and gonadal tissues of virginoparae of the vetch aphid, *Megoura viciae* Buckton. **Entomol. exp. appl.** 56: 269-275.

Brückner, D. 1976. The influence of genetic variability on wing symmetry in honeybees (*Apis mellifera*). **Evolution** 30: 100–108.

Bruslé, S. 1962. Chronologie du développement embryonnaire des femelles parthénogénétiques de *Brevicoryne brassicae* (Aphididae, Homoptéres). **Bull. Soc. Zool. France** 87: 396–418.

Bulmer, M. G. 1980. The Mathematical Theory of Quantitative Genetics. Clarendon Press, Oxford.

Calow, P. 1977a. Ecology, evolution and energetics: a study in metabolic adaptation. **Adv. Ecol. Res.** 10: 1–60.

Calow, P. 1977b. Conversion efficiencies in heterotrophic organisms. **Biol. Rev.** 52: 385–409.

Calow, P. 1979. The cost of reproduction – a physiological approach. **Biol. Rev.** 54: 23–40.

Calow, P. 1981a. Invertebrate Biology. A functional approach. Croom Helm, London.

Calow, P. 1981b. Resource utilization and reproduction. *In* C. R. Townsend and P. Calow (eds.), *Physiological ecology: an evolutionary approach to resource use.* pp. 245–270, Blackwells, Oxford.

Campbell, A. 1974. Seasonal changes in abundance of the pea aphid and its associated parasites in the southern interior of British Columbia. Ph. D. Thesis, Simon Fraser University, Burnaby, British Columbia.

Causton, D. R. 1977. A biologist's mathematics. Edward Arnold, London.

Causton, D. R., and Venus, J. C. 1981. The biometry of plant growth. Edward Arnold, London.

Chakraborty, R. 1987. Biochemical heterozygosity and phenotypic variability of polygenic traits. **Heredity** 59: 19–28.

Charnov, E. L. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. **Am. Nat.** 113: 465–480.

Charnov, E. L., and Skinner, S. W. 1984. Evolution of host selection and clutch size in parasite wasps. **Florida Entomol.** 67: 5–21.

Charnov, E. L., Los-Den Hartog, R. L., Jones, W. T., and van den Assem, J. 1981. Sex-ratio evolution in a variable environment. **Nature** (Lond.) 289: 27–33.

Chow, F. J., and Mackauer, M. 1984. Inter- and intraspecific larval competition in *Aphidius smithi* and *Praon pequodorum* (Hymenoptera: Aphidiidae). **Can. Ent.** 116: 1097–1107.

Cloutier, C. F. 1978. A study of the host-parasite association between the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae), and some of its hymenopteran parasites: growth and food utilization during parasitism. Ph. D. Thesis, Simon Fraser University, Burnaby, British Columbia.

Cloutier, C. F. 1986. Amino acid utilization in the aphid *Acyrthosiphon pisum* infected by the parasitoid *Aphidius smithi*. **J. Insect Physiol.** 32: 263–267.

Cloutier, C., and Mackauer, M. 1979. The effect of parasitism by *Aphidius smithi* (Hymenoptera: Aphidiidae) on the food budget of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). **Can. J. Zool.** 57: 1605–1611.

Cloutier, C. F., McNeil, J. M., and Regniére J. 1981. Fecundity, longevity, and sex ratio of *Aphidius nigripes* (Hymenoptera: Aphidiidae) parasitizing different stages of it host, *Macrosiphum euphorbiae* (Homoptera: Aphididae). **Can. Ent.** 113: 193–198.

Clutton-Brock, J. H., and Harvey, P. H. 1978. Mammals, resources and reproductive strategies. **Nature** (Lond.) 273: 191–195.

Cody, M. L. 1966. A general theory of clutch size. **Evolution** 20: 174–184.

Cohen, M. B. 1985. Biology and Ecology of *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae). M. Sc. Thesis, Simon Fraser University, Burnaby, British Columbia.

Cohen, M. B., and Mackauer, M. 1986. Lupine aphid, *Macrosiphum albifrons* (Homoptera: Aphididae): distribution and hymenopterous parasites in British Columbia. **Environ. Entomol.** 15: 719–722.

Collins, A. M., Rinderer, T. E., Harbo, J. R., and Brown, M. A. 1984. Heritabilities and correlations for several characters in the honey bee. **J. Hered.** 75: 135–140.

Corbet, S. A. 1968. The influence of *Ephestia kuehniella* on the development of its parasite *Nemeritis canescens*. **J. Exp. Biol.** 48: 291–304.

Cornuet, J. M. 1982. Représentation graphique de populations multinormales par des ellipses de confiance. **Apidologie** 13: 15–20.

Cowley, D. E. 1987. Developmental quantitative genetics of *Drosophila melanogaster*. Ph. D. Thesis, University of Wisconsin, Madison.

Cowley, D. E., and Atchley, W. R. 1990. Development and quantitative genetics of correlation structure among body parts of *Drosophila melanogaster*. **Am. Nat.** 135: 242–268.

Crick, F. H. C., and Lawrence, P. A. 1975. Compartments and polyclones in insect development. **Science** 189: 340–347.

Crozier, R. H. 1977. Evolutionary genetics of the hymenoptera. **Annu. Rev. Entomol.** 22: 263-288.

Dawson, P. J. 1977. Life history strategy and evolutionary history of *Tribolium* flour beetles. **Evolution** 31: 227-229.

Derr, J. A. 1980. The nature of variation in life history characters of *Dysdercus bimaculatus* (Heteroptera: Pyrrhocoridae), a colonizing species. **Evolution** 34: 548-557.

Dingle, H., Brown, C. K., and Hegmann, J. P. 1977. The nature of genetic variance influencing photoperiodic diapause in a migrant insect *Oncopeltus fasciatus*. **Am. Nat.** 111: 1047-1059.

Dixon, A. F. G. 1985. Aphid Ecology. Blackie, New York.

Dixon, A. F. G. 1987. Parthenogenetic reproduction and the rate of increase in aphids. *In* A. K. Minks and P. Harrewijn (eds.), *Aphids, their biology, natural enemies and control*. World crop pests, Volume 2A, pp. 269-287, Elsevier, Amsterdam.

Dobzhansky, T., Lewontin, R. C., and Pavlovsky, D. 1964. The capacity for increase in chromosomally polymorphic and monomorphic populations of *D. pseudoobscura*. **Heredity** 19: 597-614.

Doutt, R. L. 1959. The biology of parasite hymenoptera. **Ann. Rev. Entomol.** 4: 161-182.

Duncan, A., and Klekowski, R. Z. 1975. Parameters of an energy budget. *In* W. Grodzinski, R. Z. Klekowski and A. Duncan (eds.), *Methods for ecological bioenergetics*, pp. 97-147, Blackwells, Oxford.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. SIAM, Monograph 38, CBMS-NSF.

Eickwort, K. R. 1969. Differential variation of males and females in *Polistes exclamans*. **Evolution** 23: 391-405.

Elliot, N. C., and Kieckhefer, R. W. 1989. Effects of constant and fluctuating temperatures on immature development and age-specific life tables of *Rhopalosiphum padi* (L.) (Homoptera: Aphididae). **Can. Entomol.** 121: 131-140.

Ewens, W. J. 1976. Remarks on the evolutionary effect of natural selection. **Genetics** 83: 601-607.

Falconer, D. S. 1989. Introduction to Quantitative Genetics. Longman Scientific and Technical, U. K.

Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. **Oecologia** 14: 317-326.

Fenchel, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). **Oecologia** 20: 19-32.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Gaston, K. J. 1988. The intrinsic rate of increase of insects of different sizes. **Ecol. Entomol.** 14: 399-409.

Gebhardt, M. D., and Stearns, S. C. 1988. Reaction norms for development and weight at eclosion in *Drosophila mercatorum*. **J. Evol. Biol.** 1: 335-354.

Gehring, W. J., and Nothiger, R. 1973. The imaginal discs of *Drosophila*. *In* S. J. Counce and C. H. Waddington (eds.), *Developmental Systems: Insects. Vol. 2*, pp. 211-290, Academic Press, New York.

Gerling, D., Roitberg, B. D., and Mackauer, M. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae). **J. Insect Behaviour** 3: 501-514.

Giesel, J. T. 1986. Genetic correlation structure of life history variables in outbred wild *Drosophila melanogaster*: effects of photoperiod regimen. **Am. Nat.** 128: 593-603.

Giesel, J. T., and Zettler, E. E. 1980. Genetic correlations of life-historical parameters and certain fitness indices in *Drosophila melanogaster*: r_m, r_s, diet breadth. **Oecologia** 47: 299-302.

Giesel, J. T., Murphy, P. A., and Manlove, M. N. 1982a. The influence of temperature on genetic interrelationships of life history traits in a population of *Drosophila melanogaster*: what tangled data sets we weave. **Am. Nat.** 119: 464-479.

Giesel, J. T., Murphy, P. A., and Manlove, M. N. 1982b. An investigation of the effects of temperature on the genetic organization of life history indices in three populations of *Drosophila melanogaster*. *In* H. Dingle and J. P. Hegmann (eds.), *Evolution and genetics of life histories*, pp. 189-207, Springer-Verlag, New york.

Gilbert, J. J., and Williamson, C. E. 1983. Sexual dimorphism in Zooplankton (Copepoda: Cladocera and Rotifera). **Annu. Rev. Ecol. Syst.** 14: 1-33.

Gilbert, N. C., Gutierrez, A. P., Fraser, B. D., and Jones, R. E. 1976. Ecological Relationships. W. H. Freeman, San Francisco, CA.

Gilbert, N., and Gutierrez, A. P. 1973. A plant-aphid-parasite relationship. **J. Anim. Ecol.** 42: 323-340.

Gillespie, J. H., and Turelli, M. 1989. Genotype-environment interactions and the maintenance of polygenic variation. **Genetics** 121: 129-138.

Grant, B., Burton, S., Contoreggi, C., and Rothstein, M. 1980. Outbreeding via frequency-dependent mate selection in the parasitoid wasp, *Nasonia vitripennis* Walker. **Evolution** 34: 983-992.

Grodzinski, W. 1975. Energy flow through a vertebrate population. *In* W. Grodzinski, R. Z. Klekowski and A. Duncan (eds.), *Methods for ecological bioenergetics*, pp. 65-94, Blackwells, Oxford.

Gupta, A. P., and Lewontin, R. C. 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. **Evolution** 36: 934-948.

Hagen, K. S., and van den Bosch, R. 1968. Impact of pathogens, parasites, and predators on aphids. **Annu. Rev. Entomol.** 13: 325-384

Hamilton, T. H. 1961. The adaptive significance of intra-specific trends of variation in wing length and body size among bird species. **Evolution** 15: 180-195.

Hazel, W., Brandt, R., and Grantham, T. 1987. Genetic variability and phenotypic plasticity in pupal colour and its adaptive significance in the swallow tail butterfly *Papilio polyxenes*. **Heredity** 59: 449-455.

Henkelman, D. H. 1979. A study of weight variation in *Aphidius smithi* (Hymenoptera: Aphidiidae), a parasite of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). M. Sc. Thesis, Simon Fraser University, Burnaby, British Columbia.

Hopper, K. R. 1986. Preference, acceptance, and fitness components of *Microplitis croceipes* (Hymenoptera: Braconidae) attacking various instars of *Heliothis virescens* (Lepidoptera: Noctuidae). **Environ. Entomol.** 15: 274-280.

Howell, J., and Fisher, R. C. 1977. Food conversion efficiency of a parasitic wasp, *Nemeritis canescens*. **Ecol. Entomol.** 2: 143-151.

Hughes, A. L., and Hughes, M. K. 1986. Paternal investment and sexual size dimorphism in North American passerines. **Oikos** 46: 171-175.

Hume, L., and Cavers, P. B. 1982. Geographic variation in a widespread perennial weed *Rumex crispus*. The relative amounts of genetic and environmentally induced variation among populations. **Can. J. Bot.** 60: 1928-1937.

Hurlbutt, B. 1987. Sexual size dimorphism in parasitoid wasps. **Biol. J. Linn. Soc.** 30: 63-89.

Istock, C. A., Zisfein, J., and Zimmer, H. 1975. Ecology and evolution of the pitcher-plant mosquito. 2. The substructure of fitnes. **Evolution** 30: 535-547.

Johannsen, W. 1911. The genotype concept of heredity. **Am. Nat.** 45: 129-159.

Johnson, B. 1957. Studies on the degeneration of flight muscles of alate aphids. I. A comparative study of the occurrence of muscle breakdown in relation to reproduction in several species. **J. Insect Physiol.** 1: 248-266.

Johnson, B. 1959. Studies on the degeneration of the flight muscles of alate aphids. II. Histology and control of muscle breakdown. **J. Insect Physiol.** 3: 367-377.

Jones, R. L., and Lewis, W. J. 1971. Physiology of the host-parasite relationship between *Heliothis zea* and *Microplitis croceipes*. **J. Insect Physiol.** 17: 921-927.

Jowyk, E. K., and Z. Smilowitz. 1978. A comparison of growth and developmental rates of the parasite *Hyposoter exiguae* reared from two instars of its host, *Trichoplusia ni*. **Ann. ent. Soc. Am.** 71: 467-472.

Kafatos, F. C. 1981. Structure, organization and developmental expression of the chorion multigene families. **Am. Zool.** 21(3): 707-714.

Kambhampati, S. 1987. Inter- and intraspecific variation in introduced and native parasites (Hymenoptera: Aphidiidae) of the pea aphid in North America: life history traits, thermal coefficients and morphology. Ph. D. Thesis, Simon Fraser University, Burnaby, British Columbia.

Kerr, W. E. 1974. Advances in cytology and genetics of bees. **Annu. Rev. Entomol.** 19: 253-268.

Kindlmann, P., and Dixon, A. F. G. 1989. Developmental constraints in the evolution of reproductive strategies: telescoping of generations in parthenogenetic aphids. **Functional Ecol.** 3, 531-537.

King, B. H. 1987a. Sexual size dimorphism in parasitoid wasps. **Biol. J. Linn. Soc.** 30: 63-89.

King, B. H. 1987b. Offspring sex ratios in parasitoid wasps. **Q. Rev. Biol.** 62: 367-396.

Klekowski, R. Z., and Duncan A. 1975. Physiological approach to ecological energetics. *In* R. Grodzinski, Z. Klekowski and A. Duncan (eds.), *Methods for ecological bioenergetics*, pp. 15-64, Blackwells, Oxford.

Knapp, S. J., Bridges, W. C. Jr., and Yang, M. 1989. Nonparametric confidence interval estimators for heritability and expected selection response. **Genetics** 121: 891-898.

Kováč, L. 1987. Overview: Bioenergetics between chemistry, Genetics, and Physics. **Current Topics in Bioenergetics** 15: 332-372.

Lande, R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. **Genetics** 94: 203-215.

Law, R. 1979. The cost of reproduction in annual meadow grass. **Am. Nat.** 113: 3-16.

Lawrence, P. O. 1981. Interference competition and optimal host selection in the parasitic wasp, *Biosteres longicaudatus*. **Ann. Entomol. Soc. Am.** 74: 540-544.

Lawrence, P. O., Baranowski, R. M., and Greany, P. D. 1976. Effect of host age on development of *Biosteres longicaudatus*, a parasite of the Caribbean fruit fly, *Anastrepha suspensa*. **Florida Entomol.** 59: 33-39.

Lees, A. D. 1959. The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton. I. The influence of these factors on apterous virginoparae and their progeny. **J. Insect Physiol.** 3: 92-117.

Lenski, R. E., and Service, P. M. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. **Ecology** 63: 655-662.

Lerner, I. M. 1954. Genetic homeostasis. Oliver and Boyd, London.

Levins, R. 1963. Theory and fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. **Am. Nat.** 97: 75-90.

Lewis, W. J. 1970. Study of species and instars of larval *Heliothis* parasitized by *Microplitis croceipes* (Cresson). **J. econ. Entomol.** 63: 363-365.

Lewontin, R. C. 1965. Selection for colonizing ability. *In* H. G. Baker and G. L. Stebbins, (eds.), *The Genetics of Colonizing Species*, pp. 77-91, Academic Press, New York.

Lewontin, R. C. 1974. The analysis of variance and the analysis of causes. **Am. J. Hum. Genet.** 26: 400-411.

Liu, S. S. 1985. Development, adult size and fecundity of *Aphidius sonchi* reared in two instars of its aphid host, *Hyperomyzus lactucae*. **Entomol. exp. appl.** 37: 41-48.

Liu, S. S., Morton, R., and Hughes, R. D. 1984. Ovipositional preference of a hymenopterous parasite for certain instars of its aphid host. **Entomol. exp. appl.** 35: 217-220.

Livshits, G., and Kobyliansky, E. 1985. Lerner's concept of developmental homeostasis and the problem of heterozygosity level in natural populations. **Heredity** 55: 341-353.

Llewellyn, M. 1972. The effect of the lime aphid, *Eucellipterus tiliae* L. (Aphididae) on the growth of the lime *Tilia x vulgaris* Hyne. I. Energy requirements of the aphid population. **J. Appl. Ecol.** 9: 261-282.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. **Ecology** 58: 763-774.

Mackauer, M. 1973. Host selection and host suitability in *Aphidius smithi* (Hymenoptera: Aphidiidae). *In* A. D. Lowe (ed.), *Perspectives in Aphid Biology*, pp 20-29, Ent. Soc. N. Z. Bull. 2.

Mackauer, M. 1983. Quantitative assessment of *Aphidius smithi* (Hymenoptera: Aphidiidae): fecundity, intrinsic rate of increase, and functional response. **Can. Ent.** 115: 399-415.

Mackauer, M. 1986. Growth and developmental interactions in some aphids and their hymenopterous parasites. **J. Insect Physiol.** 32: 275-280.

Mackauer, M., and F. J. Chow. 1986. Parasites and parasite impact on aphid poulations. *In* G. D. McLean, R. G. Garret and W. G. Ruesink (eds.), *Plant Virus Epidemics*, pp. 95-118, Academic Press, Sydney.

Mackauer, M., and Finlayson, T. 1967. The hymenopterous parasites (Hymenoptera: Aphidiidae et Aphelinidae) of the pea aphid in Eastern North America. **Can. Entomol.** 99: 1051-1082.

Mackauer, M., and Kambhampati, S. 1984. Reproduction and longevity of cabbage aphid, *Brevicoryne brassicae* (Homoptera: Aphididae), parasitized by *Diaeretiella rapae* (Hymenoptera: Aphidiidae). **Can. Ent.** 116: 1605-1610.

Mackauer, M., and Kambhampati, S. 1988a. Parasitism of aphid embryos by *Aphidius smithi*: some effects of extremely small host size. **Entomol. exp. appl.** 49: 167-173.

Mackauer, M., and Kambhampati, S. 1988b. Sampling and rearing of aphid parasites. *In* A. K. Minks and P. Harrewijn (eds.), *Aphids, their biology, natural enemies and control, Volume B*, pp. 205-216, Elsevier, Amsterdam.

Marshall, D. R., and Jain, S. K. 1968. Phenotypic plasticity of *Avena fatua* and *A. barbata*. **Am. Nat.** 102: 457-467.

Mertins, J. W. 1985. Hyperparasitoids from pea aphid mummies, *Acyrthosiphon pisum* (Homoptera: Aphidiidae) in North America. **Ann. Entomol. Soc. Am.** 78: 186-197.

Messenger, P. S. 1964. Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. **Ecology** 45: 119-131.

Miles, L. R., and King, E. G. 1975. Development of the tachinid parasite, *Lixophaga diatraeae*, on various developmental stages of the sugar cane borer in the laboratory. **Environ. Entomol.** 4(5): 811-814.

Mitton, J. B., and Grant, M. C. 1984. Association among heterozygosity, growth rate and developmental homeostasis. **Ann. Rev. Ecol. Syst.** 15: 479-499.

Morrison, D. F. 1976. Multivariate statistical methods. 2nd edition. McGraw-Hill, New York.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. **Heredity** 59: 181-197.

Mukai, T., Cordellino, R. A., Watanabe, T. K., and Crow, J. F. 1974. The genetic variance for viability and its components in a local population of *Drosophila melanogaster*. **Genetics** 69: 385-398.

Murdie, G. 1969. The biological consequences of decreased size caused by crowding or rearing temperatures in apterae of the pea aphid, *Acyrthosiphon pisum* (Harris). **Trans. R. Ent. Soc. Lond.** 121: 443-455.

Murdoch, W. 1966. Population stability and life history phenomena. **Am. Nat.** 100: 1-11.

Murphy, P. A., Giesel, J. T., and Manlove, M. N. 1983. Temperature effects on life history variation in *Drosophila simulans*. **Evolution** 37: 1181-1192.

Narasimham, A. U. 1984. Comparative studies on *Tetrastichus hagenowii* (Ratzeburg) and *Tetrastichus* (Waterston), two primary parasites of cockroach ootheca, and on their hyperparasite *Tetrastichus* spp. [*T. miger* (Nees) group] (Hymenoptera: Eulophidae). **Bull. Entomol. Res.** 74: 175-189.

Nealis, V. G., Jones, R. E., and Wellington, W. G. 1984. Temperature and development in host-parasite relationships. **Oecologia** 61: 224-229.

Nechols, J. R. and Kikuchi, R. S. 1985. Host selection of the spherical mealybug (Homoptera: Pseudococcidae) by *Anagyrus indicus* (Hymenoptera: Encyrtidae): Influence of host stage on parasitoid oviposition, development, sex ratio, and survival. **Environ. Entomol.** 14: 32-37.

Nechols, J. R., and Tauber, M. J. 1977. Age-specific interaction between the green house whitefly and *Encarsia formosa*: Influence of host on the parasite's oviposition and development. **Environ. Entomol.** 6: 143-149.

Nevo, E. 1973. Adaptive variation in size of cricket frogs. **Ecology** 54: 1271-1281.

Newton, C., and Dixon, A. F. G. 1990. Pattern of growth in weight of alate and apterous nymphs of the English grain aphid, *Sitobion avenae* (Fab.). **Entomol. exp. appl.** 55: 231-238.

Nijhout, H. F. 1981. Physiological control of moulting in insects. **Amer. Zool.** 21: 631-640.

Ochieng'-Odero, J. P. R. 1990. Critical, pupal and adult weights in the size related metamorphosis of the black lyre leafroller *Cnephasia jactatana*. **Entomol. exp. appl.** 54: 21-27.

Opp, S. B., and Luck, R. F. 1986. Effects of host size on selected fitness components of *Aphytis melinus* and *A. lingnanensis* (Hymenoptera: Aphelinidae). **Ann. Entomol. Soc. Am.** 79: 700-704.

Owen, R. E. 1989. Differential size variation of male and female bumblebees. **J. Hered.** 80: 39-43.

Pianka, E. R. 1983. Evolutionary ecology. Third edition. Harper and Row, New York.

Polaszek, A. 1986. The effect of two species of hymenopterous parasite on the reproductive system of the pea aphid, *Acyrthosiphon pisum*. **Entomol. exp. appl.** 40: 285-292.

Polhemus, M. S., Bush, J. L., and Rothenbuhler, W. C. 1950. Mating systems in honey bees. **J. Hered.** 16: 151-155.

Pond, C. M. 1981. Storage. *In* C. R. Townsend and P. Calow (eds.), *Physiological ecology: an evolutionary approach to resource use*, pp. 190-219, Blackwells, Oxford.

Postlethwait, J. H., and Schneiderman, H. A. 1973. Developmental genetics of *Drosophila* imaginal discs. **Annu. Rev. Genet.** 7: 381-431.

Price, T., Kirkpatrick, M., and Arnold, S. J. 1988. Directional selection and the evolution of breeding date in birds. **Science** 240: 798-799.

Randolph, P. A., Randolph, J. C., and Barlow, C. A. 1975. Age-specific energetics of the pea aphid, *Acyrthosiphon pisum*. **Ecology** 56: 359-369.

Reznick, D. N., Perry, E., and Travis, J. 1986. Measuring the cost of reproduction: a comment on papers by Bell. **Evolution** 40: 1338-1344.

Ricklefs, R. E. 1979. Adaptation, constraint and compromise in avian postnatal development. **Biol. Rev.** 54: 269-290.

Rinderer, T. E. 1977. Measuring the heritability of characters of honeybees. **J. Apic. Res.** 16: 95-98.

Riska, B. 1986. Some models for development, growth and morphometric correlation. **Evolution** 40: 1303-1311.

Roberts, E. P., and Willis, J. H. 1980. The cuticular proteins of *Tenebrio molitor* II. Patterns of synThesis during postembryonic development. **Devel. Biol.** 75: 70-77.

Robertson, F. W., and Reeve, E. C. 1952. Heterozygosity, environmental variation and heterosis. **Nature** (Lond.) 17: 286-287.

Roff, D. A. 1981. On being the right size. **Am. Nat.** 118: 405-422.

Roff, D. A., and Mousseau, T. A. 1987. Quantitative genetics and fitness: Lessons from *Drosophila*. **Heredity** 58: 103-118.

Rose, M. R. 1982. Antagonistic pleiotropy, dominance, and genetic variation. **Heredity** 48: 63-78.

Rose, M. R. 1984. Genetic covariation in *Drosophila* life history: untangling the data. **Am. Nat.** 123: 565-569.

Rose, M. R., and Charlesworth, B. 1981a. Genetics of life-history in *Drosophila melanogaster*. I. Sib analysis of adult females. **Genetics** 97: 173-186.

Rose, M. R., and Charlesworth, B. 1981b. Genetics of life-history in *Drosophila melanogaster*. II. Exploratory selection experiments. **Genetics** 97: 187-196.

Rotheray, G. E., Barbosa, P., and Martinat, P. 1984. Host influences on life history traits and oviposition behaviour of *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae). **Environ. Entomol.** 13: 243-247.

Salt, G. 1938. Experimental studies in insect parasitism VI. Host suitability. **Bull. Ent. Res.** 29: 223-246.

Salt, G. 1940. Experimental studies in insect parasitism VII. The effects of different hosts on the parasite *Trichogramma evanescens* Westwood. **Proc. R. Ent. Soc. Lond.** Ser. A. 15: 81-95.

Salt, G. 1968. The resistance of insect parasites to the defense reactions of their hosts. **Biol. Rev.** 15: 96-119.

Sandlan, K. 1979. Sex ratio regulation in *Coccygomimus turionella* Linnaeus (Hymenoptera: Ichneumonidae) and its ecological implications. **Ecol. Entomol.** 4: 365-378.

SAS. 1985. SAS users guide: statistics. SAS Institute, Cary, North Carolina, USA.

Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. **Ecology** 55: 291-303.

Scheiner, S. M., and Goodnight, C. J. 1984. The comparison of phenotypic plasticity and genetic variation in populations of the grass *Danthonia spicata*. **Evolution** 38: 845-855.

Scheiner, S. M., Caplan, R. A., and Lyman, R. F. 1989. A search for trade-offs among life history traits in *Drosophila melanogaster*. **Evol. Ecol.** 3: 51-63.

Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. **Annu. Rev. Ecol. Syst.** 17: 667-693.

Schmalhausen, I. I. 1949. Factors of Evolution. McGraw-Hill, New York.

Scriber, J. M., and Slansky, F., Jr. 1981. The nutritional ecology of immature insects. **Annu. Rev. Ent.** 26: 183-211.

Sequeira, R., and Mackauer, M. 1987. Host instar preference of the aphid parasite *Praon pequodorum* (Hymenoptera: Aphidiidae). **Entomol. Gen.** 12: 259-265.

Sequeira, R., and Mackauer, M. 1988. Effects of parasitism by *Praon pequodorum* on age-specific fecundity and population growth of the pea aphid, *Acyrthosiphon pisum*. **Entomol. exp. appl.** 48: 179-185.

Sheridan, W. F. 1988. Maize developmental genetics: genes of morphogenesis. **Annu. Rev. Genet.** 22: 353-385.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. **Am. Nat.** 131: 124-131.

Sibly, R. M., and Calow, P. 1986. Physiological ecology of animals: an evolutionary approach. Blackwells, Oxford.

Sibly, R., Calow, P., and Nichols, N. 1985. Are patterns of growth adaptive? **J. theor. Biol.** 112: 553-574.

Slansky, F., Jr. 1981. Insect nutrition: an adaptationist's perspective. **Florida Entomol.** 65: 45-71.

Slansky, F., Jr. 1986. Nutritional ecology of endoparasitic insects and their hosts: an overview. **J. Insect Physiol.** 32: 255-261.

Smilowitz, Z., and Iwantsch, G. F. 1973. Relationships between the parasitoid *Hyposoter exiguae* and the cabbage looper, *Trichoplusia ni*: Effects of host age on developmental rate of the parasitoid. **Environ. Entomol.** 2: 759-763.

Snell, J. W., and King, C. E. 1977. Lifespan and fecundity patterns in rotifers; the cost of reproduction. **Evolution** 31: 882-890.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, San Francisco.

Soldan, T., and Starý, P. 1981. Parasitogenic effects of *Aphidius smithi* (Hymenoptera, Aphidiidae) on the reproductive organs of the pea aphid *Acyrthosiphon pisum* (Homoptera; Aphididae). **Acta ent. Bohem.** 78: 243-253.

Southwood, T. R. E. 1966. Ecological methods with particular reference to the study of insect populations. Methuen, London, UK.

$SPSS_X$ 1983. $SPSS_X$ Users Guide. McGraw-Hill, SPSS Inc., Chicago, IL.

Starý, P. 1970. Biology of aphid parasites with respect to integrated control. Dr. W. Junk, The Hague.

Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. **Annu. Rev. Ecol. Syst.** 8: 145-171.

Stearns, S. C. 1980. A new view of life history evolution. **Oikos** 35: 266-281.

Stearns, S. C. 1982. The role of development in the evolution of life histories. *In* J. T. Bonner (ed.), *Evolution and Development*, pp. 237-258, Springer-Verlag, Berlin.

Stearns, S. C. 1983a. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. **Amer. Zool.** 23: 65-75.

Stearns, S. C. 1983b. The influence of size and phylogeny on patterns of covariation among life history traits in the mammals. **Oikos** 41: 173-187.

Stearns, S. C. 1984. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. **Am. Nat.** 123: 56-72.

Stearns, S. C., and Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. **Evolution** 40: 893-913.

Sternberg, P. W. 1990. Genetic control of cell type and pattern formation in *Caenorhabditis elegans*. **Adv. Genet.** 27: 63-116.

Strand, M. R. 1986. The physiological interactions of parasites with their hosts and their influence on reproductive strategies. *In* J. Waage and D. Greathead (eds.), *Insect parasitoids*, pp. 97-136, Academic Press, London.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *In* M. K. Hecht, B. Wallace and G. T. Prance (eds.), *Evolutionary Biology, Vol. 21*, pp. 127-178, Plenum Press.

Sutherland, W. J., Graffen, A., and Harvey, P. H. 1986. Life history correlations and demography. **Nature** (Lond.) 320: 88.

Sweeney, B. W., and Vannote, R. L. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. **Science** 200: 444-446.

Takagi, M. 1985. The reproductive strategy of the gregarious parasitoid, *Pteromalus puparum* (Hymenoptera: Pteromalidae). I. Optimal number of eggs in a single host. **Oecologia** 68: 1-6.

Takagi, M. 1986. The reproductive strategy of the gregarious parasitoid, *Pteromalus puparum* (Hymenoptera: Pteromalidae). II. Host size discrimination and regulation of the number and sex ratio of progeny in a single host. **Oecologia** 70: 321-325.

Tepedino, V. J., Thompson, R., and Torchio, P. F. 1984. Heritability for size in the megachilid bee *Osmia lignaria propingna* Cresson. **Apidologie** 15: 83-88.

Thoday, J. M. 1953. Components of fitness. **Symp. Soc. Exptl. Biol.** 7: 96-113.

Thompson, S. N. 1982. Effects of parasitization by the insect parasite *Hyposoter exiguae* on the growth, development and physiology of its host *Trichoplusia ni*. **Parasitology** 84, 491-510.

Thompson, S. N. 1983a. Biochemical and physiological effects of metazoan endoparasites on their host species. **Comp. Biochem. Physiol.** 74 B 2: 183-211.

Thompson, S. N. 1983b. The nutritional physiology of *Trichoplusia ni* parasitized by the insect parasite, *Hyposoter exiguae*, and the effects of parallel feeding. **Parasitology** 87: 15-28.

Thompson, S. N. 1986. The metabolism of insect parasites (parasitoids): an overview. **J. Insect Physiol.** 32: 421-423.

Tinkle, D. F. 1969. The concept of reproductive effort and its relation to the evolution of life histories in lizards. **Am. Nat.** 103: 427-434.

Travis, J., Emerson, S. B., and Blouin, M. 1987. A quantitative-genetic analysis of larval life-history traits in *Hyla crucifer*. **Evolution** 41: 145-156.

Tsitsipis, J. A., and Mittler, T. E. 1976. Embryogenesis in parthenogenetic and sexual females of *Aphis fabae*. **Entomol. exp. appl.** 19: 263-270.

Uichanco, L. B. 1924. Studies on the embryogeny and postnatal development of the aphididae with special reference to the history of the "Symbiotic organ", or "Mycetom." **Philippine J. Science** 24: 143-247.

van Alphen, J. J. M., and Vet, L. E. M. 1986. An evolutionary approach to host finding and selection. *In* J. Waage and D. Greathead (eds.), *Insect parasitoids*, pp. 23-61, Academic Press, London.

van Bergeijk, K. E., Bigler, F., Kaashoek, N. K., and Pak, G. A. 1989. Changes in host acceptance and host suitability as an effect of rearing *Trichogramma maidis* on a factitious host. **Entomol. exp. appl.** 52, 229-238.

van den Assem, J. 1971. Some experiments on sex ratio and sex regulation in the Pteromalid *Lariophagus distinguendus*. **Neth. J. Zool.** 21: 373–402.

van den Assem, J. 1976. Male courtship behaviour, female receptivity signal and size differences between the sexes in Pteromalinae (Hym., Chalcidoidea Pteromalidae), and comparative notes on other Chalcidoids. **Neth. J. Zool.** 26: 535–548.

van den Bosch, R., Lagace, C. F., and Stern, V. M. 1967. The interrelationship of the aphid, *Acyrthosiphon pisum*, and its parasite, *Aphidius smithi*, in a stable environment. **Ecology** 48: 993–1000.

van den Bosch, R., Schlinger, E. I., Lagace, C. F., and Hall, J. 1966. Parasitization of *Acyrthosiphon pisum* by *Aphidius smithi* a density dependent process in nature (Homoptera: Aphididae) (Hymenoptera: Aphidiidae). **Ecology** 47: 1049–1055.

van Noordwijk, A. J., van Balen, J. H., and Scharloo, W. 1988. Heritability of body size in a natural population of the Great Tit (*Parsus major*) and its relation to age and environmental conditions during growth. **Genet. Res.** 51: 149–162.

Veuille, M. 1980. Sexual behaviour and evolution of sexual dimorphism in body size in *Jaera* (Isopoda: Asellota). **Biol. J. Linn. Soc.** 13: 89–100.

Via, S. 1984. The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interactions in larval performance on different host plant species. **Evolution** 38: 881–895.

Vinson, S. B. 1972. Effect of the parasitoid *Campoletis sonorensis* on the growth of its host, *Heliothis virescens*. **J. Insect Physiol.** 18: 1509–1514.

Vinson, S. B., and Iwantsch, G. F. 1980. Host regulation by insect parasitoids. **Q. Rev. Biol.** 55: 145–165.

Waage, J. K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. *In* J. k. Waage and D. Greathead (eds.), *Insect parasitoids*, pp. 63–95, Academic Press, London.

Waage, J. K., and Ng, S. M. 1984. The reproductive strategy of a parasitic wasp I. Optimal progeny and sex allocation in *Trichogramma evanescens*. **J. Anim. Ecol.** 53: 401–416.

Waddington, C. H. 1957. The strategy of the Genes. George Allen and Unwin, London.

Waldbauer, G. P. 1968. The consumption and utilization of food by insects. **Adv. Insect Physiol.** 5: 229–288.

Werren, J. H. 1984. A model for sex-ratio selection in parasitic wasps: local mate competition and host quality effects. **Neth. J. Zool.** 34: 81-96.

Werren, J. H., and Simbolotti, G. 1989. Combined effects of host quality and local mate competition on sex allocation in *Lariophagus distinguendus*. **Evol. Ecol.** 3: 203-213.

White, M. J. D. 1973. Animal Cytology and Evolution. Third Edition, Cambridge University Press, U. K.

Willis, J. H. 1974. Morphogenetic action of insect hormones. **Annu. Rev. Entomol.** 19: 97-111.

Willis, J. H. 1986. The paradigm of stage-specific gene sets in insect metamorphosis: time for revision! **Arch. Insect Biochem. Physiol.** 9: 47-57.

Wright, S. 1931. Evolution in mendelian populations. **Genetics** 16: 97-159.

Wright, S. 1968. Evolution and the genetics of populations, Vol. I: genetic and biometric foundations. The University of Chicago Press, Chicago, IL.

Wylie, H. G. 1966. Some effects of female parasite size on reproduction of *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae). **Can. Ent.** 98: 196-198.

Yund, M. A., and Germeraad, S. 1980. *Drosophila* development. *In* T. P. Leighton and W. F. Loomis, Jr., (eds.), *The molecular genetics of development*, pp. 237-360, Academic Press, New York.