

Covariance of adult size and development time in the parasitoid wasp *Aphidius ervi* in relation to the size of its host, *Acyrthosiphon pisum*

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Summary

Adult size (in terms of dry weight; DW) and development time (T_p) of the solitary parasitoid *Aphidius ervi* varied when reared in different nymphal instars of its host, apterous virginoparae of the pea aphid (*Acyrthosiphon pisum*). Parasitoid DW increased with an increase in the DW of the host at parasitization, from the first to the third aphid instar. Female wasps gained 1.1 times more in DW than their male counterparts in all four host classes, but T_p did not significantly differ between the sexes. Parasitoid DW was consistently more variable than T_p . The two traits covaried positively with an increase in host size from the first to the third instar, but they varied independently in parasitoids from fourth-instar hosts. The host size (and stage) at the time of parasitization imposes constraints on the growth and development of immature *A. ervi* that are reflected in the pattern of covariation between DW and T_p . When growing in aphids below a certain size threshold, parasitoids can maximize fitness by a trade-off between DW and T_p . Consequently, the assumption implicit in host-size models of parasitoid oviposition decisions – that females incur a relatively greater reduction in size (used as an index of fecundity) than males when developing in poor quality hosts – can be falsified.

Keywords: *Aphidius ervi*; adult size; development time; host size; covariation; life-history strategy; parasitoid; pea aphid

Introduction

Adult size at maturity and development time are key determinants of a species' life history and population growth. In many insect parasitoids, adult size is positively correlated with fecundity (Lawrence, 1981; Waage and Ng, 1984; Liu, 1985; Takagi, 1985; Opp and Luck, 1986; Mackauer and Kambhampati, 1988). As the effects of size on lifetime reproductive success differ from those of development time, the benefits of increased size (e.g. in terms of decreased adult mortality through predation) may be offset by a corresponding increase in development time (Lewontin, 1965; Roff, 1981).

In organisms growing at a constant rate, an increase in body size can be achieved only at the cost of increased development time. Alternatively, an increase in size with a concomitant decrease in development time will depend on an increase in the growth rate (Sibly *et al.*, 1985; Stearns and Koella, 1986). Because growth rates can vary only within the limits imposed by developmental and genetical constraints (Stearns, 1980), variability in phenotypic traits is ultimately the result of resource partitioning between competing functions, such as rates of

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cellular growth and differentiation, fecundity and survivorship (Murdoch, 1966; Boggs, 1981).

Developmental patterns and genetic connections between traits can result in correlated responses or trade-offs in different environments (Murphy *et al.*, 1983; Bell, 1984a,b). Consequently, patterns of covariation between fitness-related traits may be indicative of the life-history strategy adopted by different species.

Here we examine patterns of phenotypic variation in *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae), a solitary endoparasitoid of the pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae). We describe variation in adult size (as measured by dry weight) and development time of the parasitoid in relation to host size, an index of resource availability. We show that parasitoids utilize resources first to maximize size and then to minimize development time. Parasitoid size and development time are positively correlated only when both traits are limited by the size and growth potential of the host. The observed pattern of covariation between adult size and development time suggests that, in *A. ervi*, these traits are functionally independent and result from sequentially expressed (genetic) developmental programs. We discuss our findings with regard to parasitoid life-history strategies and host choice and show that some of the assumptions underlying host-size models can be falsified.

Materials and methods

All experiments were conducted with laboratory colonies of *A. ervi* in controlled environment chambers at $20 \pm 0.2^\circ\text{C}$, 65% r.h., and continuous light. We reared apterous virginoparae of the pea aphid on broad-bean plants, *Vicia faba* L. cv. 'Broad Windsor', potted in garden-mix soil. To obtain hosts of the same age and size, we caged adult aphids ($n = 100$) on about 30 young bean plants for 4-h periods. All offspring produced were reared as a cohort until they reached the

Table 1. Age (± 2 h) and mean ($\pm s$) dry weight (in μg) of pea aphid hosts at time of parasitization by *Aphidius ervi* and numbers and F_1 sex ratio of eclosed wasps in each instar class.

Replicate	Host instar			
	L ₁	L ₂	L ₃	L ₄
<i>Replicate 1</i>				
Host age	22	46	70	118
Host DW	39 \pm 6	64 \pm 9	93 \pm 7	284 \pm 47
<i>Replicate 2</i>				
Host age	24	48	72	120
Host DW	42 \pm 4	68 \pm 8	104 \pm 9	247 \pm 19
<i>Replicate 3</i>				
Host age	26	50	74	122
Host DW	44 \pm 5	75 \pm 6	111 \pm 9	262 \pm 45
<i>Wasps</i>				
Total n	278	259	244	255
F_1 sex ratio*	0.17	0.21	0.14	0.44

* The sex ratio is given as the proportion of females among all F_1 offspring.

desired age. In this manner, we produced four classes of experimental aphids aged 22, 46, 70, and 118 (± 2) h, corresponding to the four nymphal instars (L_1 – L_4).

From each instar cohort, we selected 120 aphids and divided these into four groups of 30 individuals each. Aphids were placed singly into a gelatin capsule (size OO) which contained a 2–3-day-old female of *A. ervi*. All wasps were mated and had been caged with aphids for 2 h prior to the experiment so that they would gain experience in handling hosts. To avoid superparasitism, we permitted wasps to strike a host only once with the ovipositor. We used three different wasps to parasitize each group of 30 aphids, a procedure that could be completed in about 15 min. We estimated the host dry weight (DW) at the time of parasitization by selecting 20 experimental aphids at the mid-point of the parasitization interval; the aphids were killed with carbon dioxide, oven-dried for 3 days, and then individually weighed on a Mettler UM3 electronic microbalance. The entire experimental procedure was replicated three times for each aphid instar (Table 1).

Parasitized aphids were transferred, in groups of 30 each, to bean plants in screened plastic cages (15.5 cm in diameter \times 4 cm high); the plants were standing in bottles with tap water. All cages were kept in a controlled environment chamber at $20 \pm 0.2^\circ\text{C}$, 65% r.h., and continuous light. On day 12 after parasitization, mummified aphids (i.e. dead aphids that contained a parasitoid pupa) were removed from the plants and placed singly in gelatin capsules (size OO). We arranged the capsules in rows, identified by host instar and replicate number, and attached them with scotch tape to white cardboard; the capsules in the environment chamber were then placed under a video camera and monitored continuously. Using this procedure, we were able to determine the exact times when wasps had eclosed from the mummy and hence to estimate the individual development times from oviposition to adult eclosion (T_p).

Eclosed wasps were left in the capsules to die. They were then oven-dried for 3 days and weighed to determine their DWs, as above.

We compared the data on parasitoid DW and T_p by nested ANOVA, treating all classification factors as fixed effects. Sample sex ratios, calculated as the proportion of females among all offspring produced, were transformed to their arcsine values prior to analysis. To examine the statistical relationship between DW and T_p , we used multivariate discriminant analysis, including host instar at the time of parasitization, replicate number, mummy length, parasitoid DW and T_p as variables. For all analyses, we used the SPSS_x library of statistical programs (SPSS_x, 1983). Confidence ellipses (95%) for bivariate scatterplots and discriminant function scores were computed according to the method of Cornuet (1982).

Results

Aphid DW at the time of parasitization increased within instars and with replication number because aphids continued to grow during the 4-h period needed to complete each trial (Table 1). Successful parasitism was very high in all host classes, with adult wasps eclosing from 97.6% of the total of 1061 aphids that became mummified. Parasitoids required about 8–8.5 days to complete larval development and an additional 5–6 days to eclose as adults (see below). Aphids parasitized in the L_1 stage died in the fourth-instar stage, whereas those parasitized in the L_3 and L_4 stages died as adults. In comparison, among the hosts parasitized in the L_2 stage, 45% died in the fourth-instar stage and the remainder (55%) as adults. We assigned adult parasitoids, separately by sex, to one of five classification groups based on the host stage at the time of parasitization and at the time of death (instar 4 or adult), as follows: L_1 , L_2 (iv), L_2 (a), L_3 , and L_4 (Table 2).

Parasitoid DW differed significantly between groups ($F = 442.93$; $df = 4, 1006$; $p < 0.001$), replicates within groups ($F = 2.12$; $df = 10, 1006$; $p = 0.021$), and sexes within replicates

Table 2. Mean ($\pm s$) of development time (in h) and dry weight (in μg) of *Aphidius ervi* males and females reared in the four nymphal instars (L₁ to L₄) of pea aphid at $20 \pm 0.2^\circ\text{C}$, 65% r.h., and continuous light.

Host instar; replicate no.	<i>n</i>	Development time		Dry weight		
		Mean $\pm s$	C.V.	Mean $\pm s$	C.V.	
<i>Males</i>						
L ₁ ;	1	76	319.1 \pm 8.2	2.57	155 \pm 11	7.10
	2	72	316.2 \pm 7.8	2.47	155 \pm 10	6.45
	3	84	321.1 \pm 11.6	3.61	158 \pm 13	8.23
L ₂ (iv);	1	44	316.4 \pm 7.6	2.40	164 \pm 15	9.15
	2	37	315.6 \pm 10.9	3.45	159 \pm 14	8.81
	3	6	331.3 \pm 14.5	4.38	158 \pm 11	6.96
L ₂ (a);	1	26	327.0 \pm 10.4	3.18	194 \pm 15	7.73
	2	27	325.1 \pm 12.9	3.97	207 \pm 20	9.66
	3	65	328.9 \pm 10.0	3.04	202 \pm 20	9.90
L ₃ ;	1	70	333.9 \pm 8.3	2.49	220 \pm 23	10.95
	2	56	339.4 \pm 12.6	3.71	221 \pm 23	10.41
	3	85	333.3 \pm 11.1	3.33	218 \pm 22	10.09
L ₄ ;	1	49	311.1 \pm 8.5	2.76	234 \pm 25	10.68
	2	48	312.5 \pm 12.2	3.90	219 \pm 19	8.68
	3	45	316.2 \pm 10.9	3.45	217 \pm 19	8.76
<i>Females</i>						
L ₁ ;	1	11	323.9 \pm 6.9	2.13	166 \pm 10	6.02
	2	25	319.5 \pm 7.5	2.35	174 \pm 10	5.75
	3	10	326.0 \pm 8.5	2.61	173 \pm 13	7.51
L ₂ (iv);	1	14	323.7 \pm 8.0	2.47	180 \pm 13	7.22
	2	12	318.5 \pm 9.8	3.08	186 \pm 16	8.60
	3	4	327.9 \pm 4.6	1.40	176 \pm 7	3.98
L ₂ (a);	1	6	328.4 \pm 8.4	2.56	215 \pm 10	4.65
	2	9	326.0 \pm 12.6	3.87	219 \pm 12	5.48
	3	9	335.1 \pm 8.2	2.45	213 \pm 13	6.10
L ₃ ;	1	15	337.2 \pm 7.4	2.19	236 \pm 15	6.36
	2	12	335.4 \pm 9.5	2.83	231 \pm 21	9.09
	3	6	333.1 \pm 10.0	3.00	238 \pm 11	4.62
L ₄ ;	1	43	312.6 \pm 4.6	1.47	247 \pm 17	7.29
	2	34	315.2 \pm 6.5	2.06	246 \pm 13	5.28
	3	36	320.2 \pm 10.3	3.22	244 \pm 23	9.43

($F = 13.50$; $df = 15, 1006$; $p < 0.001$). In comparison, mean development times, T_p , differed significantly between groups ($F = 90.71$; $df = 4, 1006$; $p < 0.001$) and replicates within groups ($F = 4.96$; $df = 10, 1006$; $p < 0.001$) but not between the sexes ($F = 1.68$; $df = 15, 1006$; $p > 0.05$). Aphids parasitized as L₄ produced a significantly higher proportion of F₁ female parasitoids than those parasitized in any of the younger instars (1-way ANOVA, $F = 10.59$; $df = 4, 14$; $p = 0.001$; followed by Student–Newman–Keuls test, $p < 0.05$) (Table 1).

DW and T_p of individual parasitoids increased as host size at parasitization increased from L₁ to L₃ (Fig. 1A). However, parasitoids developing in L₄ hosts did not increase further in size (1-way ANOVA, $F = 2.64$; $df = 1, 351$; $p = 0.105$), but they did develop significantly faster

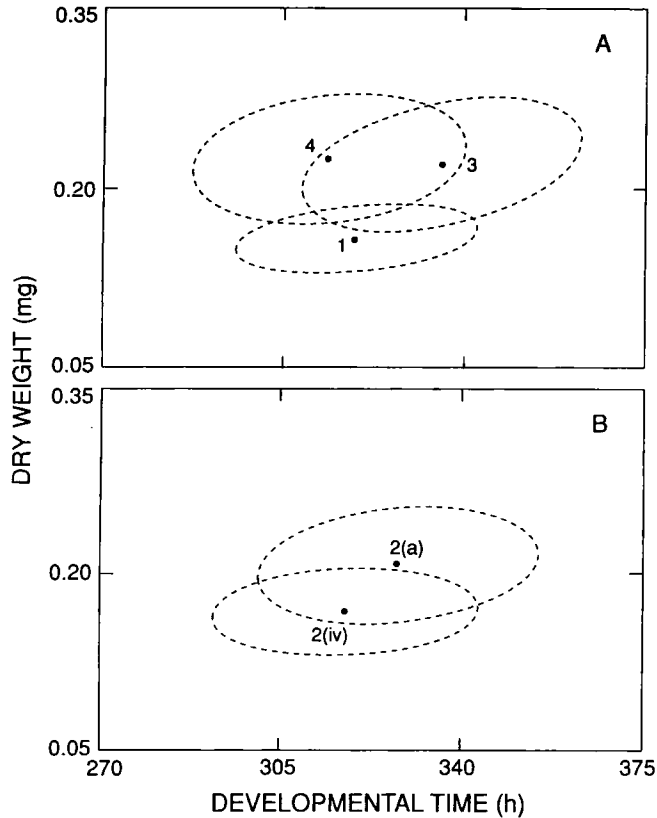


Figure 1. Pattern of covariation between dry weight (DW) and development time in *Aphidius ervi* males reared in different nymphal instars of the pea aphid. (A) Hosts that were parasitized in the first instar (1) produced parasitoids with lower DW than their counterparts from hosts parasitized in the third (3) and fourth instars (4). (B) Hosts parasitized in the second instar produced small males if the host died in the fourth-instar stage (2_{iv}) and large males if the host died as an adult (2_a). For each group, the centroid of a 95% confidence ellipse is indicated by a dot (●).

($F = 28.61$; $df = 1, 351$; $p < 0.001$) than their counterparts in L_3 hosts. Parasitoids from L_2 aphids fell into two distinct clusters, with those emerging from 'fourth-instar' and 'adult' mummies sharing the characteristics of, respectively, parasitoids from L_1 and L_3 hosts (Fig. 1B). Female wasps were generally larger than males, but total development times did not differ significantly between the sexes, regardless of variations in host size at the time of parasitization (Table 2; Fig. 2A, B).

Parasitoid DW was consistently more variable than T_p , with females showing less relative variability than males in general (Spearman rank-correlation test, one-tailed hypothesis, $n = 15$, for DW: $r_s = 0.764$; $p < 0.001$; for T_p : $r_s = 0.970$; $p < 0.001$) (Table 2). However, coefficients of variation in parasitoid DW and T_p did not increase with an increase in the mean host DW at the time of parasitization, with the possible exception of male DW (Spearman's $r_s = 0.618$; $n = 15$; $p < 0.01$).

Multiple discriminant analysis showed that *A. ervi* males from L_1 hosts were tightly clustered and separated along discriminant function 1 from their counterparts that had developed in L_3 and

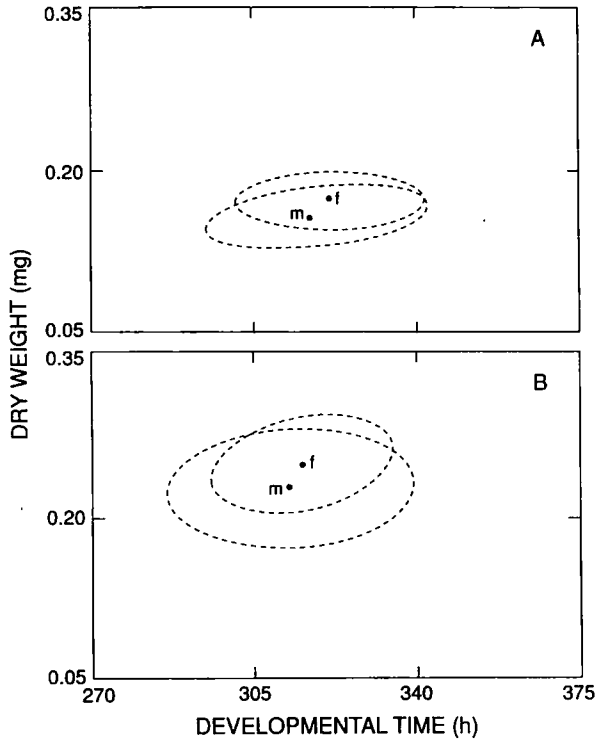


Figure 2. Pattern of covariation between dry weight (DW) and development time in *Aphidius ervi* males (m) and females (f) reared in pea aphids that were parasitized in the first (A) and fourth (B) nymphal instar. For each group, the centroid of a 95% confidence ellipse is indicated by a dot (●).

L_4 hosts (Fig. 3A). Similarly, *A. ervi* males from L_2 hosts were separated along DF 1 into two clusters, one including individuals that had eclosed from ‘instar iv’ and the other from ‘adult’ mummies (Fig. 3B). Differences in mummy size and DW (which are positively correlated; Henkelman, 1979; Liu, 1985) contributed most to the separation by DF 1 (eigenvalue = 3.373; canonical correlation = 0.878; $\chi^2 = 1524.9$; $p < 0.001$) of parasitoids from L_1 and L_2 (iv) hosts

Table 3. Standardized coefficients of canonical discriminant functions (DF) 1 and 2 for the classification of *Aphidius ervi* males reared in different nymphal instars of the pea aphid. Classification based on four variables: replicate number, mummy length, adult dry weight (DW), and total development time (T_p).

Variable	DF 1	DF 2
Replicate number	-0.191	-0.101
Mummy length	0.800	0.156
Adult dry weight	-0.192	1.052
Development time	0.417	-0.381
% of variance	85.47	13.47

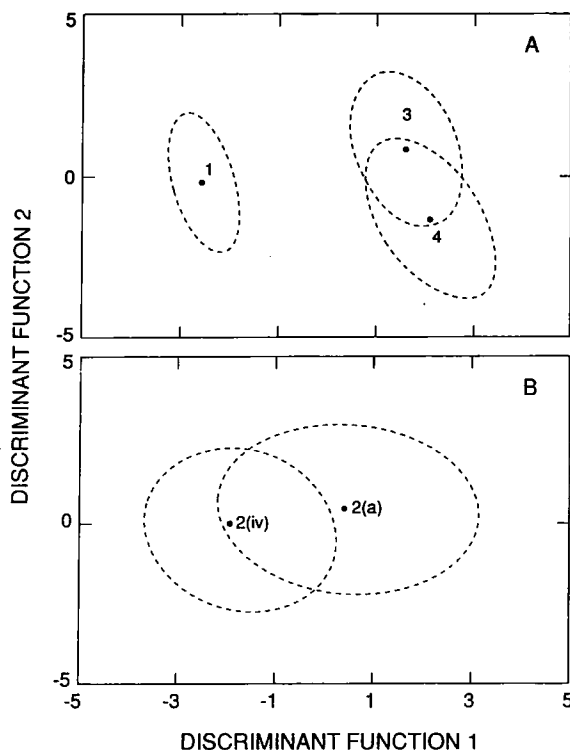


Figure 3. Classification of *Aphidius ervi* males by multiple discriminant analysis; the analysis included host instar at time of parasitization, replicate number, mummy size, parasitoid dry weight, and development time as variables. (A) Parasitoids reared on L₁ hosts (1) were separated along discriminant function 1 from parasitoids reared on L₃ (3) and L₄ (4) hosts. (B) Parasitoids reared on L₂ hosts formed two clusters in accordance with the time of host death in the fourth-instar (2_{iv}) or adult stage (2_a). For each group, the centroid of a 95% confidence ellipse is indicated by a dot (●).

from the remaining groups, whereas DF 2 (eigenvalue = 0.531; canonical correlation = 0.589; $\chi^2 = 366.7$; $p < 0.001$) separated parasitoids from L₂ (a) and L₃ from those from L₄ hosts, mainly based on differences in T_p (Table 3). (The results for *A. ervi* females were similar to those for males and are not shown.)

Female DWs were 1.10-times higher on average than those of males (1-way ANOVA, $F = 115.3$; $df = 1, 1034$; $p < 0.001$), representing the upper tail of a unimodal frequency distribution, with about 25% overlap between male and female DWs. It is worth noting that the ratio of female:male DWs varied little across host instars. Although males were generally the first to eclose in all host classes, the difference between the means of male and female T_p was not statistically significant (1-way ANOVA, $F = 2.73$; $df = 1, 1034$; $p = 0.10$).

Discussion

Most models of parasitoid host choice and progeny allocation assume that, in solitary species, parasitoid adult size is determined by host size, used as an index of host quality (e.g. Charnov, 1979; Charnov *et al.*, 1981; Werren, 1984; Waage, 1986; King, 1989; Werren and Simbolotti, 1989). When host size varies, wasps are expected selectively to place fertilized eggs (= daughters)

in large 'high quality' hosts and unfertilized eggs (= sons) in small 'low quality' hosts. Although parasitoid size is an increasing function of host size in many host-parasitoid systems (Hurlbutt, 1987), our study has shown that, in *A. ervi*, this function is not linear throughout the range of available host sizes.

In *A. ervi*, adult DW at eclosion is proportional to the maximum DW of the final-instar larva at the time of host death (Sequeira and Mackauer, 1991). Wasps developing in aphids that died during the fourth instar were considerably smaller than their counterparts from aphids that had died as adults (Table 2). Although L₄ hosts contained, at the time of parasitization, up to four-times more DW mass than L₃ hosts (Table 1), this difference was not reflected in increased parasitoid DW, a fact suggesting that the adult size of *A. ervi* approached an upper limit in L₃ hosts. Physical constraints imposed by the determinate growth pattern of aphids or genetical constraints on parasitoid size, or both, may be involved.

Developing in the same host classes, *A. ervi* females achieved a consistently higher DW than males (Table 2), evidence that females had a higher growth rate under identical conditions. The ratio of 1.10 between female:male DW was remarkably constant across all host instars; this suggests a sex-specific difference in the growth rate of immature *A. ervi*. It is worth noting that male DW was more variable than female DW, independent of host size at the beginning of parasitism (Table 2). Female DW is expected to have lower variability if developmental homeostasis is greater in the diploid females than in the hemizygous males (White, 1973; Owen, 1989).

Parasitoids required less time to complete development in L₁ than in L₃ hosts (Table 2), possibly because of constraints that aphid growth and gonadal development (Brough *et al.*, 1990) impose on parasitoid resource acquisition. Parasitoids developing in L₃ hosts showed a depressed growth trajectory, characterized by a delay in the exponential growth phase and a concomitant increase in T_p (Sequeira and Mackauer, 1991). By comparison, *A. ervi* developing in L₄ hosts required less time from oviposition to eclosion than their counterparts in L₃ hosts, evidence that parasitoids utilized the additional L₄ resources to reduce T_p rather than to increase DW (Fig. 1a).

A fundamental assumption of all host-size models is that male and female reproductive success is differentially affected by low host quality, with male fitness declining relatively less than female fitness (Charnov *et al.*, 1981; Charnov, 1982; Werren, 1984; King, 1988). Consequently, males from small hosts are expected to eclose at the same time as females from relatively larger hosts. As our data on *A. ervi* show, this assumption may not be valid in general. Host size variation affected T_p similarly in both sexes, although some *A. ervi* males eclosed earlier than females in all host classes. Because development times often are estimated from eclosion samples taken once a day rather than continuously, as in our study, some estimates may lack the precision necessary for the evaluation of correlated responses and hence should be interpreted with caution.

The coefficient of variation for T_p was greater in males than in females and less than half that for DW (Table 2). In a similar study on *Aphidius smithi*, Mackauer (1986) also found DW to be about twice as variable as development time. He suggested that differences in the coefficient of variation between these two traits reflect the differential influence of DW and T_p on fitness, with the time-to-first-offspring being relatively more important than total fecundity, i.e. size (Lewontin, 1965).

Parasitoid species are thought to respond to host-related constraints on their growth and development mainly by regulating host physiology and development (Vinson and Iwantsch, 1980; Lawrence, 1986; Stoltz, 1986; Strand, 1986). Although parasitism by *A. smithi* is known to affect aphid feeding and nutrition (Cloutier and Mackauer, 1979; Cloutier, 1986), there is no evidence that *A. ervi* in any way 'regulates' pea aphid growth to its own benefit. Any changes in the growth (Sequeira and Mackauer, 1991) and physiology (Cloutier and Mackauer, 1979; Mackauer and Kambhampati, 1984) of parasitized aphids could be due to homeostatic responses. The

observed pattern of covariation (Figs 1 and 2) can be interpreted as the result of developmental responses of the immature parasitoid to host-related constraints. Host resources are being allocated by *A. ervi* first to maximize adult size, which is correlated with maximum larval weight, and then to minimize development time (Sequeira and Mackauer, 1991). If this is correct, it would imply that the nutritional ecology of the immature parasitoids is controlled by different genetic subprograms during different stages of development (for related information, see Nijhout, 1981; Sternberg, 1990).

Roff's (1981) study on the evolution of body size in *Drosophila melanogaster* showed that the fitness consequences of delayed development could be traded off against increased size (i.e. fecundity), with the result that different combinations of size and development time will be optimal in different environments. Although several assumptions underlying Roff's (1981) model do not hold for species of parasitoids, the model provides important insights into the potential for trade-offs between the fitness consequences of different life-history parameters. In *A. ervi*, trade-offs between adult size and development time may be important only for parasitoids developing in a limited range of host sizes, specifically L₁ to L₃ hosts. In contrast, L₄ hosts contain sufficient resources for parasitoids to achieve both a large size and a short development time. Consequently, two life-history tactics are conceivable in *A. ervi* depending on host choice. For wasps developing in aphids that are below a certain age/size threshold at the time of parasitization, the optimal combination of life-history traits is determined by trade-offs. However, for parasitoids developing in hosts above that threshold, fitness can be maximized independent of any trade-offs.

The pattern of covariation between size and age at maturity varies between different parasitoid species. For example, DW may be positively correlated with host size while T_p varies non-linearly (Salt, 1940; Jones and Lewis, 1971; Miles and King, 1975; Nechols and Tauber, 1977). In some species, the pattern of covariation between DW and T_p can be positive (Arthur and Wylie, 1959; Vinson, 1972; Lawrence *et al.*, 1976) and negative in others (Smilowitz and Iwantsch, 1973; Nechols and Kikuchi, 1985). Which of several possible strategies will be optimal depends on the phenology and the age or size structure of the host population and, also, on the fitness consequences for parasitoids adopting different strategies. Thus the distribution of host sizes in the environment could have an important effect on the correlational structure between phenotypic traits in the parasitoid and ultimately influence the evolution of adaptive host selection behaviour.

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