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A QUANTITATIVE GENETIC ANALYSIS OF THERMAL SENSITIVITY IN THE LOCOMOTOR PERFORMANCE CURVE OF *APHIDIUS ERVI*

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Abstract.—The thermal sensitivity of locomotor performance in *Aphidius ervi*, a parasitic hymenopteran, conforms to the "jack-of-all-trades is master of none" model of specialist-generalist trade-offs. Performance breadth and maximal performance at the phenotypic level are negatively correlated in both sexes. A strong, negative genetic correlation was found for males, but not for females. In males, the broad-sense heritability of performance breadth was about 0.16, and that of maximum walking velocity was about 0.29. Neither heritability was significantly different from zero in females. The broad-sense heritability of body mass was about 0.3 in females and 0.6 in males, with a strong negative genetic correlation between size and maximum velocity in males only. These data provide the first quantitative genetic analysis of performance curves in eukaryotic animals, and one of the few demonstrations of the specialist-generalist trade-off that underlies much theory in evolutionary ecology.

Key words.—*Aphidius ervi*, performance curve, quantitative genetics, thermal sensitivity, trade-offs.

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Ambient temperature often limits the activity patterns of animals, particularly in ectotherms with limited thermoregulatory capacity. These limitations on activity can translate into differences in realized fitness (Kingsolver and Watt 1983; Watt et al. 1986; Lynch and Gabriel 1987) through their effects on behaviors such as running, foraging, mating, and oviposition (e.g., Burnett 1960; Huey and Stevenson 1979; Kingsolver 1983). Adaptation to extremes of temperature, as in the physiologies of Antarctic ice fish or hot springs dipterans, indicates that thermal sensitivity has a genetic basis and can respond to natural selection. The inability of these species to survive in the "normal" temperature range of closely related taxa suggests that there are limitations to the breadth of thermal adaptation (Hochachka and Somero 1984). Here I examine the quantitative genetics of temperature sensitivity and the evidence for trade-offs between performance breadth and rate.

The thermal sensitivity of an organism can be described by a performance curve, a plot of physiological activity or behavior as a function of temperature (Levins 1968; Huey and Slatkin 1976; Huey and Kingsolver 1989). The slope of the curve at any point describes the sensitivity of the organism to environmental change about that point. Key parameters of the thermal performance curve include an index of its breadth (T_{br}), the thermal conditions that maximize performance (T_{opt}), and the maximum rate of performance (u_{max}). A thermal generalist performs over a broad range of body temperatures, whereas a specialist performs well only under a narrow range of body temperatures.

Thermal performance curves provide a tool for examining the assumption of physiological trade-offs between generalists and specialists. The principle of allocation (Levins 1968, p. 14–15) proposes that a trade-off exists whereby increasing the range of resources utilized demands a reduction in performance capacity at optimal conditions. This "jack-of-all-trades is master of none" assumption permeates the ecological and evolutionary literature (Curry and Feldman 1987; Futuyma and Moreno 1988), but tests of the assumption are rare. Most comparisons of specialists and generalists are among closely related species, which may differ in a variety of ways that indirectly affect the potential trade-off, rather than among genotypes within a population. Furthermore, few of the interspecific comparisons explicitly examine the hypothesis of a negative correlation between breadth and efficiency (Futuyma and Moreno 1988). Finally, studies of trade-offs often report phenotypic correlations among traits. Evolution, however, is constrained by genetic correlations that may differ from phenotypic correlations in both magnitude and sign (Service and Rose 1985; Rose et al. 1987; Falconer 1989).

Here I test the hypothesis of negative correlation, at both the phenotypic and genetic levels, between performance breadth and performance rate under optimum conditions. I assess quantitative genetic variation in the locomotor performance curve of the wasp, *Aphidius ervi*, a solitary endoparasite of aphids. Parasitoids play an important role in controlling herbivores in natural communities and agro-ecosystems. The establishment and efficacy of introduced biocontrol agents depend on the ability of the parasitoid to locate and attack the host under the range of temperatures encountered in the new environment (Greathead 1986; Simberloff 1989; Dennill and Gordon 1990; Stiling 1990). Introduced parasitoids often become established, but are nonetheless ineffective as biocontrol agents because of their limited thermal activity range (DeBach et al. 1955; Campbell and Mackauer 1973; DeBach and Rosen 1991). Genetic studies, such as this, and selection experiments (White et al. 1970) provide both basic information on the genetics of thermal sensitivity and data critical to successful biological control programs.

The running speeds of individuals from full-sib families of *A. ervi* were measured at seven temperatures ranging from 12°C to 36°C to estimate the thermal sensitivity of locomotor performance. Locomotor performance is often used to study the thermal sensitivity of ectothermic vertebrates (e.g., Porter et al. 1973; Huey and Stevenson 1979; Bennett 1980; Spotila et al. 1989), but the methods have rarely been applied to insects. Although empirical information directly linking locomotor performance to fitness is lacking for any hymenop-

teran parasitoid, several studies offer circumstantial evidence that locomotor performance is related to female oviposition capability (Burnett 1960; Messenger 1968; Bigler et al. 1988). I will present evidence for genetic and phenotypic trade-offs between T_{br} and u_{max} in *A. ervi*, suggesting that genetic constraints influence the shape of the performance curve in both sexes. I will also examine how locomotor performance varies with body size.

Methods

Biology of the Insects

Aphidius ervi is a solitary endoparasite of several aphid species. These animals were introduced into North America during the 1960s as a biocontrol agent for pea aphids (Mackauer and Campbell 1972). Females normally oviposit a single egg within the aphid's hemocoel; within 48 h, the larva hatches. The larva completes three instars in 6–9 d while consuming its host. It then pupates within the empty aphid cuticle, forming a "mummy." Following eclosion, females have a short receptive period of a few hours during which they mate no more than once. If unmated during this period, they will lay only unfertilized haploid male eggs (Mackauer 1976; Mackauer and Kambhampati 1988; King 1989). Although females may oviposit more than one egg per host at low aphid densities in the laboratory, only a single wasp will successfully complete development in each host. For this study, I used pea aphids (*Acyrthosiphon pisum* Harris) reared on broad beans (*Vicia faba* L., cv. Banner) at 55–65% RH on a 16L: 8D cycle, with daytime temperatures of 20 ± 0.5°C and night temperatures of 10 ± 0.5°C. Under these conditions, aphid reproduction is exclusively parthenogenetic and all offspring are female. Pea aphids complete four nymphal instars before molting to the reproductive stage.

Experimental Design

In June 1991, I collected several hundred mummies and mated female *A. ervi* from three commercial organic pea fields near Mt. Vernon, Skagit County, Washington; these formed the base population for this study. For each generation, I haphazardly chose 150 to 200 mass-mated females for reproduction. Groups of 10 to 20 females were each placed in a mesh-topped paper can (10 cm D, 15 cm H) with about 200 aphids of all instars and a small amount of cut vegetation. The cans were placed inside an environmental chamber at the conditions described above. The chambers were illuminated by 16 × 150W fluorescent tubes and 8 × 100W incandescent bulbs. After removing the parasitoids, the parasitized aphids were transferred to potted beans (8–10 plants per pot). Each pot was caged with a vented mylar cylinder (15 cm D, 30 cm H) buried in the soil and covered at the top with mosquito netting. The pots were placed in trays of water and returned to the environmental chambers. The parasites and their hosts developed in environmental chambers for 9 d, by which time most pupated to form mummies. The mummies were removed from the plants. Half were returned to the environmental chambers to complete development (4–6 d), while the other half were stored under refrigeration (36 ± 2°C) up to four weeks to prevent eclosion. Each week, the mummies were combined with a mixture of mummies from previous weeks in a large (0.5 m H, 0.5 m W., 1.0 m L) flight cage for eclosion and mating. Each generation took 16 d from egg to mated, ovipositing adult. These rearing procedures minimized selection on mating and oviposition while maintaining as much genetic variation as possible.

Two sets of full-sib families were reared for testing, one in June 1992, the other in January 1993. Several attempts failed to obtain large numbers of half-sib females, due to the short life span of males and the shorter receptive period of females (Sequeira and Mackauer 1992). For each experiment, I chose 60 randomly mated females to form the parental stock. Each female was placed inside a vented mylar cage (10 cm D, 30 cm H) enclosing a pair of potted bean plants and 25–30 five-day-old aphids (early third instar) for 24 h. The parasitoid was then removed; the parasitized aphids returned to the environmental chambers to complete development inside the cages. The mummies of each family were collected, placed individually in vials to prevent mating, and held under rearing conditions until eclosion. At eclosion, up to 5 males and 5 females were collected from each family and placed in clear plastic vials (15 mm D, 70 mm H) for testing. Only active individuals in good condition with fully hardened wings were used for performance testing.

Testing Locomotor Performance

Assaying the thermal sensitivity of locomotor performance requires testing each individual under a range of temperatures that spans the thermal activity range of the population. Preliminary studies showed that below 12°C, fewer than 5% of the parasites could walk and that above 36°C, most individuals died within 1–2 h. Because I needed to test all individuals at all temperatures on a single day, I had to limit the number of test temperatures to seven: 12, 16, 20, 24, 28, 32, and 36°C. All animals remained in an environmental chamber at 22 ± 1°C between tests to minimize acclimation effects. The order of the test temperatures was 16, 24, 12, 20, 28, 32, 36°C for both experiments. Because temperatures above 28°C can cause irreversible changes in behavior, including death in some individuals, performance at high temperatures had to be assessed last.

Testing was done in a walk-in environmental chamber programmed for the test temperature. About one-third of the animals were taken into the chamber and allowed to equilibrate to the test temperature for a few minutes. The natural propensity towards negative geotaxis was exploited to assess performance. The vial containing an individual was inverted; I then timed how long the insect took to walk from bottom to top (distance traveled ~70 mm) with a stopwatch. The first time was recorded unless the insect was not on the bottom of the vial at the start or if it flew instead of walked. Fewer than 5% of the individuals flew during these trials, however if an individual flew on both the first and the second trial, the flight time from the second trial was recorded. Any individual that did not traverse the distance within one minute was assigned a time of infinity. Flies tested in this manner seem to approach maximum locomotor rate; knocking the animal to the bottom of the vial elicits an escape response. Families were randomized during testing, but the order in

which each individual was tested did not vary across test temperatures. For analysis, the walking times were transformed into velocities. At the end of all seven trials, the wasps were killed by freezing and wet masses were recorded within 24 h.

The Traits

Most of the analysis that follows considers four performance traits. T_{opt} is the temperature at which an individual walked fastest; u_{max} is the velocity at T_{opt}. T_{br} is an index, analogous to the second moment of area about a neutral axis:

$$T_{br} = \sqrt{\sum \left[\frac{u_i(T_i - T_{opt})}{u_{max}}\right]^2}, \quad (1)$$

where u_i is walking velocity at temperature T_i. This index describes the distribution of relative velocity about a central point, in this case about T_{opt}. The velocities, u_i, are standardized to u_{max} to remove spurious correlations between T_{br} and u_{max}. Finally, *area* is the estimated area of the performance curve; here it is simply the sum of velocities at all temperatures. Wet body *mass* provides a morphological trait for comparison with the performance traits.

Statistics

Only families that produced two or more individuals of a sex were included in the analysis. Three of the continuous traits (*mass*, T_{br} and u_{max}) were log transformed before analysis to improve their fit to a normal distribution. Broad-sense heritability estimates for the performance traits, wet mass, and performance at each of the seven test temperatures were computed using standard haplodiploid models of inheritance (Collins et al. 1984). Males are haploid and produce genetically homogeneous sperm, so the coefficient of relatedness among siblings is 3/4 for full sisters and 1/2 for brothers (Bulmer 1980). Males and females are analyzed separately because of the asymmetry in relatedness of brothers and sisters. The covariance among male siblings (σ_{FS}) estimates $1/2V_A$ while the covariance among female siblings estimates $3/4V_A + 1/2V_D$. Full-sib analysis does not allow the partitioning of variance due to dominance or maternal effects, so here

$$h^2 = \frac{V_G}{V_P}. \quad (2)$$

For males,

$$V_G = 2\sigma_{FS} = V_A + V_{EC}, \quad (3)$$

and for females,

$$V_G = \frac{4}{3}\sigma_{FS} = V_A + \frac{2}{3}V_D + \frac{2}{3}V_{EC}, \quad (4)$$

where V_G is the genetic variance, V_A is the additive genetic variance, V_D is the dominance variance, and V_{EC} is variance due to a common environment. Heritabilities and genetic correlations were computed by standard methods using ANOVA to partition the variance (Becker 1984; Falconer 1989) and by restricted maximum likelihood (REML, Shaw 1987).

I computed the 95% confidence intervals for the ANOVA estimates following Becker's (1984) methods. These estimates are extremely conservative since their statistical properties are unknown for unbalanced designs. I ran a permutation test on the data as a second method to test the significance of the heritability estimates. Using the observed distribution of family sizes in the first and second experiments, individuals were drawn without replacement and randomly assigned to a family within their original experimental group. The male and female datasets were each permutated 1000 times. I report the proportion of permuted populations in which the heritability or genetic covariance is as great as or greater than the estimated value.

REML provides a more robust estimate of the variance components than ANOVA for an unbalanced design, while eliminating some biases of maximum likelihood estimates (Shaw 1987). One advantage of maximum likelihood estimates is the relatively straightforward significance testing. The log likelihood for the null hypothesis (L_0) is computed and compared with the maximum of L (L_{max}) using the likelihood ratio, or G, test. The significance of G is determined from a χ^2 distribution with the degrees of freedom set by the difference between the number of parameters estimated in L_{max} and those estimated in L_0 (Shaw 1987). Here G tests the maximum likelihood parameter estimate against the null hypothesis that there is no genetic variation (i.e., $h^2 = 0$) for the trait.

Preliminary analyses revealed that the distributions of virtually all variables differed between the two groups of full-sibs. Because approximately 10 generations passed between the experiments, these differences could be due to natural selection in the laboratory or they could reflect differences in the sampled genotypes. Alternatively, minor unplanned differences in making the performance measurements might be responsible for these errors. In the estimates of heritability and genetic correlations that follow, I included "experiment" as a random factor with two levels in the statistical model and used the "family-nested-in-experiment" variance component to estimate V_A. The magnitude of the experiment variance component for a given trait was always less than 10% of V_A. For all other analyses, the effect of "experiment" was removed by ANOVA and the residuals were back-transformed to the scale of the original data. All means, variances, and nonparametric statistics reported use this transformed data.

The REML estimation was performed using software developed by Frank and Ruth Shaw based on the methods described in Shaw (1987). All other analyses were performed using Splus (StatSci Inc. 1993). Tablewide significance throughout the paper was assessed using a sequential Bonferroni technique (Rice 1989).

The "jack-of-all-trades" hypothesizes a trade-off between performance breadth and maximum velocity, resulting in a negative correlation at the phenotypic or genetic level. Kendall's coefficient of rank correlation (τ) is used to assess the phenotypic correlation, as well as the correlations among performance at the seven different temperatures because of violation of the assumption of bivariate normality. The variance-covariance components outlined above were used to compute the genetic correlations by standard methods (Becker 1984; Falconer 1989).

TABLE 1. Mean and SE family size and count of families included in the analysis for the two blocks of full-sib families (see Methods: experimental design).

	Females			Males		
	Mean	SE	*N*	Mean	SE	*N*
Block A	4.22	0.200	36	4.17	0.171	41
Block B	3.69	0.122	32	3.51	0.126	37

Kirkpatrick's method for infinite dimensional traits (Kirkpatrick 1988; Kirkpatrick and Heckman 1989; Kirkpatrick and Lofsvold 1989; Gomulkiewicz and Kirkpatrick 1992) provides a second method of assessing the trade-off between specialists and generalists. The method searches for relationships within a variance-covariance matrix in a manner analogous to a principal components analysis. In place of a set of univariate principal components, one gets a set of multivariate curves, or reaction norms. A series of n orthogonal functions (the eigenfunctions) define the series of n curves that define the pattern of genetic variance and covariance, where n is the number of environmental states measured. The first eigenfunction describes the dominant reaction norm; the second describes the second most important reaction norm, etc. The eigenvalue associated with each eigenfunction is proportional to the genetic variance available for changes represented by that eigenfunction. The reaction norms can be visualized by fitting a cubic spline to the function over the range of environmental conditions.

Two aspects of the analysis may detect trade-offs in the covariance structure of the performance curve. First, one or more zero eigenvalues denote an absence of genetic variation in one or more reaction norms of the complex trait. Second, within each of the n reaction norms, trade-offs between performance in different environments are characterized by the eigenfunction's crossing of the zero axis. For that component of the covariance matrix, positive values for some environmental states are associated with negative values in other states. Interpreting these patterns is limited in that if the first eigenfunction does not intersect the zero axis, the second must by definition. Thus, if the first eigenfunction is always positive, one can only conclude that selection for increased performance in one environment causes increased performance in all environments. Trade-offs may affect other components of the variance-covariance matrix, but they do not constitute the predominant effect. The crossing of the axis in the second, third, etc., eigenfunctions provides neither evidence for nor against a trade-off.

RESULTS

Summary Statistics

The mean number of sibs per family, the standard error of the mean, and the number of families included in the analysis for each of the two experiments are shown in Table 1. About 20% of the parents in each experiment failed to produce enough offspring of either sex to be included. Overall, 29 parents produced only males, 19 produced only females and 49 produced both. The means and standard errors, by sex, of the five performance traits and the seven measured running speeds are given in Table 2. Females are larger, faster, and have a greater area beneath their performance curves than males. Note that the large difference between mean maximum velocity (u_{max}) and the mean velocity of the population at any one temperature (u_i) results from the heterogeneity of temperatures for maximum locomotion rate (T_{opt}). The mean performance curves for females and males are plotted in Figure 1.

Phenotypic Correlations among the Traits

The correlations among walking velocities at the seven test temperatures are shown in Table 3; females are above the diagonal and males lie below in this and all correlation matrices that follow. Performance tends to be positively correlated among adjacent temperatures in both sexes, while performance at the highest temperature is negatively correlated with performance at low and intermediate temperatures, particularly in males.

The phenotypic correlations among body mass and the performance traits are given in Table 4. Both body mass and performance breadth are negatively correlated with maximum velocity. The large, positive correlation between u_{max} and *area* largely results from the crude manner in which area is

TABLE 2. Phenotypic mean and SE for female and male *Aphidius ervi*. Table-wide significance (with the top and bottom halves of table analyzed separately) is indicated by the stars adjacent to the *P*-values of the Wilcoxon rank sum test.

	Females			Males			Wilcoxon test	
	Mean	SE	*N*	Mean	SE	*N*	*Z*	*P*
Mass (mg)	582.50	7.77	270	471.33	6.41	301	10.52	0.0000***
T_{br} (°C)	8.29	0.18	270	8.76	0.19	301	−1.3868	0.1660
u_{max} (m/s)	0.0223	0.0005	270	0.0177	0.0004	301	7.9318	0.0000***
T_{opt} (°C)	28.16	0.23	270	28.11	0.23	301	−0.7632	0.4450
Area (°Cm/s)	0.29	0.01	270	0.23	0.01	301	7.8424	0.0000***
u_{12} (m/s)	0.0026	0.0001	270	0.0020	0.0001	301	3.3970	0.0007**
u_{16} (m/s)	0.0048	0.0003	270	0.0041	0.0002	301	1.0273	0.3040
u_{20} (m/s)	0.0107	0.0003	270	0.0094	0.0003	301	3.2708	0.0011**
u_{24} (m/s)	0.0146	0.0004	270	0.0120	0.0004	301	5.1191	0.0000***
u_{28} (m/s)	0.0179	0.0006	270	0.0133	0.0004	301	6.9955	0.0000***
u_{32} (m/s)	0.0164	0.0005	270	0.0121	0.0004	301	7.3462	0.0000***
u_{36} (m/s)	0.0058	0.0004	270	0.0042	0.0003	301	4.7345	0.0000***

* $\alpha = 0.05$; ** $\alpha = 0.01$; *** $\alpha = 0.001$.

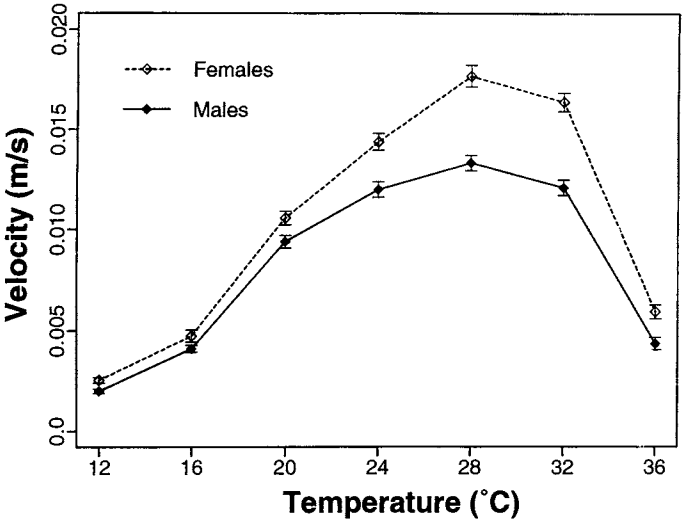

FIG. 1. Phenotypic performance curves for female and male *Aphidius ervi*. The curve describes the thermal sensitivity of walking speed.

computed and is probably not biologically significant. The relationships between T_{br}, u_{max}, and *mass*, transformed to natural logs, are plotted in Figures 2–4. The open circles represent phenotypic values; the closed squares are family means. The lines shown on the plots are reduced major axis regressions of the phenotypic values. This regression model is often used for allometric relationships and is appropriate for data in which both the x- and y-variables are subject to measurement error (Rayner 1985; McArdle 1988). Maximum rate of performance (u_{max}) and T_{br} are negatively related (Fig. 2) in females ($y = -1.882 + (-0.973)x$, 95% ci: $-0.879 < b < -1.067$, 268 df) and males ($y = -1.692 + (-1.156)x$, 95% ci: $-1.053 < b < -1.258$, 299 df). Body size is negatively correlated with u_{max} (Fig. 3) within the sexes (females: $y = 7.041 + (-1.721)x$, 95% ci: $-1.548 < b < -1.893$, 268 df; males: $y = 6.939 + (-1.805)x$, 95% ci: $-1.634 < b < -1.976$, 299 df). Body mass and performance breadth are positively correlated (Fig. 4, females: $y = -9.169 + 1.768x$, 95% ci: $1.945 < b < 1.591$, 268 df; males: $y = -7.467 + 1.562x$, 95% ci: $1.707 < b < 1.417$, 299 df).

Heritabilities and Genetic Correlations of Performance at Different Temperatures

The heritabilities of performance (REML estimates) at each of the seven test temperatures are shown in Table 5, and the genetic and environmental correlations are presented in Table 6. The correlations should be interpreted with caution because the data violate the assumption of normality. Performance at extreme temperatures is bimodally distributed, with one peak at zero velocity and the second at some intermediate value. The heritability of male performance is generally higher than that of females, and the genetic correlations are consistently larger in both sexes than the corresponding phenotypic values. The pattern of positive and negative genetic correlations in females and males is similar. Performance at high temperatures is negatively correlated with low and intermediate temperature performance, whereas performance at intermediate temperatures tends to be positively correlated with low temperature performance.

Heritabilities and Genetic Correlations of Mass, u_{max}, and T_{br}

The broad-sense heritabilities of the performance traits and body mass are shown in Table 7. In the ANOVA models, each trait for each sex was analyzed individually. I analyzed *mass*, u_{max}, and T_{br} using a single REML model for each sex to account for correlations among these variables [note: essentially identical estimates are obtained in analyzing these traits individually]; T_{br} and *area* were analyzed individually. Overall, the values estimated using ANOVA methods (Becker 1984) are similar to those from REML. Considerable genetic variation exists for wet body mass in both sexes, with males having a heritability of about 0.6 and females of about 0.3. For females, the values for u_{max} and *area* border on significance by both the permutation test of the ANOVA estimates and the G-test of the REML estimates. Males show significant genetic variation for u_{max} by both tests. T_{br} and *area* show significant genetic variation at the 5% level by the permutation test and at the 6% level by the G-test. Both the 95% confidence intervals and the G-test used here tend toward conservative conclusions (Becker 1984; Shaw 1987). If we accept these estimates, the data suggest a broad-sense heritability of approximately 0.10–0.30 for u_{max}, and a heritability of 0.10–0.20 for area beneath the performance curve. The heritability of performance breadth in males is 0.15-0.20, whereas female heritability in this trait does not differ from zero.

Traditionally, physiological traits are corrected for variation in body mass prior to analysis. I regressed body mass of males and females against their respective performance as measured by T_{br} and u_{max}, then used REML to estimate the variance components on the residuals (Table 8). Variation in

TABLE 3. Phenotypic correlations (Kendall's τ) for walking speed at seven temperatures. Females are above the diagonal, males are below. Sequential Bonferroni corrections have been applied to all tests of significance.

	u_{12}	u_{16}	u_{20}	u_{24}	u_{28}	u_{32}	u_{36}
u_{12}	—	0.16**	0.24***	0.15**	0.12*	0.05	−0.14**
u_{16}	0.23***	—	0.27**	0.10	0.15**	0.04	−0.07
u_{20}	0.12*	0.26***	—	0.33***	0.30***	0.21***	−0.09
u_{24}	0.10	0.28***	0.41***	—	0.31***	0.28***	−0.04
u_{28}	0.09	0.21***	0.25***	0.32***	—	0.26***	−0.11
u_{32}	−0.01	0.02	0.10	0.23***	0.20***	—	0.07
u_{36}	−0.20***	−0.19***	−0.22***	−0.15***	−0.21***	−0.05	—

* $\alpha = 0.05$; ** $\alpha = 0.01$; *** $\alpha = 0.001$.

TABLE 4. Phenotypic correlations (Pearson's product moment) ± SE among mass and the performance traits. *Mass*, T_{br}, and u_{max} were log-transformed prior to analysis. Females are above the diagonal, males are below. Sequential Bonferroni corrections have been applied to all tests of significance.

	Mass	T_{br}	u_{max}	T_{opt}	*Area*
Mass	—	0.14 ± 0.06	−0.11 ± 0.06***	0.21 ± 0.06**	−0.04 ± 0.06
T_{br}	0.23 ± 0.06***	—	−0.29 ± 0.06***	0.10 ± 0.06	0.15 ± 0.06
u_{max}	−0.12 ± 0.06***	−0.37 ± 0.05***	—	−0.05 ± 0.06	0.83 ± 0.03***
T_{opt}	0.14 ± 0.06	0.21 ± 0.06**	−0.08 ± 0.06	—	−0.08 ± 0.06
Area	0.00 ± 0.06	−0.00 ± 0.06	0.85 ± 0.03***	−0.14 ± 0.06	—

* $\alpha = 0.05$; ** $\alpha = 0.01$; *** $\alpha = 0.001$.

body mass may explain a small amount of the heritable variation in these performance measures, however the estimates are similar to those computed in Table 7. This is not surprising, since the correlations between T_{br}, u_{max}, and *mass* are taken into account during the REML analysis outlined in the previous paragraph.

The genetic and environmental correlations among T_{br}, u_{max}, *mass*, and *area* are presented in Table 9. I present only the REML estimates; ANOVA methods yield nearly identical results. Estimates of genetic correlations are notoriously imprecise with small- to moderate-size datasets such as this one (Shaw 1987; Falconer 1989). The estimates of standard error are extremely conservative (Becker 1984), so no significance tests will be presented. In general, male and female genetic correlations are quite different from each other. Four of seven male genetic correlations are negative, whereas all the female genetic correlations are positive and have large standard errors. All estimates of genetic correlation are larger in absolute magnitude than the corresponding phenotypic estimates in Table 4. Again, the high correlation between u_{max} and *area* is due to the manner in which area was calculated and probably has no biological significance.

I examined the genetic covariance among T_{br}, u_{max}, and *mass* to test the significance of positive and negative relationships (Table 10). The genetic covariance determines the correlated response to selection and its estimation is less

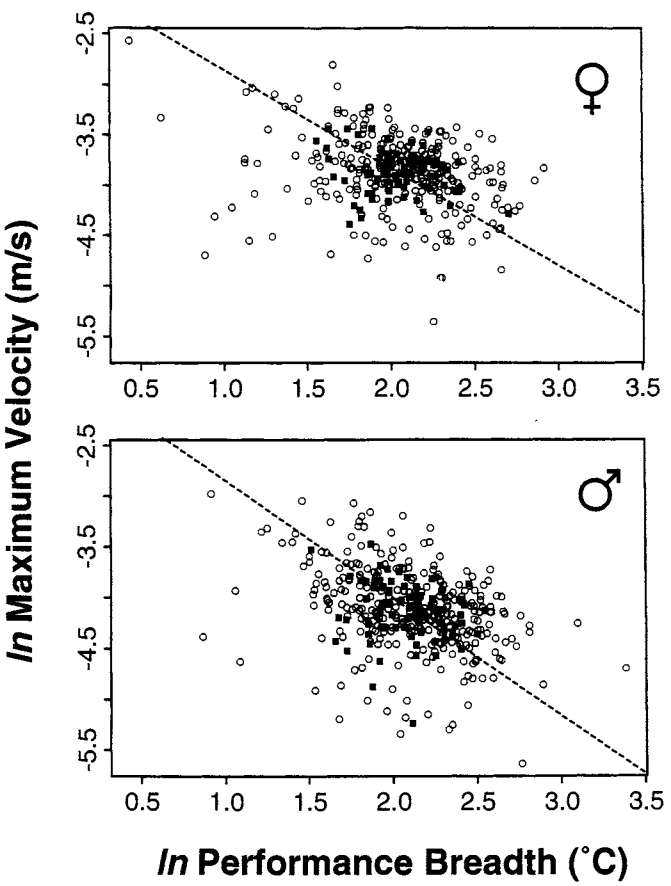

FIG. 2. Phenotypic performance breadth (T_{br}) versus maximum velocity (u_{max}) in *Aphidius ervi*. The open circles indicate individual values, the closed squares are family means. The dashed line is the reduced major axis regression on the individual values.

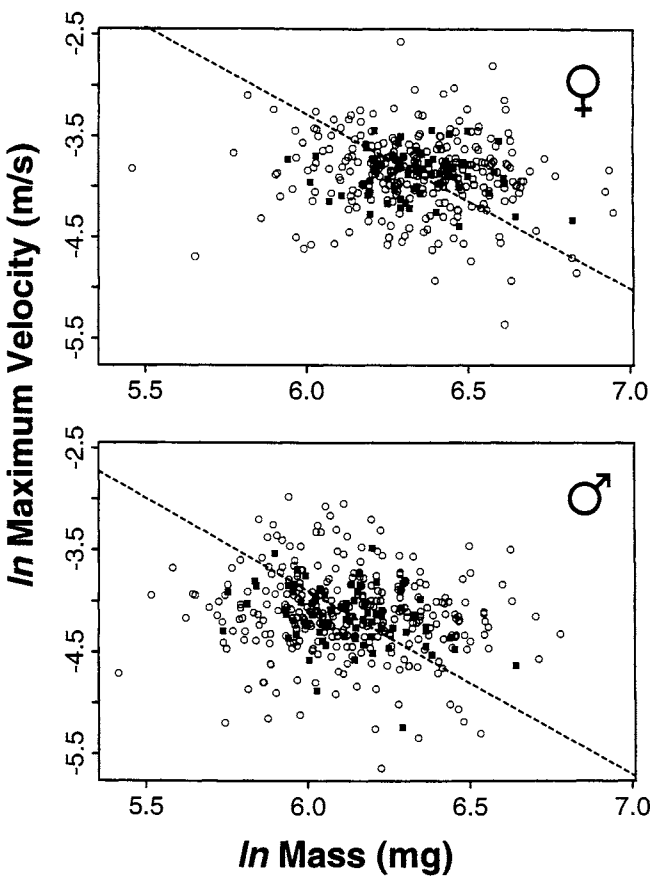

FIG. 3. Phenotypic wet mass versus maximum velocity. The open circles indicate individual values, the closed squares are family means. The dashed line is the reduced major axis regression on the individual values.

TABLE 5. Heritabilities of locomotor performance at seven temperatures, estimated using REML.

	$h^2 \pm$ SE	G	P
Females:			
u_{12}	0.18 ± 0.08	6.44	0.0093
u_{16}	0.05 ± 0.07	0.12	0.7184
u_{20}	0.08 ± 0.07	1.43	0.1620
u_{24}	−0.06 ± 0.06	0.82	0.5678
u_{28}	0.10 ± 0.08	2.08	0.1028
u_{32}	0.11 ± 0.08	2.37	0.0747
u_{36}	0.08 ± 0.07	1.60	0.2140
Males:			
u_{12}	0.19 ± 0.11	3.98	0.0461
u_{16}	0.25 ± 0.12	6.30	0.0121
u_{20}	0.05 ± 0.10	0.27	0.6031
u_{24}	0.20 ± 0.11	3.77	0.0522
u_{28}	0.12 ± 0.11	1.42	0.2338
u_{32}	0.22 ± 0.11	5.15	0.0232
u_{36}	0.31 ± 0.12	10.08	0.0015*

* $\alpha = 0.05$.

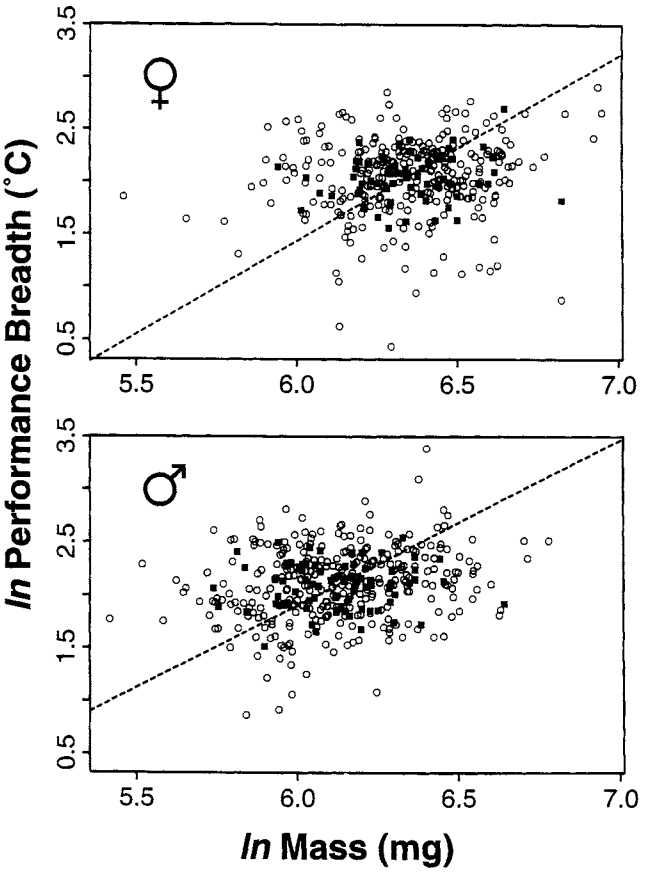

FIG. 4. Phenotypic wet mass versus performance breadth. The open circles indicate individual values, the closed squares are family means. The dashed line is the reduced major axis regression on the individual values.

subject to error than genetic correlation because only one parameter must be estimated (Lande and Arnold 1983). In the case of the ANOVA estimates, the test is the proportion of 1000 permutated data sets in which the estimated covariance was more positive (or negative, as appropriate) than the estimated value. The log-likelihood test compares the maximum likelihood estimate with the hypothesis of zero genetic covariance. The most striking observation is that u_{max} and T_{br} tend to covary negatively in males, yet positively in females (Table 9). Body size may constrain locomotor performance in males, via the negative correlation between u_{max} and *mass*, but no relationship was detected for females.

Trade-Offs in the Performance Curve

As noted above, u_{max} and T_{br} are negatively correlated at the phenotypic level in both sexes (Fig. 2, Table 4). Males exhibit a strongly negative genetic correlation, whereas the correlation for females is positive or zero (Table 9). Genetic variance-covariance matrices estimated from small data sets can impose biases that inflate the range of results by yielding negative eigenvalues in the Infinite Dimensional Analysis (Kirkpatrick and Lofsvold 1989). Because the eigenvalue is proportional to the genetic variance for the trait, negative values are not allowed. Rather than simply set all negative

TABLE 6. Genetic and environmental correlations ± SE among walking velocities at seven temperatures. Estimates for females lie above the diagonal, males lie below the diagonal. NA indicates the correlation was not estimated because of a negative variance component.

	u_{12}	u_{16}	u_{20}	u_{24}	u_{28}	u_{32}	u_{36}
Genetic:							
u_{12}	—	1.26 ± 0.89	2.01 ± 0.77	NA	0.83 ± 0.41	0.52 ± 0.40	−0.19 ± 0.47
u_{16}	1.31 ± 0.32	—	0.96 ± 0.81	NA	−0.73 ± 0.97	−0.92 ± 0.93	−0.75 ± 1.02
u_{20}	2.00 ± 1.79	1.76 ± 1.44	—	NA	1.14 ± 0.49	0.83 ± 0.49	−0.81 ± 0.79
u_{24}	0.55 ± 0.40	0.97 ± 0.27	1.05 ± 0.82	—	NA	NA	NA
u_{28}	0.82 ± 0.52	0.88 ± 0.41	1.58 ± 1.36	0.75 ± 0.35	—	0.99 ± 0.24	−0.66 ± 0.47
u_{32}	−0.21 ± 0.40	0.25 ± 0.36	−0.30 ± 0.82	0.21 ± 0.27	0.99 ± 0.44	—	0.34 ± 0.38
u_{36}	−0.41 ± 0.35	−0.37 ± 0.32	−1.23 ± 1.24	−0.23 ± 0.36	−0.70 ± 0.47	−0.22 ± 0.36	—
Environmental:							
u_{12}	—	0.03 ± 0.05	0.20 ± 0.20	0.24 ± 2.05	0.07 ± 0.08	−0.00 ± 0.00	0.03 ± 0.15
u_{16}	0.10 ± 0.13	—	0.20 ± 0.44	−0.02 ± 0.06	0.17 ± 0.58	0.07 ± 0.19	0.10 ± 0.36
u_{20}	0.04 ± 0.23	0.22 ± 0.60	—	0.52 ± 2.39	0.30 ± 0.36	0.23 ± 0.34	0.10 ± 0.26
u_{24}	0.02 ± 0.08	0.22 ± 0.19	0.36 ± 0.78	—	0.34 ± 1.46	0.33 ± 0.93	0.09 ± 0.91
u_{28}	0.03 ± 0.11	0.17 ± 0.24	0.24 ± 0.62	0.42 ± 0.47	—	0.32 ± 0.32	0.05 ± 0.12
u_{32}	0.04 ± 0.09	−0.04 ± 0.06	0.15 ± 0.84	0.34 ± 1.19	0.16 ± 0.23	—	0.29 ± 0.97
u_{36}	0.10 ± 0.11	0.12 ± 0.14	0.13 ± 0.21	0.17 ± 0.43	0.12 ± 0.12	0.34 ± 0.96	—

TABLE 7. ANOVA and REML estimates of heritability for female and male *Aphidius ervi*. For the ANOVA estimates, the upper and lower 95% confidence intervals were computed by the methods in Becker (1984). Permutation test is the proportion of 1000 runs in which the heritability of the permuted data was more extreme than the estimated heritability. REML estimates are tested using log-likelihood ratio tests against the null hypothesis of no genetic variation. Sequential Bonferroni adjustments are shown in the final column.

	ANOVA estimates				REML estimates			
	$h^2 \pm$ SE	Lower 95% C.I.	Upper 95% C.I.	Perm. test	$h^2 \pm$ SE	G	P	Adj. P
Females:								
Mass	0.29 ± 0.09	0.13	0.47	0.001	0.28 ± 0.09	11.92	0.0006	0.01
T_{br}	0.04 ± 0.07	−0.08	0.20	0.236	0.05 ± 0.07	0.51	0.4748	ns
u_{max}	0.11 ± 0.08	−0.02	0.28	0.067	0.10 ± 0.08	1.99	0.1584	ns
T_{opt}	0.10 ± 0.08	−0.04	0.26	NA	0.01 ± 0.07	0.03	0.9305	ns
Area	0.11 ± 0.08	−0.02	0.28	0.060	0.10 ± 0.08	2.06	0.0736	ns
Males:								
Mass	0.60 ± 0.13	0.36	0.86	0.000	0.60 ± 0.13	32.90	0.0000	0.001
T_{br}	0.16 ± 0.11	−0.03	0.40	0.047	0.19 ± 0.11	4.50	0.0338	0.06
u_{max}	0.29 ± 0.12	0.08	0.54	0.004	0.26 ± 0.12	5.96	0.0146	0.05
T_{opt}	−0.14 ± 0.08	−0.28	0.05	NA	−0.08 ± 0.09	0.97	0.3248	ns
Area	0.20 ± 0.11	0.004	0.45	0.023	0.20 ± 0.11	3.66	0.0556	0.06

values to zero, Kirkpatrick and Lofsvold (1989) developed a method of "squeezing" the eigenvalues by setting the smallest to zero. The "squeezed" eigenvalues account for the following proportions of the variance explained by the seven orthogonal reaction norms: (females: 0.41, 0.19, 0.14, 0.09, 0.08, 0.07, 0; males: 0.38, 0.23, 0.18, 0.08, 0.07, 0.06, 0). For both sexes, the last eigenfunction explains none of the genetic variance. This singularity in the variance-covariance matrix suggests that trade-offs will constrain evolution of the performance curve (Gomulkiewicz and Kirkpatrick 1992).

The first and second eigenfunctions from the infinite dimensional analysis are plotted in Figure 5 for females, and in Figure 6 for males. The points in these figures are the values of the eigenfunctions at the measured temperatures. The lines are cubic spline interpolations (which force a line through each data point) and should not be taken to reflect the precise shape of the reaction norms. In both sexes, the first eigenfunction describes a reaction norm in which performance at 36°C is negatively correlated with performance at intermediate temperatures. The second eigenfunction describes a reaction norm in which high and low temperature performance rates are negatively correlated. Taken together, the two eigenfunctions are consistent with the argument that trade-offs will influence evolution of the performance curve.

TABLE 8. Mass-corrected heritability estimates (REML) for performance breadth and maximum velocity.

	h^2	G	P
Females:			
T_{br}	0.03	0.25	0.6195
u_{max}	0.10	1.86	0.1729
Males:			
T_{br}	0.18	3.95	0.0468
u_{max}	0.21	3.91	0.0479

DISCUSSION

Is the "Jack-of-All-Temperatures" the Master of None?

At the phenotypic level, the clear, negative relationship between the performance breadth index and maximum velocity in both sexes (Table 3, Fig. 2) is consistent with the "jack-of-all-trades" hypothesis. The negative phenotypic relationship implies that selection for increased walking speed at the optimal temperature will also select for decreased T_{br}. For the phenotypic correlation between a pair of traits to affect the rate of evolution, both traits must have a genetic basis and share a non-zero genetic covariance. The broad-sense heritabilities of u_{max} are about 0.25 in males and 0.10 in females, and the values for T_{br} are about 0.15 in males and 0.05 in females (Table 5). For males, at least, significant genetic variation is present for these two traits. T_{br} and u_{max} exhibit a strong, negative genetic correlation of about −0.6 in males, whereas the correlation for females is positive and nonsignificant (Table 9). Genetic correlations scale the covariance between traits relative to the product of the genetic variance in the component traits, whereas the covariance between the traits determines the correlated response to selection. The permutation test of the ANOVA estimate and the G-test of the REML estimate of the covariance between T_{br} and u_{max} support the negative relationship for males (Table 10). The covariance between the traits is small and positive for females. Perhaps the heterozygosity of females masks the genetic trade-off observed in the haploid males; dominance effects may play a role in ameliorating the constraints imposed by negative genetic correlations (Mitton 1993).

One unresolved problem in dealing with a nonlinear norm of reaction is how to characterize it for statistical testing. Recent advances in evolutionary quantitative genetics have fostered an interest in reaction norm evolution (e.g., Scheiner and Goodnight 1984; Via 1984a,b; Via and Lande 1985; Scheiner and Lyman 1989; Scheiner et al. 1991). Most of these studies examine a trait in two discrete environments. With only two environments, the plasticity, or environmental

TABLE 9. Genetic and environmental correlations ± SE among the performance traits and body mass. Estimates for females lie above the diagonal, males lie below.

	Mass	T_{br}	u_{max}	*Area*
Genetic:				
Mass	—	0.67 ± 0.61	0.20 ± 0.39	0.44 ± 0.39
T_{br}	0.30 ± 0.26	—	0.49 ± 1.03	0.80 ± 0.82
u_{max}	−0.59 ± 0.23	−0.61 ± 0.28	—	1.01 ± 0.11
Area	−0.45 ± 0.28	−0.14 ± 0.41	0.87 ± 0.09	—
Environmental:				
Mass	—	0.08 ± 0.18	−0.17 ± 0.65	−0.13 ± 0.25
T_{br}	0.22 ± 0.32	—	−0.35 ± 1.79	0.11 ± 0.28
u_{max}	0.08 ± 0.06	−0.32 ± 0.32	—	0.81 ± 0.24
Area	0.17 ± 0.21	0.02 ± 0.14	0.84 ± 0.19	—

sensitivity, can be defined as the slope of the line connecting the two measures. This slope or the correlation in performance between the two environments can be treated as a quantitative trait (Scheiner and Lyman 1989). Moving to three or more environments introduces considerable complexity into the analysis, particularly if the reaction norm is nonlinear (Scharloo 1987; Via 1987). Equations can be fit to the data (e.g., Logan et al. 1976; Lynch and Gabriel 1987; Gavrilets and Scheiner 1993), however, a priori assumptions then impose constraints upon the shape of the performance curve.

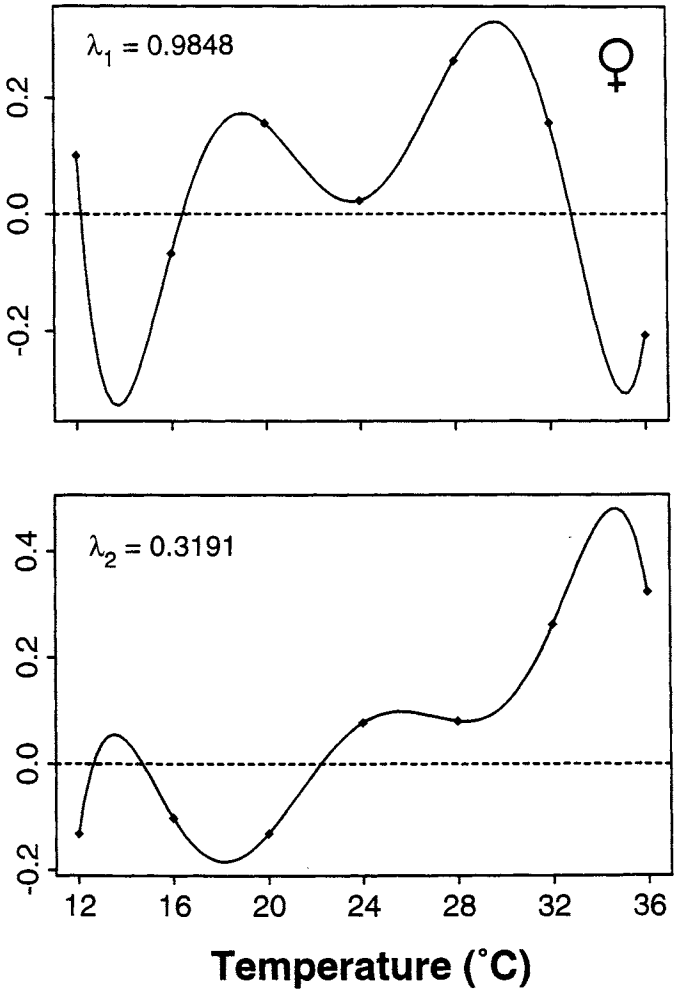

FIG. 5. Reaction norms derived from the first and second eigenvectors of the genetic variance-covariance matrix for female *Aphidius ervi* (see text for references). The eigenvalues in the upper left hand corner are proportional to the genetic variance for the reaction norm.

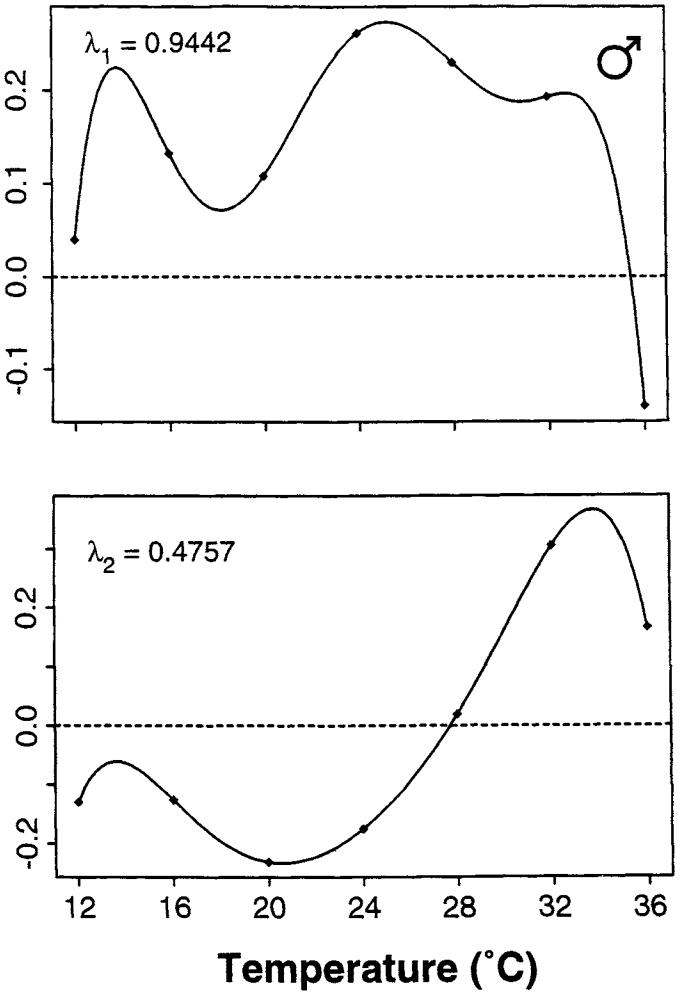

FIG. 6. Reaction norms derived from the first and second eigenvectors of the genetic variance-covariance matrix for male *Aphidius ervi* (see text for references). The eigenvalues in the upper left hand corner are proportional to the genetic variance for the reaction norm.

TABLE 10. Significance tests of the genetic covariances among performance traits and body mass. For the ANOVA estimates, the statistic is the proportion of 1000 permutations of the data in which the computed genetic covariance was more positive (or negative, as appropriate) than the estimated value. For the REML estimates, the value of the *G*-statistic is given. *P*-values are given in parentheses. Females are in the upper diagonal, males in the lower.

	Mass	T_{br}	u_{max}
ANOVA:			
Mass	—	0.086	0.304
T_{br}	0.102	—	0.300
u_{max}	0.000	0.053	—
REML:			
Mass	—	1.55 (0.2433)	0.25 (0.6870)
T_{br}	1.22 (0.2701)	—	0.39 (0.1880)
u_{max}	5.53 (0.0187)	2.80 (0.0940)	—

The breadth index used here (see Methods) provides a simple measure of the dispersion of performance about the optimum, with no a priori assumptions about the distribution of performance along the environmental gradient. The height of the curve is standardized to each individual's maximum velocity, and performance at conditions far from the optimum weights the index more heavily than performance in conditions near the optimum. Related indices of performance breadth, such as the first moment of area, yield similar results.

A second practical problem concerns the logistical trade-off between measuring multiple behavioral trials at fewer temperatures versus single trials at more temperatures. Ideally, one would like to assess an individual's performance over more than one trial per temperature so as to estimate repeatability of the trait. Multiple measures also would allow more precise estimates of the phenotype, with a corresponding increase in precision of heritability estimates (Arnold 1994). Such a design, however, would require reducing the number of temperatures at which performance was measured. Many studies have examined performance in two environments and failed to find evidence of trade-offs (reviewed in Futuyma and Moreno 1988). Increasing the number of environmental states at which performance is measured increases the resolution of the performance curve and enhances the likelihood of detecting specialist-generalist trade-offs (Gilchrist, unpubl. data). Because informal trials indicated that locomotor performance was fairly repeatable, I opted to measure single performance trials under a broader array of temperatures.

Kirkpatrick's methods for infinite dimensional traits (Kirkpatrick 1988; Kirkpatrick and Heckman 1989; Kirkpatrick and Lofsvold 1989; Gomulkiewicz and Kirkpatrick 1992) provide an extension of quantitative genetics to encompass complex traits such as performance curves and reaction norms. The analysis decomposes the performance curve into a series of reaction norms describing the major patterns of variance and covariance across the tested environmental range. The analysis provides two sources of information about trade-offs within the performance curve. First, the eigenvalues of the genetic variance-covariance matrix are proportional to the genetic variance for the trait. Zero or negative values suggest that trade-offs prevent the performance curve from evolving to maximize performance in all environments. When adjusted for the negative values, four of the eigenvalues for each sex are zero or close to it, suggesting that evolution of this trait is highly constrained.

Trade-offs can also occur within each of the eigenfunctions that describe the component reaction norms of the trait. The first eigenfunction (females: Fig. 5a; males: Fig. 6a) represents a norm of reaction having a negative pattern of covariance between performance at high temperatures and middle temperatures. The second eigenfunction (females: Fig. 5b; males: Fig. 6b) describes a reaction norm in which performance at high and low temperatures is negatively correlated. Taken together, these eigenfunctions suggest that selection for increased performance at intermediate temperatures will result in decreased performance at the extremes and vice versa, as hypothesized by the "jack-of-all-trades" model.

Evolutionary physiologists have provided evidence both for and against trade-offs between thermal specialists and generalists. In one of the earliest artificial selection experiments, Dallinger (1887) increased the heat tolerance of flagellates from under 60°C to 70°C. The selected lines were no longer able to survive temperatures of 18°C under which the original lines flourished, suggesting a trade-off between high and low temperature tolerance, but performance under optimal conditions was not assessed. Huey and Hertz (1984) measured sprint speed of agamid lizards at seven temperatures spanning the range of conditions experienced in the field and found no evidence of performance trade-offs. In fact, the fastest sprinters at optimal temperatures tended to be fast across all temperatures.

Bennett et al. (1992) provide the best explicit test of the "jack-of-all-trades" model, with a selection experiment on thermal sensitivity in the bacterium *Escherichia coli*. Clonal replicates were selected as specialists by rearing at constant temperatures of 32, 37, or 42°C, or generalists by rearing in an environment that varied each day from 32–42°C. After 2000 generations of natural selection, they found little "cost of adaptation" among the specialist lines. Performance increased at the selection temperature, but it did so with little or no reduction in performance at the other temperatures. The generalists, however, performed less well at a given temperature than the specialists at that temperature, suggesting that adaptation to a wide range of temperatures reduces performance efficiency under intermediate conditions. The data on *E. coli* and that presented in this paper are the only studies to date that assess genetic trade-offs in thermal sensitivity (Levins 1968). Both suggest that the trade-off between specialists and generalists is real, although the physiological mechanisms responsible are unknown (Hochachka and Somero 1984).

Is Hotter Really Better?

The "hotter is better" hypothesis is often cited as a reason that animals thermoregulate at high body temperatures (references in Huey and Kingsolver 1989). Because chemical systems operating at high temperature have the potential to attain higher catalytic efficiency (due to the greater absolute kinetic energy of the reactants), high body temperature might

confer an energetic advantage (Hochachka and Somero 1984). The hypothesis predicts a positive correlation between optimum temperature and maximum velocity. In *A. ervi*, I found no correlation between u_{max} and T_{opt} (Table 3).

Body Size and Performance

Body size is an important life-history trait in parasitoids. In females, selection for increased fecundity and survivorship favors large size (Charnov et al. 1981; Mackauer 1983; Opp and Luck 1986; Holloway et al. 1987), whereas large size in males can increase mating success (Grant et al. 1980). Body size also interacts with temperature to affect locomotor performance (e.g., Greenewalt 1960; Unwin and Corbet 1984; Partridge et al. 1987). Selection may favor small size in males because of the advantage in flight capacity at low temperatures (McLachlan 1986; Pivnick and McNeil 1986; McLachlan and Allen 1987; Marshall 1988; McLachlan and Neems 1989).

Mass and u_{max} show the highest heritabilities of the traits measured in this study, in part because these traits are measured directly rather than with an index and so are less subject to estimation errors. Although body size is correlated with performance, it does not account for the majority of heritable variation in either T_{br} or u_{max} (Tables 7 and 8). Sequeira and Mackauer (1992) found the heritabilities of male and female *A. ervi* body mass similar to those observed in this study. Genetic variation in the body size of *A. ervi* is probably maintained by its polyphagous habit (Mackauer and Kambhampati 1986). The species attacks and successfully completes development in aphid species and life stages that vary by over an order of magnitude in body size. The reason for the much higher heritability in males, relative to females, is unclear, but it is consistent with Sequeira and Mackauer's estimates. For a given trait, the estimates of V_E for males and females are similar; the lower heritability among females is consistently due to a small value for V_A. More detailed breeding experiments that can estimate the effects of dominance in females and maternal effects in both sexes are needed. However, the mating system of this species will make such assays extremely difficult.

Male and female *A. ervi* show a pronounced sexual dimorphism in both body size and locomotory capacity (Table 2). Females are larger and faster than males, although males may fly more frequently in nature (W. Settle, pers. comm.). Body mass and maximum velocity are negatively correlated at the phenotypic level within the sexes (Table 3, Fig. 3). Males show strong, negative genetic correlation and covariance between *mass* and u_{max} (Tables 9 and 10), whereas the effect in females is undetectable with this sample size. Conversely, larger wasps are able to locomote over a broader range of temperatures (Fig. 4). Increased body size increases thermal inertia, although the effect in animals weighing 0.5 mg should be minuscule (Bartholomew and Heinrich 1973; Willmer and Unwin 1981; Unwin and Corbet 1984). In larger organisms, thermoregulation allows specialization on a narrow range of temperatures, in spite of environmental fluctuations. Trade-offs between breadth and maximum performance may be present, but they might be concealed within the range of environmental temperatures where thermoregulation at acceptable physiological and ecological costs is possible. Theory suggests (Gilchrist 1995) that the increased performance capacity of thermal specialists may easily offset the costs of homeothermy. Further tests of the "jack-of-all-trades" model in a physiological context should concentrate on organisms, such as *A. ervi*, that are least able to regulate their internal environments in the face of external variation. It is in these organisms that the genetic variation in environmental sensitivity necessary to test the hypothesis will most likely be found.

Ecological and Evolutionary Implications of Thermal Sensitivity in Locomotor Performance

The fitness consequences of genetic variation in the thermal sensitivity of walking speed are unknown for *A. ervi* (and, for that matter, for all other insects), but several studies suggest that variation in locomotor performance or thermal sensitivity may indicate fitness differences. Bigler et al. (1988) have found that slow-walking strains of *Trichogramma maidis* are less effective at parasitizing their host's eggs under field conditions. Burnett (1960) showed that the oviposition rate of the chalcid wasp *Dahlbominus fuscipennis* was greatly reduced under low to moderate host densities at temperatures < 17.5°C or at temperatures varying from 17.5–24°C, relative to rates at a constant temperature of 20°C. Messenger (1968) found that the female oviposition ability in *Praon exsoletum* was reduced under extremes of heat and cold, and that the functional response rate in a variable environment was significantly lower than under constant conditions. All of these authors attributed the reduction in oviposition rate to a reduced searching rate on the part of females.

No behavioral studies of male *A. ervi* address the role or importance of locomotion in obtaining matings; however, male courtship success in *Drosophila* correlates with running speed (Partridge et al. 1987). In the case of *A. ervi* males, mate location is probably of greater importance than locomotion during courtship. Males appear to spend much of their active time walking over or flying about the plant surface in search of receptive females: when one is found, courtship is almost nonexistent (pers. obs.). The narrow window of mating receptivity in newly emerged females (Godfray 1990) and the short (2–4 d) lifespan of males combine to place a premium on the ability to locomote to locate mates.

The small sample sizes imposed by the difficulty of rearing undomesticated species in the lab limit the conclusions that can be drawn from this study. The data, however, suggest that genetic constraints do shape the thermal sensitivity of locomotor performance in *A. ervi*. The principle of allocation and its corollary, the trade-off between performance breadth and performance rate in specialists and generalists, pervade much of the thinking in life history theory, community ecology, and evolutionary physiology (Futuyma and Moreno 1988). This is the first quantitative genetic study of a eukaryotic organism to support the "jack-of-all-trades" hypothesis concerning a continuous environmental factor such as temperature. The methodology outlined herein can be applied to evaluate specialist-generalist trade-offs in other species and on other environmental gradients.

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