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Host-associated fitness trade-offs do not limit the evolution of diet breadth in the small milkweed bug *Lygaeus kalmii* (Hemiptera: Lygaeidae)

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Abstract Theoretical models of evolution in a temporally variable environment predict that genotypes with low variance in fitness across generations will be favored. When host use varies temporally and fitness trade-offs exist among hosts, such that an increase in performance on one host results in a correlated decrease on the other, selection for low variance in fitness across generations will favor genotypes which are generalists. Before predictions such as this can be extended to natural herbivore populations, however, it is necessary to understand the extent to which performance trade-offs limit simultaneous adaptation to multiple hosts. The experiment reported here compares two populations of the common milkweed bug, *Lygaeus kalmii* (Hemiptera: Lygaeidae) which differ in patterns of host usage. One population is largely restricted to milkweed (*Asclepias* spp.) when milkweed seeds are available, but becomes a scavenger on a large assortment of available seeds when milkweed seeds are unavailable. The second population is restricted largely to dandelion (*Taraxacum officinale*), without access to milkweed. We examine these populations to test for host-associated genetic trade-offs between specialization on dandelion (*Taraxacum*) and two species of milkweed, *Asclepias fascicularis*, which is low in cardiac glycoside content, and *A. speciosa*, which is high in cardiac glycoside content. Despite the difference in patterns of host use of the two *L. kalmii* populations, the populations did not differ in their performance on any of the host plants. Within each population, bugs performed nearly as well on each host, except that bugs had significantly lower survivorship on dandelion than on either milkweed species. Trade-offs in performance among hosts were not present in either population: estimated genetic correlations across hosts were strongly

positive. The inability of this study to detect host-associated fitness trade-offs is consistent with most published data on this topic.

Key words Genotype-environment interactions
Insect-plant interactions

Introduction

The evolution of herbivorous insect diet breadth has interested researchers for decades. Most herbivorous insects feed on few of the plant taxa available to them (Fox and Morrow 1981). Many hypotheses have been proposed to explain the observed patterns of insect diet breadth, including those which emphasize predators and parasitoids (Lawton and McNeill 1979; Bernays and Graham 1988; Fox and Eisenbach 1992), plant apparency (Feeny 1976; Rhoades and Cates 1976; Wiklund 1984; Courtney 1986; Chew and Courtney 1991), phenology (Tahvanainen 1983; Straw 1989), abundance (Wiklund 1982), or reliability (predictability) (Futuyma 1976; Cates 1981; Wiklund 1982; Chew and Courtney 1991), and the interaction between plant chemistry and the neurophysiological capabilities of insects (Ehrlich and Raven 1964; Smiley 1978; Jermy 1984; Fox and Lalonde 1993), although it is clear that no single hypothesis is sufficient to account for the observed patterns (Bernays 1991). Probably the most common explanation for specialization on a particular resource is that trade-offs exist in the ability to utilize multiple resources (Levins and McArthur 1966). For herbivorous insects, this hypothesis has usually been expressed with respect to host-associated performance trade-offs, where performance refers to any life history character that is expected to correlate with fitness.

Theoretical models of evolution in a temporally variable environment (models of "bet-hedging") predict that genotypes with low variance in fitness across generations will be favored (Segar and Brockmann 1987). When host use varies temporally, and fitness trade-offs

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exist among hosts, such that an increase in performance on one host results in a correlated decrease on another, selection for low variance in fitness across generations will favor genotypes which are generalists. Thus, while in a spatially variable environment fitness trade-offs among hosts may result in a mosaic of host-associated specialized genotypes (e.g. Via 1991), in a temporally variable environment specialization on any host may be hindered by these trade-offs such that populations are composed largely of generalist genotypes.

Before predictions such as this can be extended to natural systems, however, it is necessary to understand the extent to which trade-offs limit simultaneous adaptation to multiple hosts. A common approach used to evaluate the importance of performance trade-offs has been to use "split-family designs" in which part of a family is reared on one host, while the rest are reared on another or several other hosts. Trade-offs are evaluated by calculating the correlation between a family's performance on pairs of hosts. Negative correlations are strong evidence that trade-offs of some kind exist. Although many studies of this type have found substantial amounts of genetic variation for performance on each of the hosts they compared, little evidence has been found for genetic trade-offs across hosts (e.g., Rausher 1984; Via 1984a, b, 1991; Weber 1985; Hare and Kennedy 1986; Futuyma and Philippi 1987; James et al. 1988; Pashley 1988; Karowe 1990; Fox 1993). Of these, only Pashley (1988) and Via (1991) found evidence that trade-offs between hosts may exist: although none of Pashley's (1988) and only one of Via's (1991) correlations were statistically different from zero, most were negative and suggestive of trade-offs.

The experiment reported here compares two populations of the common milkweed bug, *Lygaeus kalmii* (Hemiptera: Lygaeidae) which differ in patterns of host usage. One population is largely restricted to its milkweed host (*Asclepias* spp.) when milkweed seeds are available, but becomes a scavenger on a large assortment of available seeds when milkweed seeds are unavailable (Wheeler 1983; Hunt 1979; Root 1986). The second population is restricted largely to dandelion (*Taraxacum officinale*) in a small field, without access to milkweed (personal observation). Milkweed (*Asclepias*) is well known to possess cardiac glycosides, which are toxic to many animals (Roeske et al. 1976), while dandelion (*Taraxacum*) does not (Heywood et al. 1977). Milkweed specialists, such as *L. kalmii*, are capable of processing, and even sequestering, cardiac glycosides (Duffey and Scudder 1972; Scudder and Duffey 1972; Isman et al. 1977), although this sequestration may result in energy costs that influence performance of nymphs (Duffey 1980). Performance trade-offs across hosts may thus be mediated by sequestration costs associated with cardiac glycosides. We examine this system to test for host-associated genetic trade-offs between specialization on *Asclepias* and specialization on *Taraxacum*.

Methods

Natural history of *Lygaeus kalmii*

Lygaeus kalmii (Hemiptera: Lygaeidae) is an aposomatically colored insect widely distributed throughout the United States and Canada (Slater and Knop 1969). In general, the feeding biology of this species is poorly understood. *L. kalmii* appears to feed almost exclusively on milkweed (*Asclepias* spp.) when milkweed is available. When milkweed is unavailable, however, *L. kalmii* either migrates to regions where suitable hosts are available (Caldwell 1974), or persist on dehisced milkweed seeds, insect carrion (such as *Eleodes*, grasshoppers, and other milkweed bugs), and other non-milkweed seeds (Hunt 1979; Root 1986), particularly composites (Wheeler 1983).

Experimental populations

Experimental populations were initiated with adult *Lygaeus kalmii* collected from *Asclepias fascicularis* (subsequently referred to as the El Dorado population) along Route 49 between Plymouth and El Dorado, El Dorado Co., California, USA, on 16 July 1989, and from *Taraxacum officinale* (subsequently referred to as the Berkeley population) in an old field behind Cragmont elementary school in Berkeley, California, USA, over multiple dates in early July 1989. Bugs from the El Dorado population were collected from widely separated plants along the entire route described above (> 10 km) to maximize genetic variance. Bugs from the Berkeley population were all collected from a single field, and appear to represent a relatively small established population: bugs have been collected on dandelion at this site since 1977 (12 years prior to this study; R. L. Caldwell, unpublished data).

The two populations in this study differ in that the El Dorado population has *Asclepias* available to it throughout July, August, and part of September, while the Berkeley population has no access to milkweed during any time of the year. *Taraxacum* seeds are continuously available to the Berkeley population, and bugs are observed feeding on these seeds all year. This *Lygaeus* population is relatively isolated from milkweed: the nearest milkweed available is approximately 6 km away (UC Berkeley Botanical garden), and the nearest established milkweed outside the Botanical gardens is over 10 km away. However, we have no estimate of gene-flow into the Berkeley population from these milkweed patches.

All field-collected bugs were maintained in plastic shoeboxes in the laboratory for one generation on *Asclepias erosa* (El Dorado population) or dandelion (Berkeley population) to insure that individuals chosen for the breeding design were virgin adults reared under similar conditions. Each population was divided between multiple shoeboxes to insure that a large proportion of the bugs would contribute to the next generation (Dingle et al. 1988). All laboratory cultures and experimental animals were maintained at 32° C, LD 14:10 in laboratory growth chambers at the University of California, Berkeley.

Egg masses were collected from these larger culture boxes and reared in 16-oz (≈ 473 ml) white plastic containers. Thus all individuals from a single egg mass were reared together, allowing all parents used in the breeding design to be selected from different egg masses.

Experimental design

Virgin males from each population (Berkeley and El Dorado) were sequentially mated to up to four virgin females from their own population (no between-population crosses were performed). Males were mated to only one female at a time, and left with the female until enough eggs were laid to cover all experimental treatments. These matings resulted in the use of 16 sires and 36 dams from the El Dorado population, and 22 sires and 58 dams from the Berkeley population.

From each half-sib family, 42 offspring were reared in groups of seven in an 8-oz (≈ 237 ml) white plastic container. Halfway through the experiment, in an effort to boost sample sizes, up to 63 offspring from each half-sib family were used. This change in procedure, plus the production of inviable eggs by some parent females, resulted in an unbalanced data set, which was accounted for in all statistical analyses.

Each experimental container was provisioned with cotton-stoppered water vials and seeds of one of the following three host species: *Taraxacum officinale*, *Asclepias fascicularis*, and *A. speciosa*. Two species of milkweed seeds were used because *A. fascicularis* seeds are low in cardiac glycoside content, while *A. speciosa* seeds are high in cardiac glycoside content (Isman et al. 1977). Dandelion seeds lack cardiac glycosides (Heywood et al. 1977).

All containers containing unhatched eggs were checked twice daily and date of hatching was recorded to the nearest half day. Because all eggs within an egg mass hatched within half a day of each other, the entire container was scored as hatched when more than two eggs in it had hatched. In all cases the other eggs in the container hatched by the next census (unless they were unviable). After 10 days, all containers were observed twice daily to estimate development time. Recently molted adults were removed from their containers. Three morphological characters were measured as estimates of body size at adult molt: right hind tibia length, pronotum width at its widest point, and width of the head between the eyes. Adults were measured at least 8 h, but within 24 h, after their adult molt, allowing their exoskeleton to harden sufficiently for handling. Following measurements, all adult females were placed individually in 8-oz (≈ 237 ml) white plastic containers with two adult males. Each female was checked twice daily to estimate the time of first egg production. Females were destroyed after producing their first clutch, while males were re-used as mates for another recently molted female.

Statistical analyses

Analyses of variance were performed on development time, age at first reproduction (post adult emergence), three morphological es-

timates of body size at adult molt, and survivorship (egg hatch to adult). The ANOVAs were performed separately for offspring of each sex within each population. Because all data sets were unbalanced, type-III sums of squares in the General Linear Models procedure of SAS were calculated (SAS Institute Inc. 1985). Family terms were treated as random effects, whereas host terms were treated as fixed effects. All morphological estimates were log-transformed before analysis.

To control for rearing dish effects, ANOVAs containing sire, dam (nested within sires), and dish (nested within dams) effects were initially calculated for each host. However, of 30 ANOVAs (5 characters on 3 hosts for 2 populations), only 5 detected significant dish effects. Because estimation of dish effects obscures detection of host and family effects (each dish has a different host, such that a large portion of the among-dam and among-host effects is detected as an among-dish effect) dish effects were deleted from all subsequent analyses.

Two types of genetic correlations were calculated for a character across hosts. Genetic correlations for the same character across environments were calculated as product moment correlations of the family means for a trait on pairs of hosts (r_G). These family mean correlations are only approximations of the true genetic correlations because each variance and covariance used in their estimation contains a fraction of the within family "error" variance or covariance, but they are expected to converge on the true genetic correlation with increasing numbers of offspring per family (Via 1984b). Because the design was unbalanced, correlations calculated from sire families are biased, so all family mean correlations were calculated on full sib families (dam families) and are thus complicated by maternal effects and non-additive components of genetic variance (Via 1984b). Standard errors of the family mean correlations were calculated by bootstrapping the correlations 1000 times and then correcting the resulting standard errors for bias (Efron 1982).

Genetic correlations were also calculated from the maximum likelihood variance component of the family \times host interactions (both sire and dam) for each pair of hosts (Yamada 1962; Fry 1992b), estimated using the restricted maximum likelihood method of the SAS Varcomp procedure (SAS Institute Inc. 1985).

Table 1 Means and SEs for three morphological estimates of size at adult molt, development time, and age at first reproduction in *Lygaeus kalmii* reared on three hosts (seeds). All means are averages of family means. Statistical comparisons within populations are with Wilcoxon signed ranks test on paired family means. Between-population comparisons are with Mann-Whitney *U*-tests (unpaired data). An italicized mean denotes a difference between populations for a character within a host. Means sharing letters

Host	Sex	Pronotum width (mm)	Head width (mm)	Tibia length (mm)	Development time (days)	Age at first reproduction (days)
Berkeley population						
<i>T. officinale</i>	F	3.81 (0.01)A	1.43 (<0.01)A	4.39 (0.02)	14.44 (0.07)	4.67 (0.14)
	M	3.54 (0.01)B	1.33 (<0.01)B	4.17 (0.02)	14.52 (0.11)	
<i>A. fascicularis</i>	F	3.80 (0.01)A	1.43 (<0.01)A	4.42 (0.02)	14.06 (0.07)	4.14 (0.10)
	M	3.53 (0.01)B	1.33 (<0.01)B	4.21 (0.01)	13.99 (0.09)	
<i>A. speciosa</i>	F	3.82 (0.01)A	1.44 (<0.01)	4.45 (0.02)	14.21 (0.08)	4.27 (0.11)
	M	3.55 (<0.01)	1.35 (<0.01)	4.24 (0.02)	14.16 (0.13)	
El Dorado population						
<i>T. officinale</i>	F	3.81 (0.02)C	1.42 (<0.01)C	4.43 (0.02)C	14.28 (0.11)C	4.67 (0.15)C
	M	3.53 (0.01)D	1.32 (<0.01)E	4.23 (0.02)D	14.11 (0.16)D	
<i>A. fascicularis</i>	F	3.81 (0.03)C	1.42 (<0.01)CD	4.42 (0.02)C	13.96 (0.07)	3.93 (0.09)
	M	3.54 (0.02)DE	1.33 (<0.01)EF	4.25 (0.02)D	14.01 (0.12)D	
<i>A. speciosa</i>	F	3.85 (0.01)	1.44 (<0.01)D	4.48 (0.02)	14.34 (0.10)C	4.22 (0.11)C
	M	3.57 (0.02)E	1.35 (<0.01)F	4.25 (0.02)D	14.42 (0.15)	

within a population are homogeneous, such that those having no letters are different from the character's mean on the other hosts (e.g., for tibia length, within the Berkeley population, females differ on all three host types, while within the El Dorado population, females reared on *Taraxacum officinale* do not differ from those reared on *Asclepias fascicularis*, but do differ from those reared on *A. speciosa*). No comparisons were made between the sexes

Table 2 Means and SEs for four estimates of survivorship of *Lygaeus kalmii* reared on three hosts (seeds). Males and females are lumped because early instars could not be sexed. All means are

averages of family means. For calculation of family means, each rearing dish was treated as a single observation within a family. Statistical comparisons and symbols are as in Table 1

Host	Number of families	Survivorship (proportion surviving)			
		Hatch to day 5	Day 5 to day 10	Day 10 to adult	Hatch to adult
Berkeley population					
<i>T. officinale</i>	59	0.49 (0.03)	0.94 (0.01)A	0.95 (0.01)A	0.43 (0.03)
<i>A. fascicularis</i>	58	0.63 (0.03)A	0.95 (0.01)B	0.93 (0.02)A	0.56 (0.03)A
<i>A. speciosa</i>	58	0.66 (0.03)A	0.91 (0.03)AB	0.94 (0.01)A	0.57 (0.03)A
El Dorado population					
<i>T. officinale</i>	35	0.52 (0.03)	0.90 (0.03)A	0.92 (0.03)AB	0.45 (0.04)A
<i>A. fascicularis</i>	34	0.63 (0.04)A	0.95 (0.02)B	0.97 (0.01)A	0.58 (0.03)B
<i>A. speciosa</i>	34	0.61 (0.03)A	0.93 (0.02)AB	0.92 (0.02)B	0.52 (0.03)AB

Table 3 Analysis of variance for adult body size of *Lygaeus kalmii* females reared on three host species (seeds) in the laboratory. All analyses are performed using SAS GLM Type III sum of squares (SAS Institute Inc. 1985), with sire and dam (nested within sires)

treated as random effects, and host treated as a fixed effect. All analyses for morphological data were performed on log-transformed data. Only ANOVAs for females are presented because ANOVAs for males are similar

Source	Mean square	F-Ratio	Pronotum width			Head width			Tibia length		
			SSE	(df)	F	SSE	(df)	F	SSE	(df)	F
Berkeley population											
Sire	MS1	MS1/MS2	0.095	(21)	1.11 ns	0.071	(21)	1.95*	0.239	(21)	2.78**
Dam (sire)	MS2	MS2/MS6	0.150	(37)	5.15***	0.064	(37)	1.79**	0.153	(37)	5.03***
Host	MS3	MS3/MS4	0.001	(2)	0.50 ns	0.007	(2)	2.97 ns	0.017	(2)	9.84***
Sire × host	MS4	MS4/MS6	0.060	(42)	1.80**	0.051	(42)	1.26 ns	0.035	(42)	1.02 ns
Dam (sire) × host	MS5	MS5/MS6	0.070	(66)	1.33*	0.048	(66)	0.75 ns	0.063	(66)	1.09 ns
Error	MS6		0.497	(629)		0.608	(630)		0.510	(621)	
El Dorado population											
Sire	MS1	MS1/MS2	0.096	(15)	2.97**	0.048	(15)	1.81 ns	0.106	(15)	3.12**
Dam (sire)	MS2	MS2/MS6	0.043	(20)	2.45***	0.035	(20)	1.56 ns	0.045	(20)	2.44***
Host	MS3	MS3/MS4	0.008	(2)	2.60 ns	0.017	(2)	5.61**	0.012	(2)	0.38 ns
Sire × host	MS4	MS4/MS6	0.042	(29)	1.65*	0.043	(29)	1.30 ns	0.044	(29)	1.63*
Dam (sire) × host	MS5	MS5/MS6	0.046	(33)	1.58*	0.049	(34)	1.27 ns	0.035	(34)	1.10 ns
Error	MS6		0.282	(321)		0.366	(323)		0.298	(312)	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant

This technique is expected to produce generally similar results to the family mean correlations, but is not complicated by maternal effects when sire variances are used. However, estimates of genetic correlations across hosts obtained in this way were highly variable and generally uninterpretable. Thus, only the family mean correlations are presented here.

All significance tests are at the 0.05 level.

Results

Despite the difference in patterns of host use of the two *L. kalmii* populations, neither population differed in their performance on any of the host plants in this experiment (Tables 1 and 2). In both populations, bugs reared on *A. speciosa* were largest, while bugs reared on

T. officinale were generally similar in size to bugs reared on *A. fascicularis*. The larger size of bugs reared on *A. speciosa* can not be accounted for by longer development time on this host because development time was longest on *T. officinale* in the Berkeley population and similar on *T. officinale* and *A. speciosa* in the El Dorado population. Survivorship of bugs tended to be fairly low during the first 5 days after hatching, and then generally greater than 90% from 5 days to adult molt (Table 2). Survivorship was consistently lowest on *T. officinale*, and approximately equal on the two milkweed species. Age at first reproduction was oldest on *T. officinale* and youngest on *A. fascicularis* in each population. Significant host, sire, and dam (within-sires) effects were detected for almost all characters analyzed (Tables 3 and

Table 4 Analysis of variance for development time, age at first reproduction (post-adult molt), and hatch-to-adult survivorship of *Lygaeus kalmii* females reared on three host species (seeds) in the laboratory. All analyses, including *F*-ratios, are described in

Source	Development time			Age at first reproduction			Hatch to adult survivorship		
	SSE	(df)	<i>F</i>	SSE	(df)	<i>F</i>	SSE	(df)	<i>F</i>
Berkeley population									
Sire	34.3	(21)	1.90*	83.9	(16)	2.02 ns	4.50	(21)	1.86*
Dam (sire)	31.8	(37)	2.32***	62.4	(24)	1.60*	4.45	(38)	2.53***
Host	13.6	(2)	12.81***	21.5	(2)	2.90 ns	1.13	(2)	9.98***
Sire × host	22.2	(42)	1.43*	111.1	(30)	3.71***	2.57	(42)	1.32 ns
Dam (sire) × host	50.8	(66)	2.08***	71.4	(39)	1.13 ns	4.23	(71)	1.29 ns
Error	241.8	(653)		548.3	(653)		9.67	(209)	
El Dorado population									
Sire	33.1	(15)	2.15*	18.9	(12)	5.49**	2.09	(15)	1.60**
Dam (sire)	19.5	(19)	2.86***	3.5	(12)	0.38 ns	1.69	(19)	2.06*
Host	8.9	(2)	7.25***	10.0	(2)	7.11**	0.66	(2)	5.711**
Sire × host	17.8	(29)	1.71*	15.5	(22)	0.92 ns	1.68	(30)	1.30 ns
Dam (sire) × host	17.8	(34)	1.46 ns	11.7	(19)	0.81 ns	1.86	(36)	1.20 ns
Error	117.2	(327)		113.9	(149)		5.05	(117)	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant

Table 3. Analyses for survivorship are based on means for each rearing dish. Only ANOVAs for females are presented because ANOVAs for males are similar

Table 5 Family mean correlations between the same character on two different hosts for *Lygaeus kalmii*. All SEs were calculated by bootstrapping the family means correlations 1000 times, and cor-

recting for bias (Efron 1982). All analyses of morphological data were performed on log-transformed data. Estimates for survivorship are for combined sexes

Environments	Sex	Pronotum width	Head width	Tibia length	Development time	Age at first reproduction	Hatch to adult survivorship
Berkeley population							
<i>Taraxacum</i> vs. <i>A. fascicularis</i>	F	0.471 (0.103)	0.359 (0.101)	0.754 (0.054)	0.120 (0.138)	-0.172 (0.146)	0.265 (0.129)
	M	0.282 (0.198)	0.462 (0.108)	0.623 (0.103)	0.668 (0.125)		
<i>Taraxacum</i> vs. <i>A. speciosa</i>	F	0.352 (0.124)	0.201 (0.113)	0.719 (0.069)	0.296 (0.124)	0.281 (0.222)	0.255 (0.126)
	M	0.346 (0.184)	0.351 (0.120)	0.627 (0.828)	0.372 (0.147)		
<i>A. speciosa</i> vs. <i>A. fascicularis</i>	F	0.493 (0.104)	0.302 (0.116)	0.693 (0.077)	0.139 (0.188)	0.582 (0.198)	0.270 (0.135)
	M	0.509 (0.125)	0.112 (0.144)	0.484 (0.145)	0.299 (0.240)		
El Dorado population							
<i>Taraxacum</i> vs. <i>A. fascicularis</i>	F	0.274 (0.169)	0.266 (0.175)	0.300 (0.176)	0.396 (0.137)	0.394 (0.155)	0.216 (0.161)
	M	0.066 (0.193)	0.579 (0.117)	0.433 (0.154)	0.489 (0.201)		
<i>Taraxacum</i> vs. <i>A. speciosa</i>	F	0.630 (0.106)	0.356 (0.107)	0.544 (0.111)	0.340 (0.193)	0.134 (0.219)	0.103 (0.173)
	M	0.544 (0.134)	0.623 (0.115)	0.439 (0.164)	0.768 (0.094)		
<i>A. speciosa</i> vs. <i>A. fascicularis</i>	F	0.492 (0.197)	-0.008 (0.204)	0.566 (0.108)	0.463 (0.136)	-0.257 (0.279)	0.243 (0.186)
	M	0.413 (0.191)	0.499 (0.108)	0.488 (0.148)	0.512 (0.221)		

4), indicating significant genetic and environmental influences on each character. Sire × host and dam (sire) × host interactions were significant for very few characters in either population (Tables 3 and 4).

The absence of significant genotype × host interactions for most characters in an analysis of variance indicates that trade-offs among pairs of hosts do not exist. The genetic correlations for all characters across hosts are consistent with this: all were positive, with the exception of the correlation between age at first reproduc-

tion on *T. officinale* and *A. fascicularis*, and age at first reproduction on *A. speciosa* and *A. fascicularis*, which were both slightly negative (although not significantly) (Table 5).

Discussion

The purpose of this investigation was to determine whether host-associated performance trade-offs exist in

the ability of *Lygaeus kalmii* to feed on dandelion (*Taraxacum*) and two species of milkweed, *Asclepias fascicularis*, which is low in cardiac glycoside content, and *A. speciosa*, which is high in cardiac glycoside content. In these experiments, estimated genetic correlations across hosts were strongly positive (Table 5), indicating that trade-offs in performance among hosts are not present.

Bugs performed almost equally well on *A. fascicularis* and *A. speciosa*, which differ substantially in cardiac glycoside content. This suggests that fitness of *L. kalmii* is insensitive to cardiac glycoside content. Variation in cardiac glycoside content influences fitness of the monarch butterfly, *Danaus plexippus* (Zalucki et al. 1990), but appears to have no effect on the fitness of either *Aphis nerii* (Groeters 1993) or another milkweed bug, *Oncopeltus fasciatus* (Isman 1977). To sequester cardiac glycosides, *O. fasciatus* uses a biophysical mechanism which does not require energy input, except for the energy to break down cardiac glycosides to their polar derivatives (Duffey et al. 1978). Our results suggest that *L. kalmii* may have a sequestration mechanism similar to that of *O. fasciatus*, and thus is capable of dealing with cardiac glycosides without incurring a physiological cost.

The only character for which bugs differed substantially on any of the hosts was nymphal survivorship. Hatch-to-adult survivorship was lower on dandelion than on either species of milkweed (Table 2). This survivorship difference was due entirely to a difference in hatch-to-5-day survivorship, indicating that only young nymphs had trouble on dandelion. Because dandelion has a much harder seed coat than either milkweed species, and seed coat hardness has a large effect on survivorship of *L. kalmii* (R. Caldwell, unpub. data) and other hemipterans (L. McLennan, pers. comm.), this low survivorship is likely to be due to difficulty in penetrating the dandelion seed coat.

With the exception of survivorship, bugs performed generally well on each of the hosts available. In addition, all family \times host interactions for the performance characters measured were small or not significantly different from zero (Tables 3 and 4). These results indicate that both populations of *L. kalmii* are relative generalists on *Asclepias* and *Taraxacum*. However, there are two ways for *L. kalmii* to be a generalist: (1) When fitness trade-offs limit the ability of an insect to specialize on pairs of hosts simultaneously, then selection for low variance in fitness across generations will favor genotypes which are compromises between high performance on either of the hosts. (2) If no fitness trade-offs exist among hosts, such that an increase in performance on one host does not result in a correlated decrease on the other host, then selection for low variance in fitness across generations will favor genotypes which are specialized on both hosts simultaneously. Although the data presented here are inadequate for distinguishing among these two types of generalists, two lines of evidence suggest that *L. kalmii* is the second of these two

types of generalist. First, trade-offs across hosts were not present in either population, and thus generalists which are a compromise between specialists on the two hosts are not expected. Second, in a comparison of the two populations of *L. kalmii* the population which experiences temporal variation in host use performed just as well on all hosts as did the population which is restricted to *Taraxacum*. Thus, this population does not appear to have sacrificed performance on any host to feed on all three hosts.

The failure of this study to detect host-associated fitness trade-offs is consistent with most other published data on this topic (reviewed in Via 1990). However, numerous concerns have been expressed about the use of split-brood designs for the estimation of genetic correlations across hosts, and these should be addressed for this study. First, genetic trade-offs are very difficult to detect using split-brood designs unless the trade-offs are very dramatic, or unless sample sizes are very large (Rausher 1988). Estimates of genetic correlations are generally very imprecise (Falconer 1989), and thus small correlations (positive or negative) require very large sample sizes to be detected. However, this is unlikely to be a problem for our results because, although many genetic correlations did not differ significantly from zero, practically all estimates were positive.

Second, the genetic correlations generally estimated are additive genetic correlations, and thus we neglect any non-additive effects, which could be important (Rausher 1988). The absence of negative genetic correlations does not necessarily imply that trade-offs do not exist. So far, however, we have a very poor understanding of the role that non-additive effects may play in the evolution of any traits (Charlesworth 1990), and no understanding of how we could actually estimate non-additive correlations in natural systems.

Third, since most genetic correlations of performance among hosts are estimated in the laboratory, they may be swamped out by the effects of increased vigor often observed under laboratory conditions, giving rise to artificial patterns of correlations (Rausher 1988; Jaenike 1990). Futuyma and Philippi (1987) and Jaenike (1990) suggest correcting data sets for this general vigor effect before estimating genetic correlations, to reduce the bias resulting from a genotype \times laboratory environment effect. In each case, their corrections have uncovered some evidence of trade-offs across hosts in *Alsophila* (Futuyma and Philippi 1987; Jaenike 1990). These corrections, however, may not always be appropriate. The correction for general vigor removes part of the genotype effect and thus inflates the estimated ratio of genotype to genotype \times environment effects, biasing estimated correlations downward. However, failure to correct for general vigor, such as in this *L. kalmii* study, may bias results upward if non-host related genotype-environment interactions are present (e.g. some genotypes perform better under laboratory conditions than other genotypes) (Rausher 1988; John Jaenike, personal communication).

The most important criticism of this and other split-brood experiments concerns the appropriate choice of hosts. Clearly, the best way to assess the importance of performance trade-offs would be to compare performance on all potential hosts, and look for patterns in observed genetic correlations. More realistically, we need to find an appropriate subset of hosts to compare, as has been done for *Colias philodice* (Karowe 1990), which has recently expanded onto *Coronilla varia*. Information on phylogenetic history may be particularly useful in allowing the selection of suitable hosts for an analysis of trade-offs by indicating evolutionary shifts in host use or diet breadth (e.g. James et al. 1988). For *L. kalmii* we have demonstrated only that performance trade-offs are not present among dandelion and two species of milkweed, and have not considered the plethora of other potential hosts which *L. kalmii* encounters in a natural environment.

The inability of most studies to demonstrate host-associated performance trade-offs has led some researchers to argue that performance trade-offs are rarely of importance in the evolution of insect diet breadth (e.g. Butlin 1987; Bernays and Graham 1988), and that we should thus turn our attention away from performance trade-offs and toward other types of trade-offs that may exist, such as trade-offs in the ability to defend against multiple types of predators. However, some selection experiments have successfully identified trade-offs. These selection experiments have circumvented many of the problems discussed above by simultaneously selecting for performance on phylogenetically very distant hosts, and have successfully detected trade-offs between some pairs of hosts (Gould 1979; Fry 1990), while not between others (Fry 1992a). As yet, however, we have insufficient data to generalize concerning the relative importance of trade-offs in influencing the evolution of insect diet-breadth. It is clear that trade-offs rarely exist among hosts which are currently utilized by an insect population (reviewed by Via 1990; Groeters 1993). It is also clear that trade-offs are frequently present among distantly related host species (Gould 1979; Fry 1990, 1992a). However, the extent to which trade-offs between hosts and non-hosts restrict the expansion or shift onto hosts which are not currently utilized by an insect population is a question for which we still have insufficient data to generalize.

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