Covariance of preference and performance on normal and novel hosts in a locally monophagous and locally polyphagous butterfly population

Abstract Covariance between preference and performance was quantified for Papilio glaucus strains derived from a locally monophagous Florida population and a locally polyphagous Ohio population. I used two-choice assays to assess relative host preferences of mothers for plant species that represent reciprocal normal and novel hosts for each population (i.e., Liriodendron tulipifera and Magnolia virginiana) and a split-brood design to quantify relative performance of their progeny on each host. Covariance between preference and proxies of performance was detected independently within each population, which is a level of genetic structure at which such covariance has rarely been documented. These results support the hypothesis that preference-performance covariance can exist in populations that have no obvious internal host-associated structure. In the Ohio strain, all proxies of performance (larval duration, pupal mass, relative growth rate, and survival) were significantly correlated with relative preference for the normal host, L. tulipifera. In the Florida strain, however, only pupal mass was correlated with maternal preference, and this correlation was not in the direction expected. Progeny that attained the heaviest mass were derived from mothers that preferred L. tulipifera, the locally rare host. The nature of the preference-performance links was not in the manner predicted by conventional optimal oviposition theory, whereby host-associated tradeoffs have been considered an implicit element. Relative performance was congruent across hosts, regardless of whether mothers preferred L. tulipifera, M. virginiana, or neither host. After considering possible genetic and nongenetic explanations that could account for preference-performance covariance in P. glaucus, I conclude that this covariance has a genetic basis. Likely, multiple genetic control mechanisms (e.g., pleiotropy and co-adaptation) integrate at the level of different trait combinations and/or a particular trait combination to generate observed patterns.

Keywords Co-inheritance · Optimal oviposition · Host choice · Tiger swallowtail · Life-history strategies

Introduction

Resource use influences the geographic distribution, abundance, and diversity of species (Andrewartha and Birch 1954; Rabinowiz 1981; Denno and McClure 1983; Van Tienderen 1997; Warren et al. 2001), and scientists have long sought to identify causal links between resource use and ecological and evolutionary pattern. In phytophagous insects, behavioral traits that determine host preferences of ovipositing females and physiological traits that determine offspring growth and survival are key determinants of resource use (Futuyma and Peterson 1985; Via 1986; Thompson et al. 1990; Restnarits 1996). A mother’s choice of host can carry significant ecological and evolutionary ramifications for her progeny, particularly when these progeny are relatively sedentary. Studies of oviposition behavior and progeny performance are thus fundamental to efforts to understand and characterize the ecology and evolution of herbivorous insects.

One primary research focus has concerned the relationship between female choice and subsequent larval performance associated with alternate host species, individuals of a given species, or alternate plant modules. Optimal oviposition theory predicts positive linkage between preference and performance when intrinsic attributes of plants are the primary selective agents affecting adaptive change (Jaenike 1978; Rausher 1983; Thompson 1988; Jaenike and Holt 1991; Thompson and Pellmyr 1991; Nylin et al. 1996; Mayhew 1997). This is because plants are highly
variable nutritional resources (Denno and McLure 1983; Feeny 1992), and females preferring hosts that support superior offspring performance should increasingly predominate the gene pool as populations of progeny deposited on inferior hosts go extinct.

This intuitively simple evolutionary expectation of a positive preference-performance correlation has proved challenging to validate. Measures of preference and performance have commonly been found to be uncorrelated (Wasserman and Futuyma 1981; Karban and Courtney 1987; Valladares and Lawton 1991; Fox 1993), despite a few cases documenting positive associations between these life-history traits (e.g., Via 1986; Singer et al. 1988; Craig et al. 1989). In fact, females often willingly oviposit on resources that are toxic to their offspring (Berenbaum 1981; Chew and Robbins 1984; Moreteau et al. 1994; Bossart and Scriber 1995a).

Various explanations have been advanced to account for the apparent lack of correspondence between preference and performance, including scenarios that consider alternative adaptive strategies (Thompson 1988; Courtney and Kibota 1996; Valladares and Lawton 1991; Fox and Lalonde 1993; Larson and Ekbom 1995; Craig et al. 1999; Cronin and Abrahmson 1999; Scheins et al. 2000; Mayhew 2001). But many interpretations have been based on studies of average measures for populations and are difficult to understand in the context of the evolution of covariance, which functions at the level of heritable differences among individuals. Interpretations are also complicated by the fact that a multiplicity of environmental and genetic factors govern evolutionary response (Craig et al. 1989; Bernays 1996; Cronin and Abrahmson 1999; Ballabeni et al. 2001; Mayhew 2001). The likelihood that any single causal interpretation will adequately describe the evolutionary integration of epistatic effects between parental and offspring characters seems small (Bernays 1991; Cheverud and Moore 1994; Wolf and Brodie 1998).

Meaningful patterns are especially difficult to sort out in polyphagous species because the evolutionary dynamics that shape insect-host associations exponentially increase in complexity as a function of relative diet breadth. Host-associated selective change is comparatively limited in scope for taxa restricted to one or a couple of host species. But as species with ever-broader diets are considered, evolutionary change derives from an increasingly intricate network of host-associated selective response (Craig et al. 1989; Bernays 1996; Cronin and Abrahmson 1999; Sadeghi and Gilbert 1999). This intricacy reflects selection operating at multiple levels; including the level of variation within individual plants, among individual plants within a given species, and among different species, for all possible species combinations of the complete host array.

*Papilio glaucus*, the eastern tiger swallowtail butterfly, is a broadly distributed, tree-feeding species associated with at least 18 different plant species from seven different families (Bossart and Scriber 1995a). But no single host is completely coincident with the distribution of the butterfly, and host-associated selective pressures differ markedly among geographic populations (Bossart and Scriber 1995b; Bossart 1998). Additionally, although most populations are locally polyphagous and encounter multiple host species, some *P. glaucus* populations are locally monophagous and are restricted to a single host taxon (Scriber 1986; Bossart and Scriber 1995b). This natural complexity that characterizes *P. glaucus* host use can be used to advantage to explore the relationship between maternal host choice and offspring performance from a novel perspective, i.e., in the context of relative diet breadth and host availability. Specifically, I collected females from a locally polyphagous *P. glaucus* population (Ohio) and a locally monophagous *P. glaucus* population (Florida), where normal and novel hosts represent the reciprocals of each other. I tested the working hypothesis that mothers prefer to oviposit on the host resource that subsequently optimizes progeny performance. To my knowledge, this study represents the first test of this hypothesis via comparative analysis of geographic populations that differ in relative diet breadth and local host availability.

### Materials and methods

#### General

Field-collected butterflies were collected as first brood adults from Highlands Co., Florida, and Lawrence Co., Ohio, and transported on ice or shipped using overnight delivery to laboratory facilities. Females were fed a 20% honey solution upon arrival and then stored at 24 °C for 24 h prior to being set up in oviposition trials. *Papilio glaucus* females exhibit seemingly complete last-stage sperm precedence (J. L. Bossart and R. C. Lederhouse, unpublished data). Thus, eggs derived from these field-collected females were assumed to represent full-sibling progeny.

#### Preference assay

Oviposition preferences were assessed in two-choice laboratory trials, comparing *Liriodendron tulipifera* and *Magnolia virginiana*. Highlands Co., Florida, populations of *P. glaucus* are virtually restricted to *M. virginiana*, the sole host occurring throughout much of peninsular Florida, whereas Ohio populations never encounter this host but regularly encounter *L. tulipifera*, one of multiple common hosts occurring in the mid-Atlantic region. Thus, these hosts represent the reciprocal normal and novel hosts for each population. Foliate sprigs presented to ovipositing females were placed in water-filled, rubber-capped plastic vials to maintain leaf freshness. *L. tulipifera* foliage was collected at least every 3rd day from various areas in the vicinity of campus and stored at 7 °C. *Magnolia virginiana* foliage was collected daily from potted trees maintained in a campus greenhouse and originally purchased as nursery stock in Florida.

Females were individually placed in clear plastic (10x20x27 cm) “shoeboxes” (Tristate Plastics) with sprigs of foliage from each host and fed a 20% honey solution daily. This protocol for assessing oviposition preferences has proved to be an effective technique for detecting legimate and biologically meaningful patterns in *P. glaucus* (Bossart and Scriber 1995b, 1999). Boxes were maintained under artificial illumination, alternating 4 h:4 h photophase. I have found that this photoperiod permits maximum oviposition, while preventing high mortality of females due to overheating. Fresh host sprigs of similar leaf surface area were positioned in opposite corners along the long side of the box towards the lights. The position of each sprig was alternated every 24 h to control for
positional effects. The position of individual boxes in relation to the light source was randomized at each feeding. Foliage was changed as needed. Eggs were counted and collected daily. Preferences were calculated as the percentage of total eggs oviposited on a given host. Preference trials lasted 4 days.

Larval performance

Progeny performance was likewise assayed on L. tulipifera and M. virginiana using a split-brood design. Assays were conducted under controlled laboratory conditions. Approximately ten newly eclosed progeny from each of 8-12 mothers tested from each population were randomly allocated to each of the two host species. Leaf freshness of foliage presented to developing larvae was maintained by placing foliage sprigs in water-filled, rubber-capped plastic vials. Larvae were reared individually to pupation in (150 cmx25 cm) screened, plastic petri dishes. Petri dishes were stacked randomly in growth chambers maintained at 24°C, 18:6 h photo:scotophase. I checked larvae daily and emptied accumulated frass and refilled water pips as necessary. Fresh foliage was provided at least every other day. Larval duration, pupal mass, and sex were recorded for each individual. Larval duration was defined as the period from day of hatch to the prepupal state, whereupon larvae cease feeding, void gut contents, and undergo a conspicuous color change from green to brown. Pupae were collected and weighed 24 h after ecysis and then placed in individual screen cages until adult emergence. Larval survival was calculated as a family percentage. Relative growth rate (RGR, in milligrams per milligram per day), which quantifies mass gained per unit time, was calculated based on an exponential growth model (Naito et al. 1991; Lederhouse et al. 1992) as,

\[ RGR = \frac{\ln(W_f) - \ln(W_i)}{D} \]

where \( W_f \) is pupal mass, \( W_i \) is initial larval mass, and \( D \) is larval duration up to the prepupal stage.

Statistics

Least square means were calculated for each family-host combination for each measure of offspring performance (i.e., pupal mass, larval duration, and RGR). Survival on each host was calculated as a family percentage. All measures of progeny performance were analyzed using the General Linear Model (GLM; Type III sum of squares, SAS 1990). Geographic strain (Florida and Ohio), larval host diet (M. virginiana and L. tulipifera), and relative preference of mothers were tested as main effects. Mothers nested within strain could not be included as a source of variation because all progeny from a given mother were associated with a single measure of preference. All model parameters were treated as fixed effects. Data were subsequently analyzed for each strain separately to clarify strain-specific patterns revealed by the full model. The interaction of preference \( \times \) strain in the full model tested whether regression slopes associated with grand means for each full-sibling family (i.e., average least square means across hosts) were congruent between strains. The interaction of preference \( \times \) larval diet in the reduced model tested for correspondence of regression slopes associated with offspring performance on each host within strains. Least square means computed from the GLM procedure for each split-brood family and family-host combination were plotted to illustrate general patterns.

Pupal mass and larval duration tend to be sexually dimorphic in P. glaucus. This dimorphism could confound statistical analysis because not all treatments ended up with equal numbers of males and females. Sex could not be introduced as a source of variation in the analysis because either males or females were absent from some family-host combinations. I quantified the relationship between males and females by comparing mean values for all 33 treatment combinations that produced pupae of both sexes. Females were significantly heavier than males on both L. tulipifera \((P=0.028, df=1,36)\) and M. virginiana \((P=0.0064, df=1,30)\). Females also required slightly longer to develop than males, but this difference was not statistically detectable on either L. tulipifera \((P>0.6, df=1,36)\) or M. virginiana \((P=0.3, df=1,30)\). To account for the significant dimorphism in pupal mass, the following regression equation was used to adjust male mass to that expected for females. Statistical methods follow those of Haukioja and Neuvonen (1985), Naito et al. (1991), and Bossart and Scriber (1995b).

\[ \text{mass}_{\text{female}} = 0.297 + 0.659 \times \text{mass}_{\text{male}} \]

\[ (P = 0.0001; df = 133; \text{r}^2 = 0.43) \]

This adjustment had no effect on conclusions. That is, no statistics changed from significant to nonsignificant when the analysis was rerun using unadjusted values of pupal mass or RGR (which incorporates pupal mass).

Results

Oviposition preference

Females differed in their relative willingness to oviposit on Liriodendron tulipifera and Magnolia virginiana (e.g., Fig. 1). Some females clearly preferred one host to the

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**Fig. 1** Relationship between larval duration (mean performance of split-brood families reared on Liriodendron tulipifera and Magnolia virginiana) and relative maternal preference for L. tulipifera for females from A Florida and B Ohio. Each mother is represented by two data points, corresponding to performance of her progeny on L. tulipifera and on M. virginiana. Decreasing preference for L. tulipifera indicates increasing preference for M. virginiana. Although eight Florida families were tested, performance on M. virginiana is represented by only seven families. Only one sibling survived in the eighth family, and the value for larval duration was missing for this individual. Least square mean performance of split-broods and relative maternal preferences are significantly correlated in the Ohio strain, but not in the Florida strain \((P=0.094 \text{ and } P=0.047 \text{ for Florida and Ohio, respectively; see Preference effects, Table 3, A, B, for statistical details})

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Table 1 Analysis of variance partitioning effects of geographic strain, larval host diet, and preferences of mothers on variation in performance of *Papilio glaucus* full-sibling progeny. Split broods were reared on *Liriodendron tulipifera* or *Magnolia virginiana*.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Pupal mass</th>
<th>Larval duration</th>
<th>Relative growth rate</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Strain</td>
<td>1</td>
<td>0.0116</td>
<td>2.43</td>
<td>6.1001</td>
<td>1.23</td>
</tr>
<tr>
<td>Larval diet</td>
<td>1</td>
<td>0.7667</td>
<td>16.11***</td>
<td>56.669</td>
<td>11.45**</td>
</tr>
<tr>
<td>Strain × larval diet</td>
<td>1</td>
<td>0.0124</td>
<td>2.62</td>
<td>1.097</td>
<td>0.39</td>
</tr>
<tr>
<td>Preference</td>
<td>1</td>
<td>0.0943</td>
<td>19.81****</td>
<td>1.707</td>
<td>0.34</td>
</tr>
<tr>
<td>Pref × strain</td>
<td>1</td>
<td>0.0075</td>
<td>1.58</td>
<td>28.277</td>
<td>5.71*</td>
</tr>
<tr>
<td>Pref × strain × diet</td>
<td>1</td>
<td>0.0001</td>
<td>0.02</td>
<td>0.210</td>
<td>0.838</td>
</tr>
<tr>
<td>Error</td>
<td>32</td>
<td>0.0048</td>
<td></td>
<td>4.951</td>
<td></td>
</tr>
</tbody>
</table>

*P*≤0.05; **P**≤0.01; ***P**≤0.001; ****P**≤0.0001  
*a* Error df=31  
*b* Values multiplied by 10^4  
*c* Values divided by 100

Table 2 Least square mean (±SE) performance of Florida and Ohio *P. glaucus* strains fed *L. tulipifera* (*Lt*) or *M. virginiana* (*Mv*).

<table>
<thead>
<tr>
<th>Larval duration (days)</th>
<th>Pupal mass (g)</th>
<th>Relative growth rate (mg/mg/day)</th>
<th>% Full-sibling survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Lt</em></td>
<td><em>Mv</em></td>
<td><em>Lt</em></td>
</tr>
<tr>
<td>Florida</td>
<td>27.28</td>
<td>(0.730)</td>
<td>34.14</td>
</tr>
<tr>
<td>Ohio</td>
<td>26.59</td>
<td>(0.600)</td>
<td>31.24</td>
</tr>
</tbody>
</table>

Table 3 Analysis of variance partitioning effects of larval host diet and preferences of mothers on variation in performance of *Papilio glaucus* full-sibling progeny. Split broods were reared on *L. tulipifera* or *M. virginiana*. Populations are analyzed separately.

(A) Florida

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Larval duration*</th>
<th>Pupal mass</th>
<th>Relative growth rate</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Larval diet</td>
<td>1</td>
<td>76.016</td>
<td>25.55***</td>
<td>0.145</td>
<td>22.16***</td>
</tr>
<tr>
<td>Preference</td>
<td>1</td>
<td>9.975</td>
<td>3.35</td>
<td>0.096</td>
<td>14.67**</td>
</tr>
<tr>
<td>Pref × larval diet</td>
<td>1</td>
<td>0.709</td>
<td>0.24</td>
<td>0.000</td>
<td>0.05</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>2.975</td>
<td></td>
<td>0.079</td>
<td></td>
</tr>
</tbody>
</table>

(B) Ohio

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Larval duration*</th>
<th>Pupal mass</th>
<th>Relative growth rate</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Larval diet</td>
<td>1</td>
<td>16.163</td>
<td>2.94</td>
<td>0.009</td>
<td>2.51</td>
</tr>
<tr>
<td>Preference</td>
<td>1</td>
<td>24.746</td>
<td>4.49*</td>
<td>0.020</td>
<td>5.53*</td>
</tr>
<tr>
<td>Pref × larval diet</td>
<td>1</td>
<td>0.346</td>
<td>0.06</td>
<td>0.000</td>
<td>0.15</td>
</tr>
<tr>
<td>Error</td>
<td>20</td>
<td>5.506</td>
<td></td>
<td>0.073</td>
<td></td>
</tr>
</tbody>
</table>

*P*≤0.05; **P**≤0.01; ***P**≤0.001  
*a* Error df=11 for Florida  
*b* Values multiplied by 10^4  
*c* Values for Florida divided by 10

other, whereas other females oviposited relatively equal numbers of eggs on both hosts. The two most common preference states displayed by Ohio females were strong preference for their normal host (7 of 12 females) and no preference for either host (4 of 12 females). The two most common preference states observed among assayed Florida females were preference for the normal host, *M. virginiana* (4 of 8 females), and preference for the novel host, *L. tulipifera* (3 of 8 females).

Larval performance

Larval host diet had a significant impact on mean performance (significant larval diet effect, Table 1). Performance was generally superior on *L. tulipifera* relative to that on *M. virginiana*, but this difference was most pronounced for Florida larvae (Table 2; larval diet effect, Table 3). For example, Florida larval families that were fed *L. tulipifera* completed development on average 7 days earlier than those that were fed *M. virginiana* (Table 2). Ohio larvae completed development on average 5 days earlier on *L. tulipifera*. Larvae developing on *L.
Fig. 2 Relationship between pupal mass (mean performance of split-brood families reared on *L. tulipifera* and *M. virginiana*) and relative maternal preference for *L. tulipifera* for females from A Florida and B Ohio. Each mother is represented by two data points, corresponding to performance of her progeny on *L. tulipifera* and on *M. virginiana*. Decreasing preference for *L. tulipifera* indicates increasing preference for *M. virginiana*. Split-brood performance on *M. virginiana* in the case of one Florida mother (i.e., the female that oviposited 50% of her eggs on *L. tulipifera*) is represented by a single individual because no other progeny survived to the pupal stage on this host. Least square mean performance of split-broods and relative maternal preferences are significantly correlated in both strains (P=0.0024 and P=0.029 for Florida and Ohio, respectively; see Preference effects, Table 3, A, B, for statistical details) and in the same direction, resulting in a species-specific correlation between preference and performance (P<0.0001, Preference effect, Table 1).

*tulipifera* also attained greater pupal mass relative to those feeding on *M. virginiana* and grew at a faster rate, although this difference between hosts was considerably smaller for Ohio full-sibling larvae (Table 2). Offspring survival was also a function of larval host diet, but relative differences across hosts were nearly identical between strains (Table 2).

Average performance on a given host was generally similar between strains (Table 2), except in the following cases. On *M. virginiana*, Florida larval families required an average of 3 days longer than Ohio larval families to complete development (F=5.52, df=1, P=0.03). This extended larval period did not convert into additional pupal mass gained, however, and consequently translated into a lower average rate of growth for Florida families (F=11.35, df=1, P=0.003). On *L. tulipifera*, Florida larval families ultimately achieved greater mass relative to Ohio families (F=28.44, df=1, P<0.0001), despite completing development in the same approximate amount of time.

Fig. 3 Relationship between relative growth rate (mean performance of split-brood families reared on either *L. tulipifera* or *M. virginiana*) and relative maternal preference for *L. tulipifera* for females from A Florida and B Ohio. Each mother is represented by two data points, corresponding to performance of her progeny on *L. tulipifera* and on *M. virginiana*. Decreasing preference for *L. tulipifera* indicates increasing preference for *M. virginiana*. Although eight Florida families were tested, performance on *M. virginiana* is represented by only seven families. Only one sibling survived in the eighth family, and the value for larval duration, which is necessary to calculate growth rate, was missing for this individual. Least square mean performance of split-broods and relative maternal preferences are significantly correlated in the Ohio strain, but not in the Florida strain (P=0.395 and P=0.012 for Florida and Ohio, respectively; see Preference effects, Table 3, A, B, for statistical details).

Covariance of preference and performance

Proxies of progeny performance were correlated with preferences exhibited by mothers (preference effects, Tables 1, 3), but the nature of the links is not easily categorized. In the case of preference and pupal mass, positive covariance between traits was observed in both strains, i.e., the relationship was species specific (preference effect, Table 1). Progeny derived from mothers that displayed relatively greater preference for *L. tulipifera* tended to develop into larger pupae regardless of whether the female originated from Ohio or Florida or whether the larval host was *M. virginiana* or *L. tulipifera*.

In all other cases, the link between preference and performance was strain specific (preference x strain interactions, Table 1). Ohio larval families that grew faster and bigger relative to other families were the progeny of females that displayed relatively greater specificity for their normal host, *L. tulipifera* (significant preference effect, Table 3, B; least square means regres-
Fig. 4 Relationship between survival (% survival of split-brood families reared on either L. tulipifera or M. virginiana) and relative maternal preference for L. tulipifera for females from A. Florida and B. Ohio. Each mother is represented by two data points, corresponding to performance of her progeny on L. tulipifera and on M. virginiana. Decreasing preference for L. tulipifera indicates increasing preference for M. virginiana. In two families (one from each strain), mothers are represented by a single data point because split-brood survival was identical on both hosts and data points lie on top of each other. Least square mean performance of split-broods and relative maternal preferences are significantly correlated in the Ohio strain, but not in the Florida strain (P=0.056 and P=0.008 for Florida and Ohio, respectively; see Preference effects, Table 3, A, B, for statistical details).

Discussion

My primary objective with the present study was to determine the extent and direction of covariance between performance of Papilio glaucescens progeny and host preferences of their mothers. Three results are particularly noteworthy. First, significant preference-performance covariance was detected within P. glaucescens populations, which supports the hypothesis that such covariance can occur among individuals of a local population. Second, patterns of covariance are not in the manner predicted by conventional optimal oviposition theory, which has generally presumed genetic tradeoffs among hosts. Finally, preference-performance covariance in this species has a genetic basis, but no single genetic explanation can wholly account for the data.

The substantial and ongoing research effort that has been targeted towards study of the preference-performance link reveals how central this relationship is to our understanding of the evolution of plant-insect associations. Generally, such links, where they have been found, have been associated with the average measures of preference and/or performance of populations (e.g., Craig et al. 1989) or with populations that are genetically structured in terms of their host affiliations (Craig et al. 1986). Here, I show that preference-performance covariance exists within populations that have no obvious internal host-associated structure. This supports the earlier work of Singer et al. (1988) and Ng (1988), who likewise demonstrated covariance between female host choice and larval performance within panmictic herbivore populations. To my knowledge, these earlier examples plus those presented here are the only cases in which such covariance has been documented at the level at which selection effects evolutionary adaptation of plant-insect associations, i.e., variation among individuals of a single gene pool. Interestingly, these earlier studies also involved a butterfly species, Euphaedra editha.

Evolution of positive covariance between preference and performance within populations has often been invoked as a mechanistic basis for a variety of host-associated evolutionary phenomena such as host specialization, host race formation, sympatric speciation, and adaptive radiation (Bush 1975, 1994; Futuyma and Moreno 1988; Singer et al. 1988; Thompson et al. 1990; Mitter et al. 1991; Via 1993; Thompson 1996; Hawthorne and Via 2001). This is to say, host-associated genetic tradeoffs have been an implicit expectation of preference-performance covariance and thus of optimal oviposition theory. Based on this theoretical foundation, I predicted that increasing preference for Liriodendron tulipifera would correspond with increasing performance on L. tulipifera, and conversely, that increasing preference for Magnolia virginiana would correspond with increasing performance on M. virginiana. Consequently, when
relative performance on each host was regressed against a single axis of relative preference for these hosts, I expected regression lines would cross. But relative performance of split-brood *P. glaucus* progeny was comparable across hosts, irrespective of whether their mothers had preferred *L. tulipifera, M. virginiana*, or neither host. Thus, while the existence of preference-performance covariance within *P. glaucus* populations is consistent with predictions of optimal oviposition theory, the nature of the specific relationship is not.

What factors might underlie preference-performance covariance in this species? Both genetic and nongenetic mechanisms can foster covariance between traits. Genetic catalysts of covariance include pleiotropy, linkage, and co-adaptation (Lynch and Walsh 1998), whereas nongenetic sources of covariance arise from environmentally induced maternal effects (e.g., Jaenike 1990).

**Genetic explanations**

The potential role of pleiotropy and linkage can be considered concurrently because the same general pattern is predicted in both cases. Specifically, when the same genes control both preference and performance (i.e., pleiotropy) or when genes controlling these traits are located in close proximity on chromosomes (i.e., are linked), increasing preference for a particular host is expected to correlate with a concomitant increase of performance on that host. But in *P. glaucus*, regressions of progeny performance on female preference were congruent across hosts, i.e., regression lines were parallel and generally positively correlated with increasing preference for a single host, *L. tulipifera*. For pleiotropy or linkage to explain this overall pattern, the genetic factors that govern *L. tulipifera* preference would have to control performance on both hosts and simultaneously negatively correlate with *M. virginiana* preference. This scenario seems unlikely. *Magnolia virginiana* should presumably act as a powerful selective constraint on the evolution of negative covariance between preference and performance, given that the Florida strain is largely confined to this host.

Response curves also should have been similar between strains if either pleiotropy or linkage were behind this covariance, because high preference for *L. tulipifera* should always necessarily couple with high performance on *L. tulipifera*; neutral preference, with intermediate performance; and low preference, with low performance. Consequently, individual data points should fall along the same general response curve, regardless of whether relative abundance of particular preference-performance genotypes differs between strains or whether a particular gamete and its associated preference-performance genotype originated from the Ohio or Florida *P. glaucus* gene pool. Although the complete congruence between strains for pupal mass adheres to this expectation, the apparent divergence in opposite directions for larval duration does not. Here, high *L. tulipifera* preference is coupled with relatively shorter larval periods in the Ohio strain, but with relatively longer larval periods in the Florida strain.

Genetic covariance can also be generated and maintained via selection for particular combinations of traits. An interpretation of co-adaptation to explain the results of this study, whereby selection favors co-inheritance of gametes that carry particular combinations of preference-performance genes (i.e., gametic phase disequilibrium, *sensu* Lynch and Walsh 1998), is inherently satisfying. Co-inheritance readily allows for evolution of positive covariance between maternal and offspring characters in combination with congruence of performance across hosts when tradeoffs in host-associated performance are absent. Additionally, the variety of responses documented between Ohio and Florida *P. glaucus* is an expected consequence of co-adaptation given the disparate selective environments experienced by these geographic populations. Optimizing selection in a heterogeneous versus uniform host environment should favor different gene combinations and lead to fundamentally different evolutionary trajectories and genetic architectures (Golmolkiewicz and Kirkpatrick 1992; Via 1993; Gothard and Nylin 1995, and references therein; Hawthorne and Via 2001).

In Ohio *P. glaucus*, a locally polyphagous population, all proxies of progeny fitness correlated positively with relative preference for the normal host, *L. tulipifera*, i.e., progeny with the highest apparent fitness derived from mothers that displayed high fidelity to their normal host, relative to those derived from less-discriminating mothers. This result makes sense if less-discriminating females are at a selective disadvantage in the heterogeneous host environment that characterizes the habitat of Ohio *P. glaucus* (note, however, Ng 1988), e.g., if generalist genotypes have a lower relative fitness than specialist genotypes on a given host.

In Florida *P. glaucus*, larval duration, relative growth, and survival were not tightly linked with host preference. This result similarly makes sense if selection to oviposit on optimal hosts is relaxed in a monophagous population, such as this, that encounters a single host species. Statistical association between unlinked traits is not predicted if the selective (or other) forces that maintain gametic phase disequilibrium are absent (Lynch and Walsh 1998).

But even though a scenario of co-adaptation readily explains much of the data, this interpretation seems to fall apart when evaluated in the context of the positive covariance between preference of Florida females for a locally rare host and progeny mass at pupation. Preference-performance links would necessarily have to arise via intraspecific host selection in this locally monophagous population. But how could selection effect positive association between preference and pupal mass when the putative selective agent, *L. tulipifera*, is locally rare?
Nongenetic explanations

The fact that no single genetic explanation seems adequate to account for these data suggests either that nongenetic mechanisms are at work or that covariance is a consequence of the integrative effect of multiple factors. What nongenetic factors might account for covariance between female choice and progeny performance in *P. glaucus*? Two possible environmentally induced sources of covariance seem relevant to consider here: maternal larval environment and physiological state of adult females.

Singer et al. (1988) suggested a possible, though unlikely, mechanism whereby maternal larval environment might generate correlation between maternal and offspring characters. This scenario hinges on two components: a genetic basis for oviposition site selection (in this case, host preference) and induced enzymes that are transmitted between generations. Positive covariance arises because preference for oviposition sites (a genetic trait) and enzymes induced via maternal larval feeding on the host (an environmental effect) are passed jointly to offspring. Correlation due to induced enzymes cannot explain the *P. glaucus* data. First, this hypothesis predicts a tradeoff in performance on alternate hosts, not the congruence across hosts seen here. Second, my random collection of adult females from the locally polyphagous Ohio population is highly unlikely to have drawn by chance the exact genotypes necessary to reveal significant correlation between mothers and their progeny, given that these field-collected mothers likely developed on different hosts. By the same token, my random collection of adult females from the locally monophagous Florida population would seem to be virtually assured of detecting significant correlation between mothers and their progeny on normal and novel hosts if induced enzymes are at work, because all field-collected mothers by definition developed on the normal host. Yet, the only significant positive correlation was associated with the host not available to effect transmission of induced enzymes between generations, i.e., pupal mass and increasing preference of *L. tulipifera*.

The physiological state of ovipositing females can also engender preference-performance covariance when physiological differences among mothers jointly influence both oviposition site selection and progeny performance. Egg load and age are the maternal characteristics most commonly cited for their effect on host selection behavior (Miller and Strickler 1984; Courtney et al. 1989; Mangel 1989; Jaenike 1990; Odendaal and Rausher 1990; Jaenike and Holt 1991; Jaenike and Papaj 1992; Minkenberg et al. 1992; Barton Browne 1993; Prokopy et al. 1994). Neither of these environmental factors seems to be a viable explanation here. To the extent that total fecundity is a legitimate proxy of egg load, this possibility can be eliminated because total fecundity does not appear to correlate with preference in this species (*r*=0.21, *P*=0.30, df=23; Bossart and Scriber 1999). Relative female age can also be discounted as an explanation because older *P. glaucus* females tend to exhibit greater fidelity to preferred hosts relative to younger females (Bossart and Scriber 1999). Consequently, progeny derived from older, more-discriminating females would have to have outperformed those from younger females to generate the positive relationships documented here. Such a scenario seems counterintuitive, is inconsistent with theoretical explanations of preference-performance correlations mediated by egg load and age (Jaenike 1990), and is apparently unsupported by published data on other species (Barbosa et al. 1986; Li et al. 1993; Scriverstava and Singh 1995; Mohagegh et al. 1998; Jann and Ward 1999; Hecus and Hoffman 2000; Harbison et al. 2001).

Conclusions

The absence of an apparent non-genetic explanation or single specific genetic explanation leaves a final interpretive option. Covariance between maternal and progeny characters in *P. glaucus* is due to the integrative effect of multiple genetic factors. For example, different trait combinations could be controlled by different genetic factors, covariance between female preference and a particular performance trait could be concurrently controlled by both pleiotropy and co-adaptation, or, finally, a given trait combination could be controlled by different genetic factors in different populations. This perspective that multiple genetic factors are responsible for preference-performance covariance is certainly not a novel or surprising conclusion. Other authors have effectively stressed the multiplicity of factors that govern, and complicate, efforts to understand the evolutionary integration of maternal and offspring characters (Bernays 1991; Cheverud and Moore 1994; Wolf and Brodie 1998).

An implicit element of this study is the perspective that host plant chemistry is a primary causal agent of evolved associations between *P. glaucus* and its host resources. Oviposition host choice in *Papilio* involves a sequential series of steps, and host chemistry is a determinant feature throughout (Feeny et al. 1983; Feeny 1991). That host preference variation for *M. virginiana* and *L. tulipifera* is heritable (Bossart and Scriber 1999) implies that chemosensory information received by ovipositing females from potential hosts is utilized or integrated differently by different genotypes. Larval development also tightly links to host plant chemistry. Larvae encounter a diversity of phytochemical constituents in their hosts (Berenbaum 1991), and genetic variation in the ability to utilize host resources is manifest in all measures of larval performance (Bossart 1998). Indeed, full-sibling Florida *P. glaucus* families utilize magnolol, a chemical constituent of *M. virginiana*, more effectively than full-sibling Ohio *P. glaucus* families (J.L. Bossart; K.S. Johnson; and J.K. Nita, unpublished data).

When relative fitness of herbivores is a function of intrinsic properties of host resources, such as plant chemistry, optimality theory predicts evolution of links between female choice and progeny performance. In two
independent analyses of preference-performance covariance, I show that such links exist between these traits at the level of variation among individuals of a single population. Such preference-performance covariance within populations, in which there is no obvious evidence of host-associated substructuring, has only rarely been documented. My comparative analysis of a locally polyphagous versus locally monophagous population proved to be a valuable strategy for evaluating potential mechanisms responsible for this covariance and for advancing our understanding of evolution of host exploitation in herbivorous species.

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