PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Fitness consequences of host use in the field: temporal variation in performance and a life history tradeoff in the moth *Rothschildia lebeau* (Saturniidae)

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Abstract That fitness varies as a function of using different hosts is a basic premise of theory addressing the ecology and evolution of oviposition behavior and host selection. Few data exist demonstrating: (1) the effects of different hosts on fitness in the field, and (2) how these effects vary spatially or temporally. Cohorts of caterpillars were followed from hatching to adulthood to test the hypotheses that: (1) hosts have significant effects on herbivore performance in nature, and (2) host "quality" for performance varies predictably (i.e., the rank order is consistent) across herbivore generations. In total, the fates of >2,000 caterpillars were followed on 238 individual host trees. Host species had significant effects on most, but not all, measured components of caterpillar performance in the field. Variation among generations was mainly quantitative rather than qualitative, with few changes in the rank order of hosts in their effects on performance. There was also a strong seasonal effect on performance such that caterpillar growth and survival were higher in the early wet season compared to the late wet season. Using estimates derived from these data, correlations among larval growth rate, larval survival, total development time, and final adult size were examined at the level of host plant species. Across generations, larval survival was consistently poor, development time was long, but final adult size attained was large on the host *Spondias mombin*. The converse was true for the host *Exostema mexicanum*. Relative performance on the host *Casearia nitida* was variable between the other two hosts. Overall, the data suggest that host use involves a predictable tradeoff between larval survival and final adult size, but argue that which is the "better" host from the female perspective will depend on the fitness consequences of producing a few, relatively large offspring versus producing more, relatively small offspring.

Keywords Family effects · Herbivore · Host plant · Offspring survival · Oviposition

Introduction

Selection of oviposition sites can have significant consequences for offspring and thus parental fitness, which should give rise to adaptive oviposition behavior (Resetarits 1996). Fitness consequences of oviposition site selection have been studied most in insects, primarily in parasitoid flies and wasps (Godfray 1994) and folivorous herbivores, the focus of this paper. That fitness varies as a result of ovipositing on different host parts, individuals, genotypes or species is a basic premise of theory addressing the evolution of oviposition strategies and host selection. This study attempts a comprehensive analysis of the effects of different host plant species on a suite of fitness-related performance variables for a lepidopteran herbivore under field conditions and across several generations in a highly seasonal Neotropical dry forest.

The relationship between host preference and offspring performance plays a central role in research on host selection (Dethier 1954; Rauscher 1983; Thompson 1988; Godfray 1994; Craig and Itami 2008) and, more generally, habitat

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selection (Jaenike and Holt 1991; Morris 2003). Within a given set of hosts, optimality theory predicts that females should preferentially place their eggs on hosts that maximize larval performance (Jaenike 1990; West and Cunningham 2002). However, empirical evidence often shows no correlation or ambiguous correlations between female preference and larval performance (Chew 1977; Singer 1984; Thompson 1988; Courtney and Kibota 1990; Jaenike 1990; Mayhew 1997, 2001; Cronin et al. 2001; Scheirs and De Bruyn 2002a; Craig and Itami 2008).

While numerous explanations have been offered to account for highly variable preference–performance relationships (Agosta 2006; Craig and Itami 2008), often overlooked is that few data actually exist to evaluate the basic premise that different hosts significantly affect fitness in nature, where multiple factors influence larval growth, development, and survival (Rausher 1981; Janzen 1985; Thompson 1988; Kessler and Baldwin 2002; Zalucki et al. 2002). The majority of data derive from controlled laboratory experiments, which ignore natural extrinsic sources of mortality and possibly other variables (e.g., microclimate, habitat, plant architecture) not replicated in the lab (Singer 1984; Thompson 1988; Mayhew 2001). The field studies that do exist have generally focused on specific stages of the life cycle, especially late larval instars. In surveying mortality data from 141 studies of 105 species of Lepidoptera, Zalucki et al. (2002) found only 11 that followed cohorts from egg laying/hatching to disappearance/pupation. To my knowledge only three studies make direct comparisons among host plant species under field conditions (Rausher 1980; Feeny et al. 1985; Moore 1989; see also Klemola et al. 2003).

Furthermore, few data exist on spatiotemporal variation in relative performance on different hosts (Roitberg et al. 1999; Cronin et al. 2001; Scheirs and De Bruyn 2002b; Heard et al. 2006). Among populations, variation in the relative rankings of different hosts for fitness coupled with gene flow could weaken (Singer and Thomas 1996) or strengthen (Nosil et al. 2006) the preference–performance relationship. Within populations, temporal variation in the relative rankings of hosts for fitness could mean these effects, while discernable, are unpredictable, thereby constraining adaptation to any particular host (Futuyma 1976; Rausher 1979; Thompson 1988; Higashiura 1989; Fry 1996; Yamaga and Ohgushi 1999; Cronin et al. 2001; van Nouhuys et al. 2003; Gripenberg et al. 2007).

The objective of this study was to examine the consequences of host plant use, at the level of host plant species, for herbivore fitness in the field over several generations in a population of the moth *Rothschildia lebeau* (Lepidoptera: Saturniidae: Saturniinae). Saturniids are particularly good organisms for studying the fitness consequences of host plant use because adults do not feed and females mate only

once. Thus, a female's fitness should be a direct function of how she distributes her offspring among hosts. The primary hypothesis tested in this study was that the herbivore's performance varies as a function of using different host plant species in nature, and that host plant effects on performance are predictable across generations. I tested this hypothesis by assaying several components of *R. lebeau* performance (larval survival, growth, development time, adult size, fecundity, and adult longevity) on its three primary dry forest host plant species in three or four consecutive generations. In each generation, full-sibling cohorts of caterpillars were placed unprotected on trees in the forest to measure larval performance. In parallel, cohorts of caterpillars were also raised on trees in large protective nets to measure adult performance. Because the data suggested a host-related tradeoff between larval survival and final adult size, I also examined correlations among estimates of four life history variables (larval growth rate, development time, survival, and final adult size) at the level of host plant species.

Materials and methods

Study system

The study was conducted in Sector Santa Rosa of the Area de Conservación Guanacaste, Guanacaste Province, northwestern Costa Rica. Santa Rosa is a 10,800-ha mosaic of regenerating lowland Pacific tropical dry forest (Janzen 2002). The biology of most organisms in Santa Rosa is dominated by the extreme seasonality of the dry forest (Janzen 1984a, 1987, 1993, 2002), with an ∼6-month rainy season (May–October) and an ∼6-month dry season (November–April), when essentially no rain falls. Many tree species, including those in this study, are deciduous and leafless during the dry season.

R. lebeau has a large geographic range, extending from extreme southern Texas, USA, to northern South America (Lemaire 1978). In Santa Rosa, *R. lebeau* produce two to three generations during the rainy season and pass the dry season as dormant pupae (Janzen 1984a). Adults emerge over a period of weeks at the start of the rains in May and produce the first, early wet season (EWS) generation of offspring that develop roughly May–July. These offspring produce the second, late wet season (LWS) generation, which is less synchronous but occurs roughly August–October. Individuals from the second generation may enter pupal dormancy or eclose and attempt a third generation before the onset of the dry season.

Adult saturniids do not feed and are short lived (Janzen 1984b; Tuskes et al. 1996). Female *R. lebeau* eclose with a full egg load (200–500 eggs) and mate once, normally on the night of eclosion. Oviposition begins the following

night when clutches of from six to 12 eggs are laid on individuals of seven possible host plant species (Table 1). The caterpillars pass through five non-toxic instars, each of which is a putative Batesian mimic of various aposematic species (Janzen 1985). The caterpillars do not disperse off of their individual host plant, which greatly simplifies experimental analyses of larval ecology and life history. Prior to pupation, ultimate instars normally crawl off of the host plant to spin a tightly woven, pendulant cocoon on a nearby branch or twig.

Three tree species are the primary hosts of *R. lebeau* in Santa Rosa (Table 1): *Casearia nitida* (Salicaceae), *Exostema mexicanum* (Rubiaceae), *Spondias mombin* (Anacardiaceae). Each species is relatively abundant with respect to the general flora and, more importantly, the set of hosts that *R. lebeau* is known to use (Table 1). It is not known whether or to what degree *R. lebeau* is selective among hosts when ovipositing, although the range of plant species that the caterpillars will develop on normally at the site is larger than the range of plant species that females use for oviposition (Janzen and Hallwachs 2007). When reared under controlled laboratory conditions in the EWS 2004 (i.e., in a common environment free from natural enemies), caterpillar growth rate and survival were much higher on a diet of *C. nitida* or *E. mexicanum* compared to *S. mombin* (Agosta 2008). These three host species are also studied here; the other four, relatively rare hosts (Table 1) are ignored.

Experimental caterpillars and host trees

All caterpillars were obtained from mating two wild parents or an experimentally reared female and a wild male. All host trees were located within and around the Santa Rosa Administration Area. For *E. mexicanum* and *S. mombin*, primarily sapling and juvenile trees were used because adults are generally not within reach of even a tall ladder.

Adult *C. nitida* are generally within reach, which allowed the use of saplings, juveniles, and adults. Trees were generally located in close proximity to trails, roads, streambeds, or edge created by firebreaks in both late-successional, closed-canopy and early-successional, open-canopy forest. Young *E. mexicanum* are found primarily in shady, closed-canopy forest, while young *S. mombin* are found primarily in sunny, open-canopy forest. *C. nitida* are abundant in both habitats, and individuals in both habitats were used in each experimental period.

In the experiments described below, all caterpillars were placed 0.5–3 m above ground level. Females have been observed ovipositing at this height (Janzen 1985) and the caterpillars are routinely observed feeding and resting at this height in both adult and juvenile trees (general observation).

Longitudinal cohort experiments

Cohorts of caterpillars were followed from hatching to disappearance/pupation to estimate larval survival and growth in the field as a function of host plant species in the EWS (first generation) and LWS (second generation) of 2005 and 2006. A cohort was initiated by transferring usually ten, but sometimes as few as seven, newly hatched, full-sibling caterpillars onto the leaf of a sufficiently leafy branch of a host tree. Bands (~6 cm) of sticky resin (Tanglefoot, Grand Rapids, Mich.) were applied to the base of branches or small trees supporting cohorts to ensure that the disappearance of caterpillars could be attributable to mortality rather than movement to another part of the crown. The disadvantage was that small, non-flying invertebrate predators (e.g., ants, spiders) were at least partially excluded by the bands of resin. When at least one caterpillar in a cohort survived through the penultimate instar, the original branch was often near defoliation. Remaining caterpillars were then moved to a new branch or the branch of a neighboring tree.

Table 1 Summary of host plant records 1978–2006 for wild-caught *Rothschildia lebeau* from upland Sector Santa Rosa, Area de Conservación Guanacaste, Guanacaste Province, northwestern Costa Rica (Data from Janzen and Hallwachs (2007)), also given are the relative abundances of *R. lebeau's* host plant species from a 640-m by 240-m plot in 80+ year-old secondary dry forest (Data from B. Enquist, unpublished plant census data 1996, Bosque San Emilio)

Species	Family	No. of records[a]	Percent of records	Relative abundance (%)
Casearia nitida	Salicaceae	57	32.4	29.8
Exostema mexicanum	Rubiaceae	51	29.0	48.8
Spondias mombin	Anacardiaceae	41	23.3	13.9
Zuelania guidonia	Salicaceae	12	6.8	2.1
Swietenia macrophylla	Meliaceae	6	3.4	1.1
Coutarea hexandra	Rubiaceae	5	2.8	1.0
Zanthoxylum setulosum	Rutaceae	4	2.3	3.5

[a] Records compiled based on three criteria: (1) they represent haphazardly collected, wild-caught individuals, (2) they are from upland Sector Santa Rosa, (3) the host plant species from which they were collected is unambiguous

Cohort survivorship was estimated by counting caterpillars approximately daily until all either died, as indicated by their disappearance or the presence of a carcass, or pupated. Cocoons were collected and brought back to the lab to record their fate (adult moth, parasitoid, or death by unknown cause).

Larval growth rate was estimated by measuring the average resting length of caterpillars in the cohort after 2 weeks (15 days) of feeding. Although this is not technically a rate, I showed previously that initial neonate mass is only very weakly correlated with subsequent day-15 mass within and among *R. lebeau* families (Agosta 2008), and thus simply measuring size at day 15 is an adequate comparative measure of the rate of growth over this period. To verify that day-15 length was positively correlated with day-15 mass (Agosta 2008), regressions between mass and resting length for a group of caterpillars raised in nets for 15 days on each host plant species were examined. Analysis of covariance verified that the relationship between mass and length was similar among host plant species (results not shown). Since larval instar is so closely correlated with day-15 size (Agosta 2008), I do not report larval instar as a response variable.

Replication was achieved by following multiple cohorts from each *R. lebeau* family (2–6 cohorts/family per host) on multiple trees (1 cohort/tree) of each host species during each experimental period (Table 2). Thus, individual cohort was the fundamental unit of observation in all analyses. Host-specific survival was measured as the median survival time of each cohort, which was calculated as the number of days that 50% of the cohort survived. Median survival times were log-transformed to meet assumptions of normality and analyzed using ANOVA with Host plant species, Season and Year as the main effects. The random factor Family was also included in this model to estimate its variance component and test whether the other effects were significant when accounting for variation among families. Families were nested within seasons, which resulted in a mixed factorial nested design ANOVA. This analysis and all other analyses were conducted using JMP 5.1 (SAS

Institute, Cary, N.C.). Mixed-model ANOVAs were conducted using the restricted maximum likelihood approach. Additionally, the proportion of caterpillars surviving to adulthood on each host plant species in each period was examined, although statistical comparisons were generally precluded because of the extremely small number of caterpillars that survived to adulthood.

Average cohort resting length after 15 days of feeding (day-15 length) was also analyzed using ANOVA. Data were log-transformed to meet assumptions of normality. As with the analysis of median cohort survival time, family was included as a nested random factor to estimate its variance component. Growth data were not collected for the LWS 2006. For this and all analyses involving size and growth in nets (below), the fixed-factor Period (EWS 2005, LWS 2005, EWS 2006) was used to examine temporal effects (instead of the factors Season and Year as above). For all analyses involving ANOVA, post-tests were conducted on main effects when appropriate using Tukey–Kramer honestly significant difference (HSD) with a significance criterion of $P < 0.05$.

Growth in nets

Few caterpillars survived to adulthood in the cohort experiments described above. In order to test the effect of host plant species on adult performance variables, caterpillars were reared from hatching to pupation in large protective nets on host trees in parallel to the cohort experiments. In general, 25–50 caterpillars were reared per net on from three to five individual trees (1 net/tree) per host plant species in each generation. The positions of nets within and among trees were changed routinely as the caterpillars began to defoliate branches in the late instars.

Cocoons collected from nets were weighed to obtain pupal weights (pupa + cocoon). Newly eclosed adults were weighed and their forewing length (FWL) was recorded. Males were maintained individually in inflated clear plastic bags to record longevity (number of days alive). Females were mated with free-flying wild males, then similarly maintained in plastic bags for egg laying. Egg load was measured by counting laid eggs plus the few mature unlaid eggs normally left in the abdomen. Egg size was measured by taking the average mass of ten individually weighed, randomly selected eggs.

The rearing design in nets differed between 2005 and 2006. In 2005, each net contained caterpillars that had all hatched on the same day and which were derived from one to two families, allowing accurate measurement of total development time (number of days from hatching to eclosion). In 2006, genetic diversity was increased by rearing from four to five families per net. This design required that caterpillars with different hatch dates (up to 2 weeks apart)

Table 2 Number of cohorts of *R. lebeau* caterpillars followed on each host plant species during each experimental period/generation, also given are the number of *R. lebeau* families that cohorts were derived from in each experimental period

Host plant species	Experimental period/generation			
	EWS 2005	LWS 2005	EWS 2006	LWS 2006
C. nitida	22	34	20	11
E. mexicanum	16	26	20	11
S. mombin	19	26	21	12
No. of families	5	9	5	3

EWS Early wet season, *LWS* late wet season

Table 3 ANOVA results for the effect of host plant species and time on the various *R. lebeau* performance variables examined in this study

Response	Source	DF	SS/% var	*F* ratio	*P*
Median survival time	Host	2	14.25	13.80	<0.0001
	Season	1	5.63	10.89	<0.01
	Year	1	2.78	5.38	<0.05
	Host × Season	2	1.87	1.81	0.18
	Host × Year	2	0.91	0.89	0.42
	Season × Year	1	0.69	1.34	0.25
	Host x Season x Year	2	0.72	0.70	0.50
	Family [*Season*]	20	23.98		
	Family [*Season*] × *Host*	36	7.13		
	Residual		73.85		
Day-15 length	Host	2	0.07	1.03	0.37
	Period	2	0.77	12.11	<0.001
	Host × Period	4	0.30	2.35	0.08
	Family [*Period*]	16	38.2		
	Family [*Period*] × *Host*	26	6.4		
	Residual		55.35		
Pupal mass	Host	2	4.76	3.61	<0.05
	Period	2	1.63	1.24	0.31
	Host × Period	4	1.20	0.46	0.76
	Net [*Host*, *Period*]	19	38.35		
	Residual		61.64		
Development time					
Female	Host	2	0.03	3.87	<0.05
	Period	1	0.11	25.23	<0.0001
	Host × Period	2	0.04	4.51	<0.05
	Error	38	0.17		
Male	Host	2	0.04	10.48	<0.001
	Period	1	0.20	109.69	<0.0001
	Host × Period	2	0.01	2.57	0.087
	Error	48	0.09		
Adult FWL					
Female	Host	2	232.77	9.25	<0.001
	Period	2	23.66	0.94	0.40
	Host × Period	4	64.68	1.29	0.29
	Error	59	742.25		
Male	Host	2	769.38	27.00	<0.0001
	Period	2	335.39	11.77	<0.0001
	Host × Period	4	375.00	6.58	<0.001
	Error	88	1254.02		
Fecundity					
Egg load	Host	2	2921.32	0.24	0.79
	Period	2	2122.81	0.18	0.84
	Host × Period	4	41207.89	1.70	0.17
	Error	50	303238.02		
Egg size	Host	2	0.11	0.64	0.53
	Period	2	0.13	0.72	0.49
	Host × Period	4	0.02	0.07	0.99
	Error	50	4.76		

Table 3 continued

Random effects and their variance components are indicated by *italics*. *FWL* Forewing length

Response	Source	DF	SS/% var	*F* ratio	*P*
Male longevity	Host	2	0.66	3.28	<0.05
	Period	2	1.47	7.32	<0.01
	Host × Period	4	0.87	2.18	0.08
	Error	73			

be reared in the same net, which precluded any accurate measurement of total development time. However, since siblings were evenly allocated among the three host species upon hatching, comparing the means of the distributions of eclosion dates for the group of individuals raised on each host plant species should reflect differences in total development time. Thus, for EWS 2006 total development time was estimated in terms of Julian day of the date of eclosion, and this variable was included in the examination of correlations among performance variables described below.

Rearing caterpillars in nets resulted in the following response variables: pupal mass, adult mass, adult FWL, total development time, egg load, egg size, male longevity. These variables were analyzed individually using the same basic ANOVA model described previously. Development time data were arcsine-square root transformed to meet assumption of normality. For pupal mass, sample sizes per net were relatively large, which permitted the inclusion of the factor Net as a random variable. For the other variables, samples sizes per net were relatively small due to: (1) high mortality in the pupal stage, and (2) separation of the data by sex. Therefore, Net was not included as a random factor in these analyses (i.e., data were pooled across nets for each host species).

Host-related correlations among performance variables

The correlations among four performance variables at the level of host species were examined using estimates derived from the above experiments: average cohort day-15 resting length (an estimate of larval growth rate), median cohort survival time (an estimate of larval survival), total development time, pupal mass (adult size). Data were pooled across families since there was little variation in performance resulting from family-by-host plant species interactions ("Results" section and Agosta 2008). For each variable, all data were standardized relative to the mean within-period, across-host response (e.g., average pupal mass across hosts in EWS 2005) using the *Z*-transformation. I then calculated the mean relative response for each performance variable on each host plant species in each period and examined the correlations among the standardized variables. Although the combined raw data on development time represented two types of measurements (see above), *Z*-transformed data are dimensionless and therefore

both types of measures could be included in the calculation of correlations. Because of small sample sizes per sex, data for males and females were combined for both development time and pupal mass, which was used as the measure of adult size and included both pupae that ultimately eclosed and those that ultimately died. For the relatively small number of pupae that did eclose, I examined the correlations for each sex separately (i.e., using sex-specific pupal mass and development time) for comparison with the combined-sex analysis.

Results

Larval survival and growth rate

Sample sizes for the number of cohorts followed per host plant species per generation are given in Table 2. Overall, 238 cohorts derived from 22 families were followed. Most mortality was inferred by the disappearance of caterpillars, but 133 caterpillar carcasses were observed. Most carcasses were of fourth and fifth instars found still attached to the plant with no obvious signs of predation or parasitism.

Over the course of the study and across host plant species, survival to the adult stage for caterpillars raised outside of nets was <1% (Electronic supplementary material S1). Of 2,027 newly hatched caterpillars placed out experimentally, 85 survived to spin a cocoon. Of these 85 pupae, 17 produced adults. The remaining cocoons were either parasitized ($n = 37$) or contained dead pre-pupae or pupae ($n = 31$). Survival was highest in EWS 2005 on *C. nitida* (Electronic supplementary material S1). In the LWS 2005 and EWS 2006, essentially no caterpillars survived, with the exception of two (0.6%) from *C. nitida* (Electronic supplementary material S1). For all periods combined, significantly more caterpillars survived to adulthood on *C. nitida* than on *E. mexicanum* or *S. mombin* ($\chi^2 = 8.31$, $df = 2$, 2,024, $P < 0.02$; Electronic supplementary material S1).

Median cohort survival time was always lower or as low on *S. mombin* compared to *C. nitida* or *E. mexicanum* (Fig. 1a). Moreover, there were no changes in the rank order of hosts in terms of median cohort survival time among generations (Table 4). Variation among families accounted for ~30% of the variation in median cohort survival times with only ~7% of this variation resulting from a
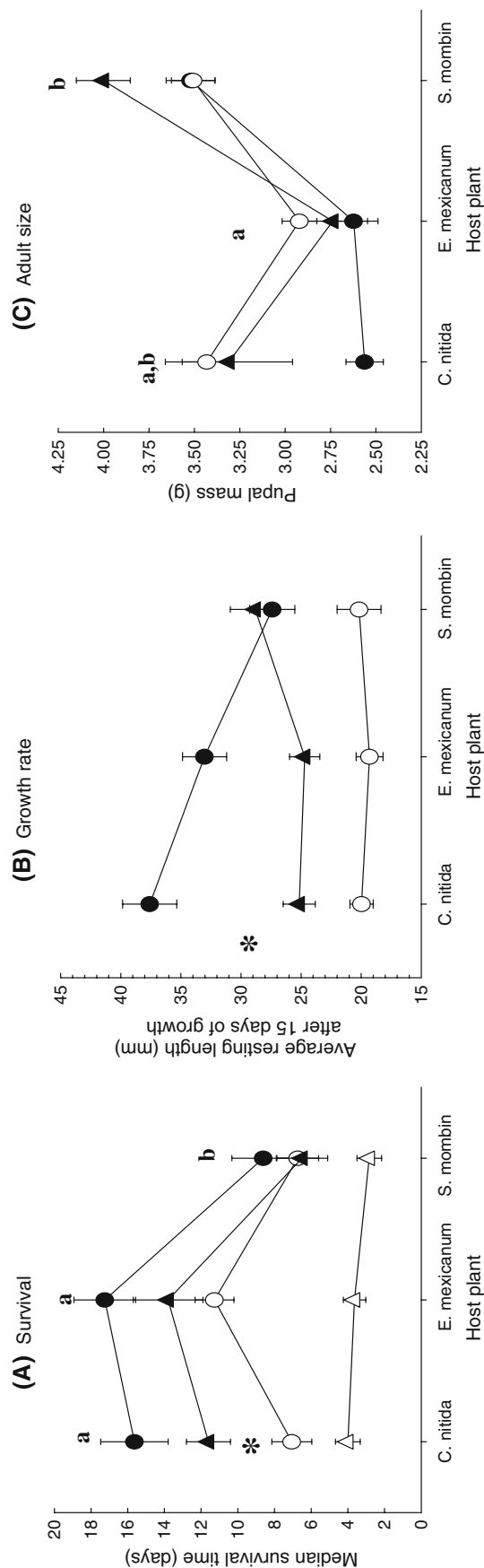
Fig. 1 Effect of host plant species on the larval survival, growth rate, and final adult size of *Rothschildia lebeau* in the field. Data given as mean ± SE. *Circles* 2005, *triangles* 2006, *filled symbols* early wet season, *closed symbols* late wet season. *Different letters* indicate significant differences between host species. *Asterisk* indicates a significant difference between the early wet season and late wet season

family-by-host interaction (Table 3). Interactions between host plant species, season, and year were not significant, but all three main effects were significant (Table 3, Fig. 1a). Median cohort survival time was longer in 2005 (LS mean ± SE = 7.5 ± 1.1 days, *n* = 142) than in 2006 (5.2 ± 1.2 days, *n* = 94) and longer in the EWS than in the LWS (Fig. 1a). Moreover, there was a main effect of host plant species on median cohort survival time, which was about twice as short on *S. mombin* than on *E. mexicanum* or *C. nitida* (Fig. 1a). There was no significant difference between the latter two species.

Thus, within each EWS generation, survival time on *S. mombin* was much lower than on *C. nitida* or *E. mexicanum*. Within each LWS generation, survival times were either equivalent among the three host plant species (LWS 2006) or else equivalent between *S. mombin* and *C. nitida*, but higher on *E. mexicanum* (LWS 2005). Thus, depending on the generation, *S. mombin* was either the poorest or an equally poor host for *R. lebeau* survival.

In contrast to survival, there was no overall effect of host plant species on caterpillar day-15 length across generations, as variation among generations in the relative effects of hosts on day-15 length was unpredictable (Table 3, Fig. 1b). This resulted from three different rank orders of host plant species in each generation, ranging from highest growth on *C. nitida*, to highest growth on *S. mombin*, to no difference among the hosts (Table 4). Variation among families accounted for ~45% of the variation in day-15 length, with only ~7% of this variation resulting from a family-by-host interaction (Table 3). The interaction between host plant species and period was marginally non-significant (*P* = 0.08). Period had a significant main effect: caterpillars were larger after 15 days of feeding in the EWS 2005 and EWS 2006 compared to the LWS 2005 (Fig. 1b).

Adult size, development time, fecundity, and longevity

Across generations, there was a generally predictable effect of host plant species on *R. lebeau* adult size. Despite variation in the relative effect of *C. nitida* on pupal mass, *S. mombin* always produced relatively large pupae while *E. mexicanum* always produced relatively small pupae (Table 4). Variation among nets accounted for ~38% of the variation in pupal mass. There was no significant interaction between host plant species and period and no overall effect of period on pupal mass (Table 3, Fig. 1c). However,

Table 4 Summary of variation in the relative rankings of host plant species for *R. lebeau* performance

Performance variable	Period/generation					
	EWS 2004[a]	EWS 2005	LWS 2005	EWS 2006	LWS 2006	Across-generation, host plant main effect?
Percent survival[b]	C, E > S	C > E, S	C > E, S	NS	–	Yes, C > E = S
Median survival time	–	C, E > S	E > C, S	C, E > S	NS	Yes, C, E > S
Growth rate (day-15 size)	C > E > S	(C > S) ≈ E	S > C, E	NS	–	No
Pupal mass	–	S > C, E	S > C > E	S, C > E	–	Yes, (S > E) ≈ C
Development time						
Female	–	NS	(C > E) ≈ S	–	–	No
Male	–	S > C, E	NS	–	–	Yes, S > C, E
Adult FWL						
Female	–	S > C, E	NS	S > C, E	–	Yes, (S > E) ≈ C
Male	–	S > C > E	(S > E) ≈ C	C > E = S	–	Yes, (S > E) ≈ C
Fecundity						
Egg load	–	NS	NS	NS	–	No
Egg size	–	NS	NS	NS	–	No
Male longevity	–	(S > E) ≈ C	NS	NS	–	Yes, (S > E) ≈ C

Within periods, ranks determined by one-way ANOVAs followed by Tukey–Kramer honestly significant difference (HSD). Across periods, ranks determined by multi-factorial ANOVAs in Table 3 followed by Tukey–Kramer HSD. *C Casearia nitida*, *E Exostema mexicanum*, *S Spondias mombin,* > significant difference between hosts ($P < 0.05$), = no difference between hosts ($P > 0.05$), ≈ host was intermediate between other hosts, *NS* no significant host plant effect, *dash* data were not available; for other abbreviations, see Table 2

[a] From Agosta (2008)

[b] Within-period ranks determined by comparing the raw data. Across-period main effect determined by χ^2-test (see "Results")

there was a significant main effect of host plant species on pupal mass: caterpillars reared on *S. mombin* were larger than those reared on *E. mexicanum* (Fig. 1c). Pupal mass obtained on *C. nitida* was intermediate between the other two hosts and not significantly different from either.

Pupal mass was highly correlated with adult mass and FWL for females (mass, $r = 0.73$, $n = 64$, $P < 0.0001$; FWL, $r = 0.77$, $n = 65$, $P < 0.0001$) and males (mass, $r = 0.82$, $n = 96$, $P < 0.0001$; FWL, $r = 0.82$, $n = 94$, $P < 0.0001$). Adult mass and FWL were also highly correlated (females, $r = 0.83$, $n = 63$, $P < 0.0001$; males, $r = 0.85$, $n = 94$, $P < 0.0001$), therefore, only the results of analyses using FWL as a measure of adult size are presented.

For female FWL (Electronic supplementary material S2), the interaction between period and host plant species was not significant, nor was there a significant effect of period (Table 3). There was, however, a main effect of host plant species on female FWL, which was significantly larger on *S. mombin* (LS mean ± SE = 66.10 ± 0.63 mm, $n = 39$) than on *E. mexicanum* (61.52 ± 0.94 mm, $n = 18$). Female FWL on *C. nitida* (63.37 ± 1.41 mm, $n = 13$) was intermediate and not significantly different from that on the other hosts.

For male FWL (Electronic supplementary material S2), there was a significant interaction between host plant species and period, and thus no main effect of host plant species (Table 3). Males grew significantly larger on *S. mombin* in both the EWS and LWS 2005, but grew larger on *C. nitida* in EWS 2006 (Table 4).

Thus, examination of adult size for females and males separately resulted in the same general rank order of hosts as that observed for pupal mass, with two exceptions (Table 4). For female FWL, host plant species had an overall effect with significantly larger individuals produced on *S. mombin* in two of three generations. However, in one generation, no overall effect of host plant species was observed. For male FWL, there was a significant host-by-period interaction. In two of three generations, FWL was largest for individuals raised on *S. mombin*; however, in one generation it was largest for those raised on *C. nitida*. Thus, for female FWL the rank order of hosts did not change among generations, although in one generation the effect was neutral. For male FWL, the rank order of hosts varied among generations. However, taken as whole, data on pupal mass and sex-specific FWL indicate a general pattern whereby *S. mombin* produces relatively large adults and *E. mexicanum* produces relatively small adults. Relative adult size obtained on *C. nitida* was variable.

Total development time from hatching to eclosion was positively correlated with female ($r = 0.37$, $n = 43$, $P = 0.014$) and male FWL ($r = 0.39$, $n = 49$, $P < 0.01$).

Since the largest individuals were generally those from *S. mombin*, individuals from *S. mombin* should have had the longest development times, followed by those from *C. nitida*. For males, this was partially the case, with a significant main effect of host plant species on development time. Males took significantly longer to develop on *S. mombin* (LS mean $\pm$ SE = 63.2 $\pm$ 1.2 days, $n = 20$) compared to *C. nitida* (58.4 $\pm$ 1.9 days, $n = 16$) or *E. mexicanum* (55.1 $\pm$ 1.4 days, $n = 18$); however, there was no statistical difference between the latter two species. For females, the effect of the interaction between host plant and period on development time was significant, and thus there was no main effect of host plant species (Table 3). Development time was longest on *S. mombin* in EWS 2005 (the difference was not significant; Table 4), but longest on *C. nitida* in LWS 2005.

As a whole, the data on development time were rather inconclusive, likely because of high variance and small sample sizes (Electronic supplementary material S2). For the analysis of correlations among performance variables presented below, development time data were combined with additional data from 2006 (see "Materials and methods"). This resulted in development times that, for males at least (see below), were generally longest on *S. mombin*, shortest on *E. mexicanum*, and intermediate on *C. nitida* (Fig. 2a).

Both egg load ($r = 0.58$, $n = 58$, $P < 0.0001$) and egg size ($r = 0.28$, $n = 58$, $P = 0.037$) were positively correlated with female FWL; however, neither measure of fecundity differed significantly among host plant species or periods (Table 3, Electronic supplementary material S2).

Male longevity was positively correlated with FWL ($r = 0.39$, $n = 82$, $P < 0.001$), and the generally larger *S. mombin* males lived ~2 days longer than the smaller *E. mexicanum* males (Electronic supplementary material S2). There were significant main effects of period and host plant on longevity (Table 3). Males in EWS 2006 (LS mean = 11.4 $\pm$ 1.1 days, $n = 35$) lived longer than males in EWS 2005 (8.6 $\pm$ 1.1 days, $n = 37$) and LWS 2005 (7.6 $\pm$ 1.1 days, $n = 10$). Moreover, males from *S. mombin* lived longer (10.1 $\pm$ 1.1 days, $n = 32$) than those from *E. mexicanum* (8.0 $\pm$ 1.1 days, $n = 32$), while longevity on *C. nitida* (9.2 $\pm$ 1.2 days, $n = 18$) was intermediate and not significantly different from that on the other hosts.

Host-related correlations among performance variables

Larval growth rate was not significantly correlated with any of the other performance variables (Fig. 2a). Development time was negatively correlated with larval survival and positively correlated with adult size, while larval survival was negatively correlated with adult size (Fig. 2a). In sum, across generations, use of *S. mombin* was associated with low caterpillar survival, extended development time, and large adult size (Fig. 2a). On the other hand, use of *E. mexicanum* was associated with high survival, short development time, and small adult size (Fig. 2a). Relative performance on *C. nitida* was variable: depending on the generation, it was similar to *S. mombin*, similar to *E. mexicanum*, or intermediate between the two. However, among generations, covariation in relative survival, development time and adult size on *C. nitida* were similar to the pattern observed between *S. mombin* and *E. mexicanum* (Fig. 2a).

The same general pattern was found when males and females were examined separately (see r_F and r_M-values given in Fig. 2a) with the one exception that the average female adult size was uncorrelated with average development time on these hosts. Thus the significant positive relationship between adult size and development time in the combined analysis (i.e., all pupae) appears to be driven by the data from males.

Discussion

Table 4 summarizes the within- and across-generation rankings of host plant species for the suite of performance variables measured in this study. Host plant effects on *R. lebeau* performance did manifest in nature. Depending on the variable, and in terms of the relative rankings of hosts, variation among generations in these effects ranged from clearly, or at least arguably, predictable (survival, pupal mass, female FWL, male longevity, development time), to unpredictable (day-15 length, adult male FWL), to effectively neutral (egg load, egg size). Thus, there was a host plant species main effect for most of the performance variables, which means that host plant effects on *R. lebeau* performance were generally predictable from generation to generation. The predictability of host plant effects on performance combined with the correlations among performance variables produced an emergent pattern of host use as a life history tradeoff (Fig. 2a,b): long development time, poor survival, but large adult size on *S. mombin*; short development time, high survival, but small adult size on *E. mexicanum*. Depending on the generation, development time, survival and adult size on *C. nitida* were more like on *S. mombin* or more like on *E. mexicanum*, but within generations the variables covaried in a similar manner to that observed between *S. mombin* and *E. mexicanum*.

Possible sources of systematic error in this study that may have affected the results include: (1) the exclusion of non-flying invertebrate predators (mainly ants and spiders) by tanglefoot, (2) the limited opportunity of caterpillars to select foliage within hosts, and (3) disperse off of branches near defoliation. I suspect these limitations contributed to quantitative error in the performance estimates, but I assume the
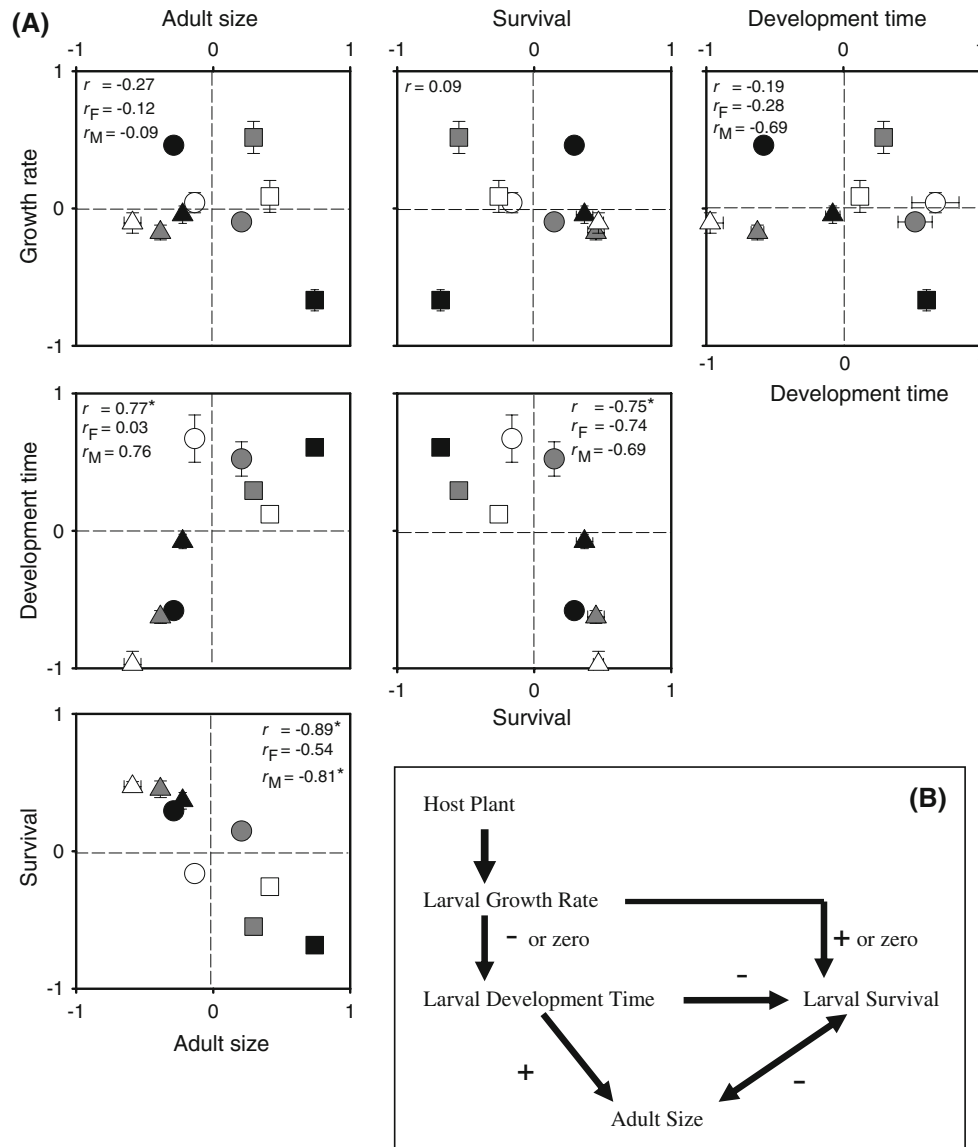
Fig. 2 a Correlations among estimates of relative *R. lebeau* performance for four major life history variables: survivorship (median cohort survival time), growth rate (day-15 resting length), total development time from hatching to eclosion, final adult size (pupal mass). Each point represents the mean ± SE response on a given host plant species in a given period/generation. *Circles Casearia nitida, tri-angles Exostema mexicanum*, *squares Spondias mombin*, *black symbols* early wet season 2005, *gray symbols* late west season 2005, *white symbols* early wet season 2006. Also given are the correlations for females (r_F) and males (r_M) separately (see "Materials and methods"). *Asterisk* indicates that the correlation is significant at $P < 0.05$. **b** Summary of the inter-correlations among the performance variables in **a**

effects were similar across hosts and thus did not affect the results qualitatively. An additional concern was that ultimate instars, which normally crawl off of the host plant to pupate on a nearby branch or twig, could simply drop off experimental branches or small trees, in which case they would have been recorded as dead when in fact they survived. When an ultimate instar did disappear from a host, the surrounding (~3 m radius) understory was searched for cocoons, but none were ever found. Therefore, if caterpillars were dropping from hosts to pupate it was not detected, and again I assume the effect was similar across hosts.

Variation among families accounted for 45 and 30% of the variation in growth and survival, respectively. Only ~7% of this variation was explained by a family-by-host interaction, indicating that within generations families exhibited a similar rank order response to the three host plant species. This result corroborates a previous laboratory experiment (Agosta 2008), which found considerable variation among families but a consistent rank order of host plant species in terms of growth and survival. The lack of a strong interaction between family and host plant species observed here and in Agosta (2008) suggests that this varia-

tion is best explained by some families performing better than others regardless of host species, as opposed to family-based performance tradeoffs on different hosts (S. J. Agosta, unpublished data).

There was an obvious inconsistency between survival measured as the number of adults produced and survival measured by median cohort survival time: almost no caterpillars survived to pupation on *E. mexicanum*, but median survival time was consistently high on this host. In theory, the number of adults produced represents a direct and absolute measure of host-related survival, but two caveats lessen the value of these data for inferring differences among hosts. First, the data do not take into account egg mortality, which if different among hosts (e.g., Moore 1989) could modify the pattern of host-related survivorship. I estimated that individuals were more than replacing themselves over the course of the study (2.7 adults produced/female; Electronic supplementary material S1). This is an overestimate because it does not include egg mortality or account for mortality of adults with remaining reproductive potential. Second, values of 0% survivorship are likely underestimates because survivorship was in general very low and because the number of caterpillars followed per host species per generation never represented the entire egg load of more than 1.1–0.5 females, respectively (Electronic supplementary material S1). Therefore, 0% survivorship in these experiments most likely reflected very low but >0% survival in the population-at-large, and differences among hosts may have existed when none were found (i.e., sample sizes were not large enough to detect very low, but non-zero survivorship). For these reasons, I believe that median cohort survival time was a more reliable comparative measure of host-specific offspring survival in this study, and my conclusions are based on it as the measure of survival.

With respect to host-related survival, two general conclusions can be drawn from these data and those of Agosta (2008). First, *S. mombin* appears to be a predictably poor host for caterpillar survival under both field and laboratory conditions (Table 4). Depending on the generation, it was the poorest host or as poor as other hosts, but never the highest quality host; however, recall that despite poor survival, the caterpillars that did survive were among the largest adults (see below). Second, the apparent survival disadvantage of using *S. mombin* relative to other hosts does not necessarily manifest in all generations. In fact, there appears to be a strong seasonal component to this effect.

Not surprisingly, there was a marked seasonal decrease in *R. lebeau* larval growth rate, development time, and survival in the dry forest, similar to that observed in some temperate systems (e.g., Rausher 1981; Doak et al. 2006). Growth rate and survival were lower and development time was longer in the LWS compared to the EWS. Presumably,

this result was at least partly driven by a general decrease in foliage quality as leaves aged (decreased leaf water and nitrogen content, increased leaf toughness and defense: Feeny 1970; Rausher 1981; Kursar and Coley 1991; Coley and Barone 1996; Coley et al. 2006). Additionally, the abundance of natural caterpillar enemies may be higher in the LWS than in the EWS (Janzen 1993), which would contribute to an overall decrease in caterpillar survival.

Although a seasonal decrease in growth and survival of caterpillars was observed across hosts, the magnitude of this effect was not equal among hosts (Fig. 2a,b): growth and survival were reduced to a much greater extent in the LWS on *C. nitida* and *E. mexicanum* compared to *S. mombin*. For example, in both years, survival on *C. nitida* and *E. mexicanum* were similar and much higher than on *S. mombin* in the EWS. In the LWS, however, survival decreased to a much greater extent on *C. nitida* and *E. mexicanum* compared to *S. mombin*, such that survival on the three hosts was more similar (2005) or equal (2006) in the LWS. Rausher (1981) observed a similar phenomenon in the butterfly *Battus philenor*, which experienced a seasonal decline in the nutritional quality of one host species, but not the other.

Larval growth rate as measured by size after 15 days of feeding (i.e., through the third and fourth instars) was uncorrelated with the other performance variables. Larval growth rate is a common response variable in studies of host use (Awmack and Leather 2002), and is thought to be a good general proxy for host plant quality because it is often correlated with development time and adult size (Nylin and Gotthard 1998). Within one generation (EWS 2005), day-15 length was highly correlated with these variables (Fig. 2a), but this pattern did not manifest in subsequent generations. In any case, the result suggests caution with regards to the use of larval growth rate as the sole indicator of host plant quality, especially since it can be uncorrelated or non-intuitively correlated with adult fitness parameters (Thompson 1988; Vanbergen et al. 2003; De Block and Stoks 2005; Moreau et al. 2006).

The correlations among larval growth, survival, development time, and final adult size—whether analyzed for males and females separately or combined—suggest that host plant use in this system involves a predictable tradeoff between larval survival and final adult size. For males, decreased survival appears to be naturally coupled with increased development time, while for females this correlation was curiously absent. The observation that male *R. lebeau* grew slowly but got bigger on the host *S. mombin* is notable because it runs counter to the traditional L-shaped reaction norm for age and size maturity predicted by life history theory (Stearns 1992; Nylin and Gotthard 1998).

The model in Fig. 2b should be treated as a current, working hypothesis to be tested with future experiments

designed to examine the relationships among the variables directly, at different levels (i.e., among individuals feeding on the same host and different hosts). As part of this working hypothesis, a better understanding of the fitness consequences of adult body size is needed to evaluate the potential ecological and evolutionary significance of this tradeoff. Thus far, I have presented only limited evidence that adult size matters in terms of female fecundity (larger females produced more and larger eggs, but this did not translate into host-related differences in fecundity) and male longevity (larger males from *S. mombin* lived longer than smaller males from *E. mexicanum*, but the relationship was weak). Elsewhere, I will show that male size is positively correlated with mating success (S. J. Agosta, unpublished data).

Finally, I point out two obvious questions that arise in light of these data which deserve further study in this and other plant–herbivore systems. First, is the picture that emerges from studying *R. lebeau* performance on primarily juvenile trees in the understory/subcanopy fundamentally different than the one that would emerge from studying performance in the tall canopies of adult trees? Second, what are the mechanisms behind the differences in host-specific growth and survival observed in the field? For *R. lebeau*, the clearest differences in performance were between *S. mombin* and *E. mexicanum*, which generally occurred in two different habitats (sunny open-canopy forest vs. shady closed-canopy forest, respectively). To what extent were the disparate effects of these hosts on *R. lebeau* performance in the field driven by plant-specific factors, habitat-specific factors, or a combination of both? To what extent can the observation that performance on *C. nitida* was consistently intermediate and more variable through time than on the other hosts be explained by the facts that: (1) individuals occur in both *Spondias*-like and *Exostema*-like habitat; and (2) a mix of juvenile and adult trees were used in the study, as opposed to the two other hosts for which primarily juveniles were used? Relatively little is known about the role of plant ontogeny in plant–herbivore interactions (Boege and Marquis 2005). A recent study with *C. nitida* in Mexico comparing herbivory on sapling vs. young reproductive trees found 3 times higher herbivore density and 66% more herbivory on saplings and higher total foliar phenolics in reproductives (Boege 2005). However, there was no difference in leaf toughness, water, or nitrogen concentrations and, moreover, no difference in the 3-day survival rates of caterpillars of a geometrid moth on sapling versus young reproductive trees. For two heteroblastic (i.e., trees with both adult and juvenile foliage) *Eucalyptus* species, Lawrence et al. (2003) found that beetle feeding was 9 times greater in the adult zone vs. juvenile zone and that beetles preferred adult foliage over juvenile foliage. Using a multifactorial approach, they concluded that plant ontog-

eny rivals other better studied plant traits known to affect herbivores.

Conclusion

Recent attention has been given to the need for more quantitative field data on spatiotemporal variation in herbivore performance as a function of different hosts since these data are critical for understanding the ecological conditions that underlie herbivore population dynamics and the ecology and evolution of oviposition and host plant-selection behavior (Roitberg et al. 1999; Cronin et al. 2001; Scheirs and De Bruyn 2002b; Heard et al. 2006; Gripenberg et al. 2007). The goal of this study was to test the hypotheses that host plant effects on herbivore performance, which are often observed in the lab, manifest in the field and that these effects are predictable across herbivore generations. For *R. lebeau* in Santa Rosa, I found that host plant species indeed had significant effects on most measured components of performance. In general, variation among generations in these effects was quantitative rather than qualitative. Most of the variation among generations was the result of changes in the relative magnitude of differences among hosts in their effects on performance, rather than changes in the rank order of hosts in their effects on performance. Thus, in the aggregate, there was a degree of predictability in the relative effects of host plant species on *R. lebeau* performance across generations, as evidenced by how larval survival, development time, and final adult size covaried at the level of host (Fig. 2).

On the other hand, there was enough variability in the relative effects of host plant species on *R. lebeau* performance to render any ranking of host plant quality based on the results from a single generation tenuous. For instance, while *S. mombin* was a poor host for caterpillar survival in each generation, relative survival on *E. mexicanum* and *C. nitida* varied from greater to equivalent with *S. mombin*, depending on the generation. Furthermore, it is clear that ranking hosts in terms of "quality" for *R. lebeau* is not a simple task of measuring one or even several performance variables. Is *E. mexicanum* a better host than *S. mombin* because development is quick and larval survival is high, or is *S. mombin* the better host because the relatively few adults that are produced are large? This of course depends entirely on whether producing more small offspring is better than producing few large offspring, the solution to which may vary through time and space. Evidence for host-related tradeoffs involving offspring growth and/or different components of survival has been found for other Lepidoptera (e.g., Mira and Bernays 2002; Singer et al. 2004). Such tradeoffs are of considerable interest because—in addition to unpredictably in relative host quality in time and space—

they are expected to add to the conditions favoring polyphagy and a risk-spreading oviposition strategy (Hopper 1999; Singer et al. 2004; Singer 2008). Furthermore, such tradeoffs can be expected to constrain selection for adaptation to any particular host and select for females that produce offspring with a broad ability to grow and survive across a set of variable hosts.

Thus, while the current data do show that *R. lebeau*'s hosts are different in terms of their effects on the performance of individual larvae, they do not elucidate which is the "better" host from the perspective of an ovipositing female. In any case, since saturniids are highly fecund yet short lived, time constraints on oviposition may be a more important factor determining *R. lebeau* host use than host plant "quality" per se. Indeed, time constraints may be one reason why the females distribute small clutches of offspring across multiple host individuals and species of potentially varying "quality" in the first place.

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