

Selection on offspring size varies within and among families in relation to host nutritional quality

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Abstract Life history theory often assumes a positive relationship between offspring size and fitness, although the strength and form of this relationship is expected to vary with environmental conditions. In arthropods, surprisingly few studies have examined the influence of larval environment on the offspring size–fitness relation. In phytophagous insects, the few studies that have examined variation in larval host plants have found a negative correlation between host plant nutritional quality and the strength of selection favoring larger offspring size, suggesting that this pattern might be general. I present experimental evidence for such a relationship in a population of the moth *Rothschildia lebeau* feeding on its three primary host plant species. Unlike previous studies, I consider the effect of offspring size on growth and survival at two levels, both among families and among siblings within families. Neonate caterpillar mass had a significant effect on growth and survival. The effect on growth, however, was weak, resulted primarily from variation among families, and did not differ among host plant diets. The effect on survival was stronger and varied among host plant diets, among families, and within families on different host plants in a manner that was generally consistent with the hypothesized negative correlation between host plant nutritional quality and the strength of selection favoring larger offspring size. Overall, results suggest that the consequences of variation in offspring size for survival within and among families are host plant-dependent in this system.

Keywords Family effects · Herbivory · Host plant · Larval growth · Lepidoptera · Phytophagous insects · Phenotypic selection · Offspring size · Offspring survival · *Rothschildia lebeau*

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Introduction

Offspring size is both a maternal and offspring trait and its consequences for parent and offspring fitness is a widely studied aspect of animal life histories (Bernardo 1996; Fox and Czesak 2000; Bernardo and Agosta 2005). A general assumption of life history theory is that larger offspring have higher fitness and therefore are favored by natural selection (e.g., Williams 1966; Smith and Fretwell 1974; Parker and Begon 1986; McGinley et al. 1987), although the strength and form of selection on any organismal trait is expected to vary spatially and temporally with environmental conditions (Endler 1986).

In arthropods, many, mostly laboratory-based studies of the effects of initial size on subsequent offspring growth and survival are consistent with the hypothesis that “bigger is better” (review in Fox and Czesak 2000). However, as pointed out by Fox and Czesak (2000), relatively few studies of offspring size in arthropods have considered its consequences in different environments. The few studies of phytophagous insects that have considered variation in larval host plant environment have found that fitness differences between large and small offspring are often greatest on host diets or under feeding conditions that are generally inferior for growth and survival (Braby 1994; Fox and Mousseau 1996; Fox 2000; Torres-Vila and Rodríguez-Molina 2002; Fox and Czesak 2006; Fischer et al. 2003a, 2006), suggesting that a negative correlation between host nutritional quality and the strength of selection favoring larger offspring size might be general (Fox and Czesak 2000).

The small collection of studies relating offspring size, offspring fitness, and host plant nutritional quality in phytophagous insects suggest a potentially widespread pattern with implications for understanding the evolution of offspring size and host plant selection. Previous studies have examined this relationship using larvae reared on different individuals within a host species (Fox 2000), on two different host species (Fox and Mousseau 1996; Fox et al. 2001; Czesak and Fox 2003; Fox and Czesak 2006), on different plant parts within a host species (Braby 1994), on an artificial versus a natural host diet (Torres-Vila and Rodríguez-Molina 2002), and by manipulating abiotic conditions and leaf age in a single host species (Fischer et al. 2003a, 2006). Here I use the three primary host plant species of a population of the moth *Rothschildia lebeau* (Lepidoptera: Saturniidae: Saturniinae) to test the hypothesis that the strength of selection favoring larger offspring size and the overall nutritional quality of hosts for growth and survival are negatively correlated. Unlike previous studies, I consider variation in offspring size at two levels, both among families and among siblings within families.

Materials and methods

Study system

Rothschildia lebeau is a large polyphagous saturniid that ranges from southern Texas, USA to northern South America (Lemaire 1978; Janzen 1984a; Tuskes et al. 1996). As in all saturniids, adult *R. lebeau* do not feed, and live for only a few days (Janzen 1984b; Tuskes et al. 1996; Agosta and Janzen 2005). All adult resources are gained as larvae and both egg load and egg size are set prior to eclosion (Jervis et al. 2005; Miller 2005). The female mates once, normally on the night of eclosion, and

can lay half or more of her 200–500 eggs the following night and >80% of her eggs within the first three nights (Miller 1983). Like many species of Lepidoptera, *R. lebeau* caterpillars are solitary feeders and do not move from the individual host plant that the female selects for oviposition.

The study was conducted in the Pacific lowland dry forest (Sector Santa Rosa) of the Área de Conservación Guanacaste, Guanacaste Province, northwestern Costa Rica (see site description in Janzen 2002). Female *R. lebeau* lay small clutches of 6–12 eggs on individuals of seven woody host plant species in five different families (Salicaceae, Rubiaceae, Anacardiaceae, Meliaceae, and Rutaceae) in this dry forest. Three tree species are by far the primary hosts (Janzen and Hallwachs 2006): *Casearia nitida* (Salicaceae) (= *C. corymbosa* in the Flacourtiaceae in older literature), *Exostema mexicanum* (Rubiaceae), and *Spondias mombin* (Anacardiaceae). Each of these tree species is relatively common in Santa Rosa, both with respect to the general flora and with respect to the set of host plants that *R. lebeau* is known to use (general observation, and B. Enquist, unpublished plant census data).

Experimental design

The experiment examined *R. lebeau* caterpillar growth, time to different developmental stages and survival on its three primary dry forest host plants (i.e., *C. nitida*, *E. mexicanum*, and *S. mombin*) and was designed to examine variation among families in these three measures of caterpillar performance. I initiated the experiment with newly hatched neonate caterpillars and terminated it after 15 days of feeding. Results therefore represent caterpillar performance through the first four instars, but not in the ultimate (fifth) instar. Termination of the experiment after 15 days of feeding represented a compromise between assessing caterpillar performance throughout the entire larval lifecycle (i.e., hatching to pupation) and having high enough survival within families for statistical comparisons. Caterpillar size and developmental stage after 15 days of feeding have been negatively correlated with total developmental time (number of days from hatching to eclosion) in this system (S. J. Agosta, unpublished data), and therefore represent a reasonable proxy of developmental rate, which in addition to overall survival is used here as a measure of host plant quality.

Eight adult female *R. lebeau* were collected from the study area at the start of the rainy season in mid-May 2004. All individuals had spent the previous dry season (December–April) as dormant pupae (Janzen 1984a). One of the females was captured as an adult at a light trap, five were collected as dormant pupae (wild cocoons) during the dry season, and two were obtained from a long-term Santa Rosa breeding colony maintained by F. Chavarria (Table 1). The female captured as an adult had already mated. The seven other females were placed in mating cages to copulate with free-flying wild males that they attracted. While the breeding colony generally produces subnormal-sized adults, the two females (F2 and F3 in Table 1) used here were similar in size to the wild-caught females. This colony is also plagued by an unknown pathogen that sometimes causes unusually high larval mortality, although neither family derived from the breeding colony females had the highest observed mortality (Table 1).

After mating, female moths were hung individually in clear plastic bags at ambient temperature under a rearing tent made of a black plastic tarp in the forest near the Santa Rosa administration area. Female *R. lebeau* readily lay eggs on the inside walls of

Table 1 Summary of initial sample sizes, average neonate masses, and caterpillar survivorship for the eight *Rothschildia lebeau* families and three host plant diet treatments used in this study

	Sample size	Average neonate mass (mg) \pm SD	Mortality (%)
Family			
F1	34	1.85 \pm 0.15	12
F2 ^a	34	2.09 \pm 0.11	59
F3 ^a	35	2.33 \pm 0.32	46
F4	35	2.30 \pm 0.28	6
F5	24	2.42 \pm 0.36	21
F6	25	1.62 \pm 0.26	76
F7	34	2.65 \pm 0.27	21
F8	36	2.31 \pm 0.52	28
Host plant			
<i>C. nitida</i>	83	2.15 \pm 0.36	29
<i>E. mexicanum</i>	88	2.27 \pm 0.48	23
<i>S. mombin</i>	86	2.21 \pm 0.41	45

^a Female from breeding colony; all other females from the wild

plastic bags. The larvae normally hatch 6–9 days later and are easily collected. All families used in the experiment hatched within 1 week of each other (25 May–1 June). Upon hatching, 24–36 neonates from each female were weighed individually (neonate mass is positively correlated with egg mass; $r = 0.64$, $n = 63$, $P < 0.0001$) and allocated among the three host plant diets (Table 1). Six of the females used in this study were a small but random sample from the general *R. lebeau* dry forest population, and the two females from the breeding colony (who mated with free-flying wild males) produced neonates with masses well within the range of masses of neonates produced by the six wild-caught females. Thus, the trait variation represented in this study (Table 1) can be considered representative of the variation found in nature and, for the six families derived from two wild parents, a random sample of neonate mass variation within this population during the study period.

Caterpillars were raised individually in clear plastic bags with the appropriate food. Plastic bags were hung under the rearing tent in a haphazard fashion with respect to family and host plant for the duration of the experiment. Caterpillars were provided small freshly cut branches with leaves of their respective diet every third day throughout the experiment. All foliage was cut from trees in and around the administration area. Each caterpillar was generally provided with a mix of young and old leaves and a mix of previously damaged and undamaged leaves and normally had access to foliage ad lib. In only two instances did caterpillars consume all available foliage by the third day.

Caterpillars were reweighed and their instar recorded after 15 days. The following response variables were recorded for each experimental caterpillar: neonate mass (mass at hatching); day 15 mass; instar reached by day 15; larval fate (i.e., lived or died by day 15).

Analyses

Data on neonate mass and day 15 mass approximated normal distributions (based on normal quantile plots), so parametric tests were used for the analyses presented below. All analyses were conducted using JMP 5.1 (SAS Institute, Cary, NC, USA).

The relative nutritional quality of the three host plant species was assessed by comparing overall patterns of growth (day 15 mass, instar reached by day 15) and survivorship (lived or died by day 15). Initially, I planned to use neonate mass as a covariate in the analysis of overall growth, however, it was only weakly correlated with day 15 mass (see below) and its inclusion as a covariate did not effect the outcome of the analysis. Likewise, there was no dependency of caterpillar development (instar reached by day 15) on neonate mass (logistic regression, $P = 0.54$). Consequently, neonate mass was not included in analyses of overall growth.

To compare relative host plant quality in terms of caterpillar growth, I used a two-way mixed-model ANOVA (Expected Mean Square method) to examine the joint effects of host plant (fixed effect) and family (random effect) on day 15 mass. Given that host plant was a significant main effect in this model, I used a Tukey–Kramer HSD test to examine differences among host plants. In addition, I examined the effect of host plant diet on the instar reached by day 15 and overall survival using χ^2 -tests.

Given overall differences in growth and survival on the three host plant diets and variation among families in the average size of neonates (Table 1), I aimed to determine (1) whether the strength of selection on neonate mass differed among host plant diets in a manner consistent with the hypothesis outlined in the Introduction, and (2) whether the effect of neonate mass on growth and survival was primarily the result of within-family or among-family variation. I tested the hypothesis that initial neonate mass influenced subsequent growth and that the strength of this relationship was different among host plant diets using Analysis of Covariance (ANCOVA). The model included day 15 mass as the response, host plant as the main effect, and neonate mass as the covariate. A significant interaction term in the initial model (i.e., test for homogeneity of slopes) would indicate that the strength (slope) of the relationship between neonate mass and day 15 mass differed among the host plant diets.

Given a significant effect of neonate mass on day 15 mass, I repeated the ANCOVA using the factor family as an additional covariate. If the effect of neonate mass on day 15 mass was non-significant when the factor family was included, then this would indicate that selection occurred primarily at the among-family level (i.e., females that produced on average larger neonates had on average larger day 15 offspring). If the effect of neonate mass on day 15 mass remained significant when the factor family was included, then this would indicate that within-family variation in neonate mass had a similar effect on day 15 mass among families (i.e., larger neonates were generally larger day 15 caterpillars, irrespective of which family they were derived from).

I tested the hypothesis that initial neonate mass influenced the probability of survival on the three host plant diets using multiple nominal logistic regression (Janzen and Stern 1998; Quinn and Keough 2002). The full model included neonate mass, host plant diet, family, and their interactions as the predictor variables, and survival (lived or died by day 15) as the nominal response variable. I followed the rules outlined in Agresti (2002) for backward elimination of non-significant terms to obtain the final model presented here. A significant host plant diet-by-neonate mass term in this model would indicate that the relationship between neonate mass and survival differed among the three host plant diets. Given that this interaction was significant, I compared the estimated regression coefficients among host plant diets to determine if the relationship varied in a manner consistent with the hypothesis

outlined in the Introduction. The likelihood ratio χ^2 -test statistic (G^2) was used for all tests of significance, which is more reliable than the Wald statistic when sample sizes are small (Quinn and Keough 2002).

Results

At the start of the experiment, there were no significant differences in the average mass of neonates allocated to the three host plant diets (One-way ANOVA: $F_{2,263} = 1.81$, $P = 0.17$; Table 1). However, there was significant variation in the average mass of neonates among families (One-way ANOVA: $F_{7,258} = 34.80$, $P < 0.0001$; Table 1). Female F7 produced on average the largest neonates. They averaged ~38% larger than neonates produced by female F6, who produced on average the smallest neonates.

Relative host plant nutritional quality

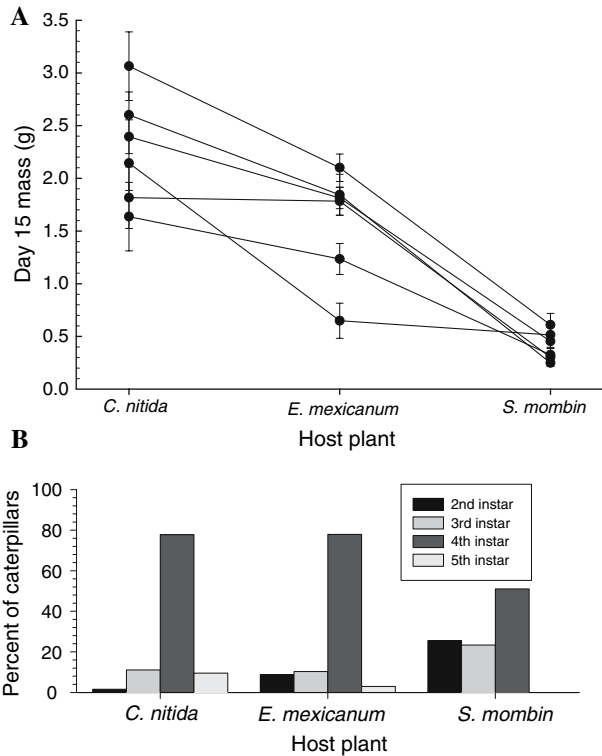
Two families were excluded from the analysis of growth because all caterpillars died on one of the three host plant diets (F2, all died on *S. mombin*; F6, all died on *E. mexicanum*). For the remaining six families, there was a significant family-by-host plant interaction on caterpillar day 15 mass (Table 2; Fig. 1a), indicating that families responded differently to the three host plant diets. However, inspection of the family responses in Fig. 1a reveals that although they cross in a few cases, families showed a similar rank order response to the host plant diets: families performed slightly better or equally well on *C. nitida* compared to *E. mexicanum* and much better or in one case equally well on *E. mexicanum* compared to *S. mombin*. Overall, the main effect of host plant diet on day 15 mass was highly significant and different among all three host plants (Tukey–Kramer HSD, $P < 0.05$), such that mass attained on *C. nitida* (mean \pm SE 2.28 ± 0.14 g, $n = 53$) was greater than on *E. mexicanum* (1.66 ± 0.08 g, $n = 59$), which was greater than on *S. mombin* (0.42 ± 0.04 g, $n = 44$).

The effect of host plant diet on caterpillar development, as measured by the instar reached by day 15, paralleled the results of the growth analysis. There was a significant effect of host plant diet on the proportion of caterpillars in each instar on day 15 ($\chi^2 = 28.34$, $df = 6$, 169 , $P < 0.0001$; Fig. 1b). By day 15, most caterpillars feeding on *C. nitida* and *E. mexicanum* had reached the penultimate (fourth) instar and some the ultimate (fifth) instar. The instar reached was much more variable on *S. mombin*; many were still in the second or third instar and none had reached the fifth instar (Fig. 1b).

Table 2 Two-way mixed-model ANOVA for the effect of host plant diet (fixed), family (random), and their interaction on the mass of *Rothschildia lebeau* caterpillars after 15 days of feeding

Factor	df	SS	F-ratio	P
Host	2	80.99	42.75	<0.0001
Family	5	14.98	3.11	0.059
Host \times family	10	9.74	2.69	<0.01
Error	138	49.91		

Fig. 1 (A) Effect of host plant diet on the growth of caterpillars from six *Rothschildia lebeau* families after 15 days of feeding. Each point represents the average \pm SE response for a group of full siblings ($4 < n < 13$). The main effect of host plant diet on day 15 mass is highly significant (Table 2) and different among all three host plants (Tukey–Kramer HSD, $P < 0.05$). **(B)** Effect of host plant diet on the instar reached by caterpillars after 15 days of feeding

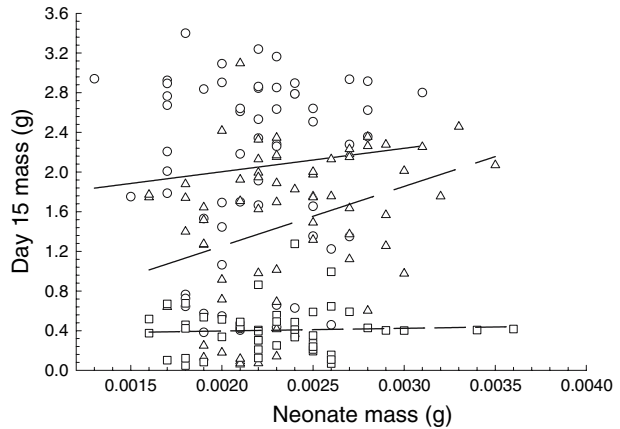


Overall, 35% of 256 caterpillars died by day 15 (ten were killed accidentally and are not included in any analyses of caterpillar fate). Highest mortality occurred on *S. mombin* (45%), followed by *C. nitida* (29%) and *E. mexicanum* (23%) ($\chi^2 = 10.82$, $df = 2$, 254, $P < 0.01$). Overall, growth, development, and survival to day 15 were lowest on *S. mombin*, which, according to the hypothesis outlined in the Introduction, leads to the prediction that selection for larger neonate size should have been strongest in this relatively low quality resource environment.

Effect of neonate mass on subsequent mass

The interaction between neonate mass and host plant diet in their effect on day 15 mass was not significant ($F_{1,172} = 1.35$, $P = 0.26$; Fig. 2) indicating that the slopes of the relationship between neonate mass and day 15 mass did not differ significantly among host plant diets. ANCOVA revealed a weak but significant effect of neonate mass on day 15 mass ($F_{1,174} = 4.74$, $P = 0.031$; Fig. 2). When family was included as a factor in the model, the significant effect of neonate mass disappeared ($F_{1,167} = 0.07$, $P > 0.75$), indicating that the effect was primarily due to variation in average neonate mass among families. This result was consistent with a positive but non-significant correlation between average neonate mass and average day 15 mass among families ($r = 0.61$, $n = 8$, $P = 0.11$).

Fig. 2 Relationship between *Rothschildia lebeau* neonate mass and mass after 15 days of feeding on *C. nitida* (circles, solid line; $n = 63$), *E. mexicanum* (triangles, long-dashed line; $n = 68$), and *S. mombin* (squares, short-dashed line; $n = 47$)



Effect of neonate mass on survival

The final logistic regression model predicting survival included a significant family-by-host plant diet and host plant diet-by-neonate mass interaction (Table 3). Inclusion of the latter interaction (and lack of a significant three-way interaction between family, host plant diet, and neonate mass) indicated that the overall relationship between neonate mass and survival differed significantly among host plant diets. Examination of the regression coefficients revealed a significant positive relationship between neonate mass and survival on a diet of *S. mombin* ($\beta = 3.15 \pm 1.38$, $G^2 = 5.20$, $P = 0.023$), but no such relationship on a diet of *C. nitida* or *E. mexicanum* (each $G^2 < 1.5$, each $P > 0.5$).

Figure 3 plots the resulting probability formula derived from the model in Table 3. For *S. mombin*, all families (with the exception of F2, which experienced 100% mortality) show a positive relationship between neonate mass and survival, which is consistent with the overall effect reported above (note that none of the individual family level regressions in Fig. 3 were statistically significant). For *C. nitida* and *E. mexicanum*, none of the families exhibit such a relationship, which is again consistent with the lack of an overall effect of neonate mass on survival reported above. However, visual inspection of Fig. 3 suggested that families with on average larger neonates tended to survive better than families with on average smaller neonates on *C. nitida* and *E. mexicanum*. This interpretation was consistent with a positive but marginally non-significant correlation among families between average neonate mass and survival on *C. nitida* ($r = 0.67$, $n = 8$, $P = 0.068$) and *E. mexicanum* ($r = 0.66$, $n = 8$, $P = 0.073$). There was no such relationship on *S. mombin* ($r = 0.12$, $n = 8$, $P = 0.78$).

Table 3 Final logistic regression model predicting *R. lebeau* survivorship after 15 days of feeding

Factor	df	G^2	P
Host	2	5.26	0.072
Family	7	60.27	<0.0001
Neonate mass	1	0.19	0.67
Host \times family	14	48.81	<0.0001
Host \times neonate mass	2	8.72	0.013

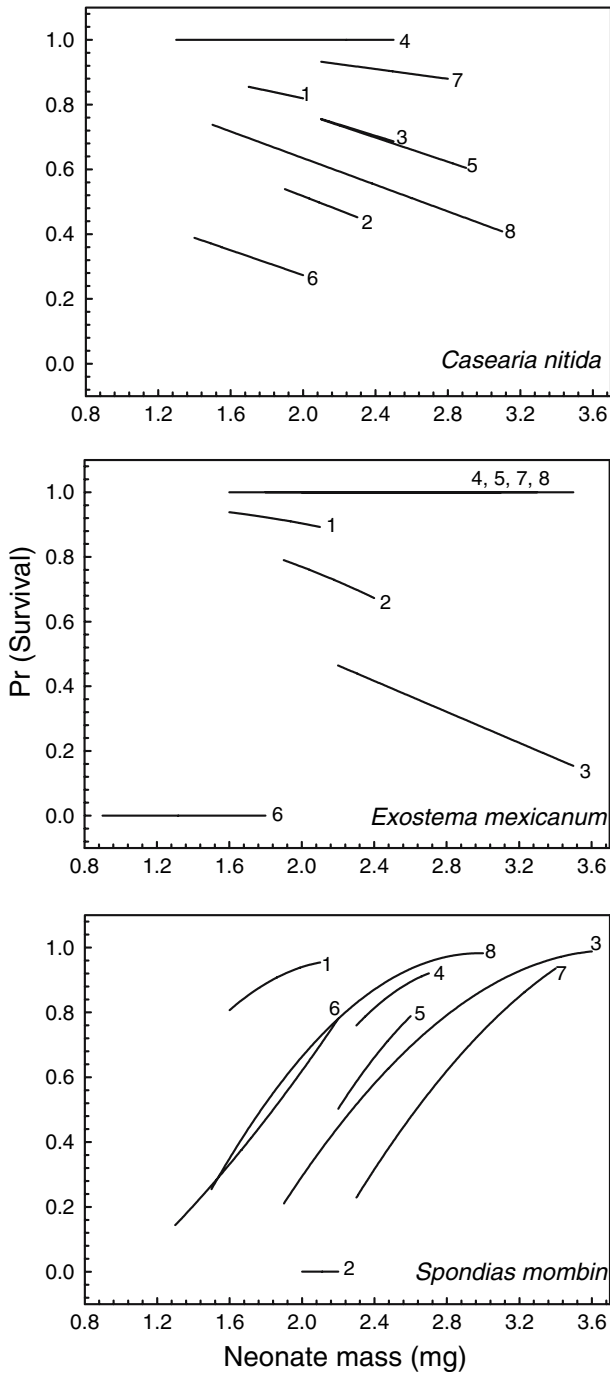


Fig. 3 Probability of survival as a function of *Rothschildia lebeau* neonate mass and family within the first 15 days of feeding on three host plant diets. Numbers correspond to the eight families listed in Table 1

Discussion

This study found evidence for selection for larger *R. lebeau* neonate mass (or some correlate; see below) in terms of growth and survivorship. In terms of growth, the relationship between initial size and subsequent size was weak at best, occurred primarily as the result of variation among families, and did not differ among host plant diets (Fig. 2). In terms of survival, the relationship between initial size and survival to later instars was significant but variable within families on different host plant diets (Fig. 3). This variability, although more complex than that observed in previous studies (see below), occurred in a manner consistent with the hypothesized negative correlation between the strength of selection favoring larger offspring size and host plant nutritional quality (Fox and Czesak 2000). More generally, results of this study were consistent with the prediction that selection on offspring size is strongest in relatively low quality resource environments (Parker and Begon 1986; Sibily and Calow 1986).

In phytophagous insects, for which female oviposition decisions so clearly determine the larval resource environment, surprisingly few studies of offspring size have considered the effects of host variation on the offspring size–fitness relation (Fox and Czesak 2000). Existing studies represent a variety of biological systems and have employed different experimental and statistical approaches to this problem (Braby 1994; Fox and Mousseau 1996; Fox 2000; Fox et al. 2001; Torres-Vila and Rodríguez-Molina 2002; Czesak and Fox 2003; Fox and Czesak 2006; Fischer et al. 2003a, 2006; this study). Nonetheless, the patterns emerging from these studies are similar. For example, Braby (1994) studied the significance of egg size in three species of satyrine butterflies (*Mycalesis* spp.). In two species, caterpillars from larger eggs had a higher probability of survival on a diet of tougher nitrogen-poor foliage than caterpillars from smaller eggs, but this fitness difference diminished when caterpillars were raised on softer nitrogen-rich foliage. Fox (2000) studied the natural range of variation in seed quality within a host species for the bruchid seed-beetle *Stator limbatus*. Results from both observational field data and experimental laboratory data showed a strong positive correlation between seed quality (mean seed-coat resistance per tree) and the intensity of selection (i) on egg size (see also Fox and Mousseau 1996; Fox et al. 2001; Czesak and Fox 2003; Fox and Czesak 2006).

This study differed from previous studies by considering variation in offspring size both among families and among siblings within families, which revealed two very different selection environments (Fig. 3). On a diet of *S. mombin*, caterpillars grew very slowly, overall survivorship was comparatively low, and larger neonates were favored regardless of which family they were derived from (i.e., there was a consistent within-family effect). On a diet of *C. nitida* and *E. mexicanum*, caterpillars grew quickly, overall survivorship was comparatively high, and there was no evidence of selection on neonate mass within families. However, there were positive family level correlations between average neonate mass and survival on *C. nitida* and *E. mexicanum*, indicating that families that produced relatively large neonates tended to survive better than families that produced relatively small neonates on these hosts. Note that family F6, which produced on average the smallest neonates, suffered the highest rates of mortality observed on these otherwise high quality hosts.

Thus, the main source of variation in offspring size-related survival differed in *R. lebeau* depending on the host plant. On the relatively high-quality hosts, variation in survival was mainly due to differences among families. While the causes of these family effects are unknown, the observed correlations between average neonate mass and survival suggest that, at least in part, families producing relatively large offspring simply performed better than those producing relatively small offspring. In contrast, on the relatively low quality host, variation in survival was due to both unknown family effects and a relatively strong size–survival relationship experienced by most families (i.e., even families producing relatively large neonates did not escape the survival consequences of variation in offspring size on the lowest quality host).

These results have at least two interesting implications for understanding the consequences of host plant use by *R. lebeau* in Santa Rosa. First, field-studies in Santa Rosa, which follow cohorts of caterpillars from hatching to disappearance/pupation have shown that survival on *S. mombin* is consistently poor relative to *C. nitida* and *E. mexicanum* (S. J. Agosta, unpublished data). This study suggests that low survivorship on *S. mombin* in the field is at least in part a consequence of a relatively strong size–survival relationship experienced by most families. Second, variation among families explains 30–50% of the variation in *R. lebeau* performance in the field when raised on these three host plants (S. J. Agosta, unpublished data). This study suggests that some of this variation results from variation in initial offspring size, but also that the level at which the size–performance relationship manifests (i.e., within- versus among-families) differs depending on the host. Thus, for this herbivore at least, an answer to the question, “What are the fitness consequences of variation in offspring size?” appears to be host specific.

While the results of this study are generally consistent with the hypothesized negative correlation between host nutritional quality and the strength of selection favoring larger offspring size, it should be noted that my experiment only considered selection during a portion of the larval lifecycle. After 15 days of feeding, most caterpillars had reached the penultimate instar, and it is possible that results would have been different had the experiment been carried-out through the ultimate instar or to the adult stage. In terms of fecundity selection, the response variable “day 15 mass” may be at best weakly correlated with final adult size and fecundity, therefore, this study should not be taken as a direct test of selection on neonate mass in terms of fecundity. Rather, this study was designed to examine viability selection, and in this regard I believe the main conclusions were unaffected by the duration of the experiment. For example, in the field (i.e., exposed to natural enemies on naturally occurring host plants) during the early wet season of the year following this study, day 15 mass was low, total development time was long (hatching to eclosion), and survival was poor on *S. mombin* relative to *C. nitida* and *E. mexicanum* (S. J. Agosta, unpublished data). Thus, my assessment of relative host plant quality in terms of caterpillar growth and survival after 15 days of feeding in this experiment is consistent with similar data that are representative of the entire lifecycle under field-conditions.

Finally, I point out that the mechanism underlying the pattern observed in this and previous studies is unclear. For leaf-chewing insects, larger offspring may possess larger mandibles and therefore may be better able to establish, process, and survive on tougher foliage (Nakasuji 1987; Braby 1994; Fischer et al. 2006). I made no attempt to relate *R. lebeau* neonate size to mandible size or to measure the

toughness of the leaves of the three food plant species. However, leaves of *S. mombin* are noticeably thicker and tougher than the leaves of *C. nitida* or *E. mexicanum* in the early wet season, which might account for the strong effect of neonate mass on survival observed when caterpillars were reared on *S. mombin*. In addition to the possibility that neonate mass acts as a correlate for mandible size, it is also possible that larger neonates are simply better provisioned (i.e., have higher stored energy reserves; Azevedo et al. 1997) than smaller neonates and therefore have an initial advantage when feeding on a low quality diet (Fischer et al. 2003b). Neither of these potential mechanisms—larger feeding apparatus or higher stored energy reserves—are mutually exclusive explanations for the repeatedly observed increased performance advantage of larger offspring when feeding on low-quality hosts.

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References

- Agosta SJ, Janzen DH (2005) Body size distributions of large Costa Rican dry forest moths and the underlying relationship between plant and pollinator morphology. *Oikos* 108:183–193
- Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken, NJ
- Azevedo RBR, French V, Partridge L (1997) Life-history consequences of egg size in *Drosophila melanogaster*. *Am Nat* 150:250–282
- Bernardo J (1996) The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am Zool* 36:216–236
- Bernardo J, Agosta SJ (2005) Evolutionary implications of hierarchical impacts of nonlethal injury on reproduction, including maternal effects. *Biol J Linn Soc* 86:309–331
- Braby MF (1994) The significance of egg size variation in butterflies in relation to host plant quality. *Oikos* 71:119–129
- Czesak ME, Fox CW (2003) Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. *Evolution* 57:1121–1132
- Endler JA (1986) Natural selection in the wild. Princeton University Press, Princeton
- Fischer K, Brakefield PM, Zwaan BJ (2003a) Plasticity in butterfly egg size: why larger offspring at lower temperatures? *Ecology* 84:3138–3147
- Fischer K, Bot ANM, Brakefield PM, Zwaan BJ (2003b) Fitness consequences of temperature-mediated egg size plasticity in a butterfly. *Funct Ecol* 17:803–810
- Fischer K, Bot ANM, Brakefield PM, Zwaan BJ (2006) Do mothers producing large offspring have to sacrifice fecundity? *J Evol Biol* 19:380–391
- Fox CW (2000) Natural selection on seed-beetle egg size in nature and the laboratory: variation among environments. *Ecology* 81:3029–3035
- Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. *Ann Rev Entomol* 45:341–369
- Fox CW, Czesak ME (2006) Selection on body size and sexual size dimorphism differs between host species in a seed-feeding beetle. *J Evol Biol* 19:1167–1174
- Fox CW, Mousseau TA (1996) Larval host plant affects the fitness consequences of egg size in the seed beetle *Stator limbatus*. *Oecologia* 107:541–548

- Fox CW, Czesak ME, Fox RW (2001) Consequences of plant resistance for herbivore survivorship, growth, and selection on egg size. *Ecology* 82:2790–2804
- Janzen DH (1984a) Weather-related color polymorphism of *Rothschildia lebeau* (Saturniidae). *Bull Entomol Soc Am* 30:16–20
- Janzen DH (1984b) Two ways to be a big tropical moth: Santa Rosa saturniids and sphingids. *Oxf Surv Evol Biol* 1:85–139
- Janzen DH (2002) Tropical dry forest: Área de Conservación Guanacaste, northwestern Costa Rica. In: Perrow MR, Davey AJ (eds) *Handbook of ecological restoration*, vol 2. Restoration in practice. Cambridge University Press, Cambridge, pp 559–583
- Janzen DH, Hallwachs W (2006) Event-based database of caterpillars, their host plants, and their parasitoids in the Area de Conservación Guanacaste, northwestern Costa Rica. <http://janzen.sas.upenn.edu>
- Janzen FJ, Stern HS (1998) Logistic regression for empirical studies of multivariate selection. *Evolution* 52:1564–1571
- Jervis MA, Boggs CL, Ferns PN (2005) Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. *Ecol Entomol* 30:359–375
- Lemaire C (1978) *Les attacidae Américains*. C. Lemaire, Neuilly-sur-Seine, France
- McGinley MA, Temme DH, Geber MA (1987) Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am Nat* 130:370–398
- Miller TA (1983) Pupal size and egg production characteristics in *Rothschildia forbesi* (Saturniidae). *J Lepidopterists' Soc* 37:174–176
- Miller WE (2005) Extrinsic effects on fecundity-maternal weight relations in capital-breeding Lepidoptera. *J Lepidopterists' Soc* 59:143–160
- Nikasuji F (1987) Egg size of skippers (Lepidoptera: Hesperidae) in relation to their host specificity and to leaf toughness of host plants. *Ecol Res* 2:175–183
- Parker GA, Begon M (1986) Optimal egg size and clutch size, effects of environment and maternal phenotype. *Am Nat* 128:573–592
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Sibly R, Calow P (1986) *Physiological ecology of animals: an evolutionary approach*. Blackwell Science, Oxford
- Smith CC, Fretwell SD (1974) The optimal balance between size and number of offspring. *Am Nat* 108:499–506
- Torres-Vila LM, Rodríguez-Molina MC (2002) Egg size variation and its relationship with larval performance in the Lepidoptera: the case of the European grapevine moth *Lobesia botrana*. *Oikos* 99:272–283
- Tuskes PM, Tuttle JP, Collins MM (1996) *The wild silk moths of North America: a natural history of the Saturniidae of the United States and Canada*. Cornell University Press, Ithaca
- Williams GC (1966) *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton